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Mridula Srinivasan
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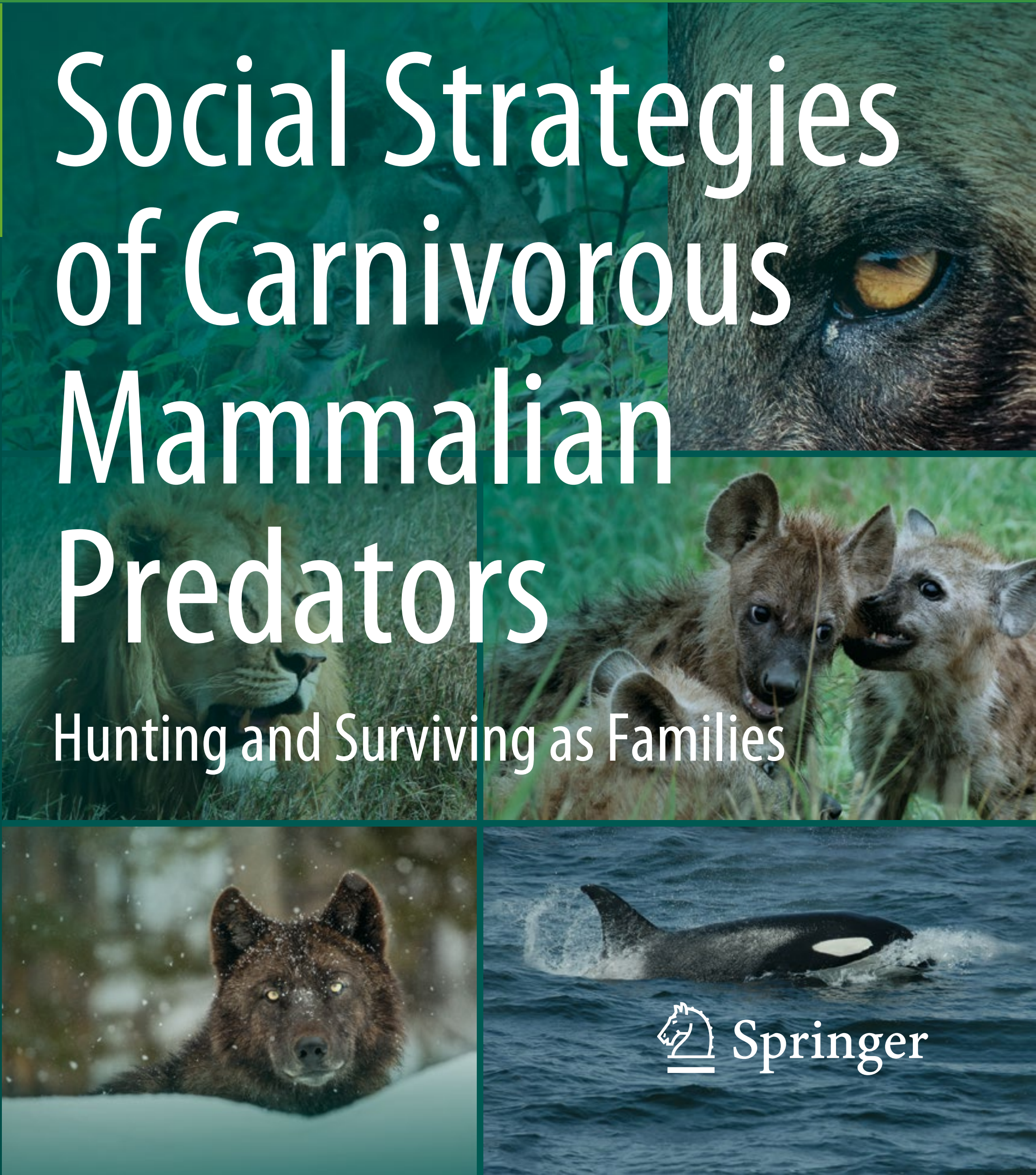

Social Strategies of Carnivorous Mammalian Predators

Hunting and Surviving as Families

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Editors

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Preface

The idea for this book started about 15 years ago when I was planning my doctoral studies. Unfortunately, the realities of completing a dissertation took over and my ideas never germinated into anything tangible. Fortunately, a few years back after chatting with my co-editor, and former Ph.D. advisor, Dr. Bernd Würsig and Éva Lörinczi (Springer Nature Publishers), I felt encouraged to develop the idea into a book proposal. Writing and editing a book for the first time is a thrilling journey—full of twists and turns and seemingly endless—but when it is finally done, it is enormously satisfying.

I am extremely grateful to Bernd—prolific author of multiple books—for his generous time and unwavering support and for helping me navigate the inevitable challenges of getting all the chapters organized.

Special thanks to Eva and Bibhuti Sharma for their extraordinary patience and support throughout this endeavor.

This effort was impossible without the contribution of the authors in this book. Their enthusiasm, commitment, and amazing contributions made my job extremely easy—I learned a lot from them and am grateful they could share their knowledge and expertise through this book. A few went through unimaginable personal challenges, yet they persevered. It is a credit to all the authors for staying dedicated to the task and coping with obstacles imposed by a pandemic and regular life and work distractions. This was one of the best collaborative projects I have worked on, and I cannot wait to work with these fine authors in some capacity in the future.

I am also indebted to all the reviewers, who took time out of their busy schedules to provide timely reviews that greatly improved all the chapters.

Thanks also to Dr. Lisa Desfosse, my boss, and the Southeast Fisheries Science Center, National Marine Fisheries Service (NMFS) for their faith and support as I balanced my leadership responsibilities with book writing.

Big gratitude to Hannah Rappoport and Britney Danials—two NOAA interns, who through their illustrations showed what incredible talents they are. They gave expression to the text through artwork and my hope to connect art with technical writing was realized through their creativity.

Alla fine e sopra tutto—I would like to thank my husband, Jolly. Without his enthusiasm, undeterred support, and constant inducements for me to complete the book, I would have forever procrastinated working on the book.

Grazie a tutti.

Mridula Srinivasan.

Contents

Chapter 1
Animals That Stay Together, Hunt Together

Mridula Srinivasan and Bernd Würsig

Abstract Social mammalian predators typically forage in groups and maintain mostly consistent membership. Within the social unit, there could be a hierarchy for allocating resources and predators may benefit from hunting together than alone. An intriguing question that this book poses is whether the benefits of cooperative hunting warrant group living or whether benefits of group living predispose animals to hunt communally. Consolidation of similar species or taxa-specific studies in a comparative context can help elucidate some of the ways different researchers are approaching questions on cooperative predation and sociality. Each chapter is dedicated to a social mammalian carnivore hunting mammalian prey. In total, we provide representative examples from five terrestrial and one marine species. We have been intentionally selective in our choices to allow a holistic synthesis of knowledge and better illustration of social unit characteristics and predation strategies. We learn that the lives of these predators are shaped by resource variability, lateral and vertical information transfer, human forces, and intrinsic life history, social, and behavioral traits. We consider impacts of human and environmental change on the social habits of these predators, specifically the potential disruption of social learning when the social structure is fragmented. As an overarching goal, the book hopes to offer insights on the value of protecting social predators to maintain ecosystem resilience.

Keywords Social predation · Mammalian predators · African lion · Asiatic lion · Killer whale · Gray wolf · Spotted hyena · African wild dog

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Artistic rendering by Britney Danials. Photo credit: Daniel Bianchetta, Killer whale (center and top right clockwise), Stotra Chakrabarti, Asiatic lions (third from top clockwise), Jacob W. Frank, Gray wolf (bottom center), Bobby-Jo Vial, African Wild Dog, Meredith Palmer, African lion (top left), Kay Holekamp, Spotted Hyena (top)

Social mammalian predators that communally hunt (e.g., killer whales—*Orcinus orca*, lions—*Panthera leo*, wolves—*Canis lupus*) can be distinguished by their social organization, cooperation (assisting each other without necessarily a common goal), coordination (engaging in synchronous actions), and role differentiation (embracing dedicated tasks in a hunt, for example). The social unit flexibility and stability, as well as familial connections within the hunting unit, can stimulate learning across multiple generations, allow the capture of large prey, and strengthen chances of survival through collective defense against predators or interlopers—this is what typifies group living predators from the occasional cooperative forager (Creel & Creel, 1995; Kruuk, 1972; Nudds, 1978; Schaller, 1972). Ecological determinants such as hunting success, habitat type, territorial or offspring defense, or resource dispersion can further dictate whether communal predators, where a group consists of two or more individuals (Gittleman, 1989; Krebs, 1978; Macdonald, 1983), always or intermittently hunt together.

The terms social predators or social predation have been variously applied to a group of animals that may forage together or exhibit cooperative foraging. We follow the definition of social predation by Lang and Farine (2017), which applies to animals that find, capture, and kill mobile prey. And under their proposed multidimensional framework, we are specifically interested in social mammalian carnivorous predators that may exhibit group foraging with mostly consistent membership, transmit signals to indicate hunt initiation, allocate resources according to a social hierarchy, and accrue multiple benefits when engaged in group hunting rather than hunting alone.

A classic question in ecology is understanding the selection pressures that contributed to the evolution and persistence of cooperative hunting in social carnivores. Are social or gregarious animals more likely to cooperatively hunt or do animals that hunt together also remain together during other activities? The answer is complex, dependent on social, as well as abiotic and biotic factors. Energetic intake per capita, hunting success, relatedness, inter- and intra-specific predation, behavior-dependent group size effects, consumption of single vs. multiple prey, prey size and abundance, and reproductive or physiological conditions confound our analyses depending on the species and foraging ecology being considered (Bekoff et al., 1984; Creel & MacDonald, 1995; Gittleman, 1989; Packer & Ruttan, 1988, Suter & Houston, 2021). Human interference or human-dominated landscapes complicate the puzzle further and transform social systems in an unpredictable manner.

Consolidation of similar species or taxa-specific studies in a comparative context can help elucidate some of the ways different researchers are approaching questions on cooperative predation and sociality. The literature is replete with examples of cooperative social hunters across multiple taxa of insects, fishes, birds, and various small and large mammalian species. Finding the connective tissue linking various taxa and species within taxa to unravel the evolution of sociality and group hunting behavior is a daunting proposition, but see Beauchamp (2014), who explored different aspects of predator–prey interactions among multiple taxa but at a superficial level.

In this book, we use a narrower lens than provided by broad taxonomic overviews such as Bertram (1978) or Curio (1976) by focusing on fewer prime mammalian predators hunting mammalian prey to explore whether social mammalian predators are successful hunters because of the benefits accrued through their social membership. Terrestrial and marine mammalian social predators have distinct social structures, incredible behavioral plasticity and adaptability, and lifestyles that merit a more in-depth examination. We do this by exploring predation strategies within a socio-ecological context of five well-established terrestrial and one marine examples of carnivorous mammalian predators that exemplify social predation in all its complexity. We further explore the potential effects of human-induced changes in the landscape and seascape, and the need for social dynamics and behavior to be integrated into conservation models, i.e., consider the preservation of the appropriate social unit rather than mere animal numbers. This exploration enters the realm of conservation and potentially human management of species and populations at the societal or cultural level, a relatively new concept of social and cultural lives that is gaining credence in terrestrial (Kuhn, 1996; Laland & Galef, 2009) and marine (Whitehead & Rendell, 2015) systems; see also Brakes et al. (2021).

Each chapter is dedicated to a social mammalian carnivore hunting mammalian prey. We have been intentionally selective in our choices to allow a holistic synthesis of knowledge and better illustration of social unit characteristics and predation strategies. While some pack hunter species such as coyotes *Canis latrans* and dholes *Cuon alpinus* were omitted from consideration, we believe the social hunter examples presented here are broadly representative of the behavioral complexity and social diversity of these and other similar cooperative mammalian hunters. The analysis presented in the various chapters is not a quantitative comparative analysis across case studies, but rather represents individualized studies. Where possible, examples are provided to compare behaviors among species.

In Chap. 2, Palmer et al. (2023) cover the extensively studied African lions (the only social felid) from eastern Africa. The authors summarize information on African lion egalitarian social structure and fission-fusion social dynamics, the interplay between lion sociality and group hunting, and adaptations of female prides and male coalitions to varied ecological factors triggering a range of lifestyles from being solitary to stable cooperative groupings across their range. In contrast, in Chap. 3, Chakrabarti et al. (2023) provide an overview of Asiatic lion sociality within an entirely human-dominated landscape marked by diverse and smaller prey and habitat variability, and yet drivers of sociality can be rather like those of African lions. In Chap. 4, Tallian et al. (2023) describe one of the most illustrious but short-lived canids, gray wolf "pack" sociality and predation strategies, which are intertwined and tested under variable anthropogenic pressures in regions with varying grades of protection. In Chap. 5, Smith and Holekamp (2023) analyze the intriguing rank-based social systems in spotted hyenas (*Crocuta crocuta*) and the physiological, morphological, and behavioral characteristics that equip them with tremendous adaptability to changing prey conditions and anthropogenic pressures. In Chap. 6, Jordan et al. (2023) focus on the African wild dog (*Lycaon pictus*)—a versatile and arguably the most social canid pack predator typified by quasi-democratic hunting behaviors, a unique feeding hierarchy, and employment of creative foraging methods to human-driven changes in their hunting grounds. Finally, Chaps. 7 and 8 focus on the only marine social predator that habitually feeds on other mammals—the killer whale. Chapter 7 by Srinivasan (2023) is a global synthesis of mammal hunting killer whale group foraging techniques that are prey dependent and heavily influenced by the cultural transmission of knowledge, democratic social systems, and ecological parameters. The interplay between multigenerational knowledge transmission, social structure and organization in modulating cooperative hunting strategies in mammal hunting killer whales is further comprehensively explained by Black et al. (2023) in Chap. 8. The authors synthesize 30 years of mostly unpublished data from Monterey, California, to provide insights into one of the longest and well-observed populations of mammal hunting killer whales.

This volume gives examples of social mammalian predators where sociality allows for often highly efficient predation. However, we do not imply that the evolution of sociality itself necessarily has social hunting as its original or main driver. Cooperative hunting is rather one of several factors, such as sexual strategies, anti-predator defense (in some cases), and communal care of young—that may contribute to various forms of mammalian sociality. But, it can also become of dominant importance through quick behavioral changes or slower processes of evolution, especially if coordinated cooperative behaviors through kinship, mutualism, or reciprocity, help them harness individual capabilities and knowledge to overcome large prey or social prey like themselves. It is not our intent to explain or duplicate the multi-variable factors concerning evolution and behavioral development of sociality, but an excellent up-to-date primer is provided by Clutton-Brock (2016). We explore overall patterns of sociality related not just to social predation in Chap. 9 (Srinivasan & Würsig, 2023).

In summary, this book offers the reader a comparative picture and a wider understanding of the evolution of sociality and the fluid social dynamics of iconic group living mammalian predators in marine and terrestrial realms. We learn that the lives of these predators are shaped by resource variability, lateral and vertical information transfer, human disturbance, and intrinsic life history, social, and behavioral traits. We consider impacts of human and environmental change on the social habits of these predators, specifically the potential disruption of social units and consequent conservation impacts. As an overarching goal, the book hopes to offer insights on the value of protecting social predators to maintain ecosystem resilience.

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Chapter 2
Social Strategies of the African Lion

Meredith S. Palmer, Natalia Borrego, and Craig Packer

Abstract Within the realm of social carnivores, lions (*Panthera leo*) are the sole representative of the large felids. While other *Felidae* may tolerate temporary associations with dependent offspring or receptive members of the opposite sex, lions are the only big cat where both males and females live in permanent social units. Each sex forms independent groups that come together to engage in a wide variety of social behaviors, including cooperative hunting, mutual defense of kills, cooperative territorial defense, and communal raising of young. Unique patterns of egalitarianism and flexible fission-fusion dynamics make this social structure distinctive among mammals. The bulk of our knowledge on the evolutionary drivers of lion sociality has been derived from extensive studies of populations inhabiting mesic and productive eastern African savanna systems. However, lions across Africa occupy a wide variety of habitat types, including arid deserts, seasonally flooded wetlands, and densely thicketed scrub. Comparison of lion behavior and interactions across their range reveals that their social strategies are highly plastic and adapt to maximize survival and fitness under prevailing local conditions. In this chapter, we first review the ultimate drivers of lion gregariousness based on research from eastern Africa and discuss how lions optimize individual fitness under constraints imposed by group-living. We then explore how variation in proximate drivers of social living (i.e., resource availability, intensity of inter- and intra-specific competition, and habitat structure) can shape the expression of social behavior. We end with a discussion of the social adaptations lions make to survive in increasingly human-dominated landscapes.

The original version of the chapter has been revised. The source line of the artistic illustration has been changed to give credit to the actual photographer – Stotra Chakrabarti. The correction to this chapter is available at https://doi.org/10.1007/978-3-031-29803-5_10

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Keywords Grouping · Territory defense · Foraging success · Cooperative hunting · Communal cub rearing · Egalitarianism · Fission-fusion · Behavioral plasticity · Human-wildlife conflict · Competition

Artistic rendering by Britney Danials. Original photo credit: Stotra Chakrabarti

On any other safari, the icebox bouncing around in the back of the truck might have contained gin and tonic, or perhaps champagne. This time, however, our unassuming plastic cooler was filled to the brim with African lion feces—the freshest and most odiferous we could find. When we trundled to a halt in the middle of the South African wildlife reserve, my job was to reach a thinly gloved hand into this container and spread the pungent, slippery scat—and its scent—into the surrounding savanna. While I rolled up my sleeves and got elbows-deep in lion droppings, the lead researcher cracked open wooden crates and began to assemble a spindly tower topped with a quartet of bullhorn speakers, each facing off in a different cardinal direction. The wires trailing down from the speakers connected a complex audio system programmed with roars (long distance communication calls) recorded from lions located many hundreds of kilometers away. Broadcasting the scent and sound of an unfamiliar group, or pride was meant to intrigue the reserve's resident lions, signaling a potential threat to be investigated. Sure enough, we soon spotted the first lioness sneaking forward through the underbrush.

Quality territories, filled with the waterholes, food resource, and denning sites needed to raise litters of cubs to adulthood, can be few and far between. The advantages of cooperatively defending a valuable site like this from intruders, such as the ones we were pretending to be, likely instigated the first evolutionary steps toward gregariousness in the solitary ancestors of today's lion. But it doesn't end with sociality. The need to remember which of your companions will back you up in a rival confrontation and who might cheat or lag behind shaped the development of social intelligence. Higher cognitive processes, such as counting and odds assessment, enable lion groups to evaluate when it is best to take on intruders and when to turn tail. While intragroup competition and other environmental restrictions have prevented closely related big cat species such as leopards and tigers from adopting a social lifestyle, lions, as we will explore in this chapter, have developed unique social structures to optimize their individual fitness within the constraints of group-living.

At our playback experiment, the lionesses take pause—two of them have emerged, but roars from three separate individuals were coming from our speakers. Lions can count and sex other lions from their calls; they can determine family from stranger, friend from foe, and evaluate whether their own group possess the strength and cohesion to stand a fighting chance. Our pride determined that their odds are poor and slunk off together without making a scene: sociality, cognition, and intelligence all at play under the circumstances in which they first evolved.

2.1 Introduction

Lions (*Panthera leo*) and their ancestors once roamed from southern Africa through southwest Asia, west into Europe, and east into India (Barnett et al., 2006; Yamaguchi et al., 2004). Fossil evidence suggests that the earliest lion-like cat appeared during the late Pliocene, eventually colonizing the entire Holarctic region to become the most widespread terrestrial large mammal of the late Pleistocene (Barnett et al., 2006; Turner & Anton, 1997). We know from early human cave paintings in Chauvet, France, depicting group-living European cave lions (*P. leo spelaea*) that sociality in these proto-lions dates back as far as this Pleistocene era (Packer & Clottes, 2000; Yamaguchi et al., 2004).

Currently, lions are found as a largely continuous population in eastern and southern Africa, in fragmented pockets of west and central Africa, and as an isolated population of ~350 lions in India (Bauer & Van Der Merwe, 2004). These populations can be broadly categorized as belonging to either African (*P. leo leo*) or Asian (*P. leo*, see Chap. 3 this book) subspecies (Bertola et al., 2016). Here, we focus on the African lion, whose current population size is estimated to fall between 16,500 and 32,000 individuals (Bacher et al., 2016; Bauer & Van Der Merwe, 2004; Riggio et al., 2012). Modern-day lion sociality is characterized by a fluid fission-fusion social organization that allows them to flexibly adapt subgrouping patterns to prevailing conditions. This behavioral plasticity results in a broad spectrum of social strategies—from solitary existence to highly cooperative social groupings—exhibited across their range (Meena, 2009).

2.1.1 Unique Among Felids: A Broad Overview of Lion Social Structure

Lions are the only felids where both sexes live in stable social groups (Bertram, 1975; Schaller, 1972) (Fig. 2.1; Box 2.1). Their social organization is based on matrilineal groups of females (“prides”) and groups of bonded males (“coalitions”), which function as separate social units that temporarily associate to mate and raise offspring (Packer et al., 1990).

2.1.1.1 Prides

Prides are stable, matrilineal groups of related females that maintain exclusive territories across multiple generations (Packer, 1986; Schaller, 1972) (Fig. 2.1). Prides can consist of a single female with dependent offspring to groups as large as 21 adults with cubs (Loveridge et al., 2016; Schaller, 1972; Van Orsdol et al., 1985). Lionesses typically have their first litter at 3–5 years of age and their reproductive lifespan can last for another 12 years (Funston et al., 2003; Packer et al., 1988).

Females are largely philopatric and the majority of female offspring are recruited into their mother’s pride; accordingly, pride members are always closely related (Gilber et al., 1991; Packer, Gilbert, et al., 1991). Cohorts of subadult females may disperse, however, when they are evicted by incoming males, upon reaching sexual

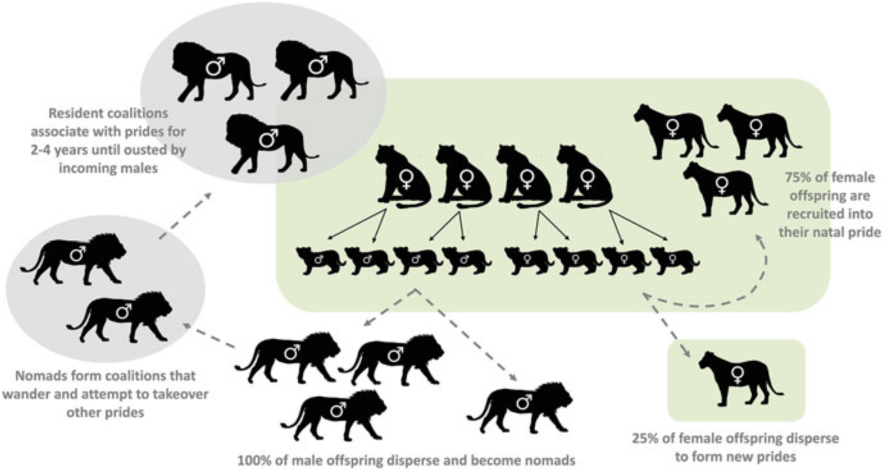

Fig. 2.1 Lion social structure: The primary unit of lion sociality is the female "pride," a group of related adult females and dependent offspring. Upon reaching maturity, most female offspring are recruited back into their natal prides while male subadults are forced to disperse. These young males wander as nomads for several years, forming permanent cooperative "coalitions" with other nomadic males. Male coalitions attempt to gain breeding rights over other prides by evicting resident males and subadults. A successful coalition typically remains associated with a pride for 2–4 years before being ousted by new incoming males. Silhouettes by Gabriella Palomo

maturity with their fathers still resident, or when surrounded by large areas of uncontested territory (Dolrenry, 2013; Pusey & Packer, 1987). Typically, dispersers form a new pride adjacent to their natal home range (Pusey & Packer, 1987; VanderWaal et al., 2009), such that neighboring prides often contain close relatives (Spong et al., 2002).

2.1.1.2 Coalitions

Male lions form life-long coalitions that compete with other groups of males for exclusive access to prides (Fig. 2.1). Young males typically disperse from their natal pride by the time they are 4 years old (range: 20–65 months; Hanby & Bygott, 1987). Groups of similar-aged males tend to depart as a group to form a coalition, while males that disperse in small cohorts (1–2 individuals) often form coalitions with unrelated singleton nomads (Packer, Gilbert, et al., 1991; Spong et al., 2002). As lion body size increases linearly with age for the first 3 years of life (Smuts et al., 1980), subadults that delay dispersal are better able to compete with older, larger males for females and territory (Elliot, Valeix, et al., 2014). Dispersing males enter a nomadic phase in which they wander outside of their natal territory and lack a stable home range (Elliot, Cushman, Loveridge, et al., 2014; Elliot, Cushman, Macdonald, et al., 2014; Hanby & Bygott, 1987; Pusey & Packer, 1987).

Coalitions cooperate to evict or kill prides' resident males, gaining reproductive benefits by killing the ousted coalition's cubs and driving away subadult male competitors and sexually immature females (Elliot, Valeix, et al., 2014; Hanby & Bygott, 1987; VanderWaal et al., 2009). Sometimes, the expelled subadults are too young to survive dispersal, resulting in "delayed infanticide" (Elliot, Valeix, et al., 2014). Following the loss of dependent offspring, females enter estrus and mate exclusively with the new males (Packer & Pusey, 1983a, 1983b). Successful male coalitions usually remain in a pride for 2–3 years, fathering only a single cohort per pride (Packer et al., 1988).

2.1.1.3 Egalitarianism

Unlike other social carnivores and many higher primates, lions do not form dominance hierarchies but act instead as "one of nature's few true democrats" (Packer et al., 2001). Female lions exhibit no disparities in reproductive output (Packer et al., 2001; Packer & Pusey, 1983b) nor display apparent feeding hierarchies (Borrego, 2020; Packer et al., 2001). Males also lack dominance structures within their coalitions. For example, access to mates is not determined by social rank but rather on a first come-first served basis, where the male who initially encounters an estrous female enters an uncontested and exclusive courtship (Packer & Pusey, 1982). Egalitarianism was likely favored by the high risks of injury or death that may result from intraspecific fighting within and between groups (Packer et al., 2001). As a result of this social equality, group members are equally affected by any factor that raises or lowers fitness of the entire group (Packer et al., 1988).

2.1.1.4 Fission-Fusion

Although the pride is a cohesive social unit, lion association patterns can be highly dynamic (Fig. 2.2). In large prides, pride-mates are often scattered into smaller subgroups throughout their territory (Mosser & Packer, 2009; Packer, 1986; Van Orsdol et al., 1985). Smaller prides, on the other hand, tend to associate more strongly to form in the biggest possible group (Valeix et al., 2009). Lions can maximize individual fitness by remaining with or leaving a group based on social or environmental factors (Higashi & Yamamura, 1993; Van Orsdol et al., 1985). The "fission-fusion" strategy provides a mechanism for maintaining benefits of large social groups for resource defense while mitigating costs of within-group competition (Mosser et al., 2009; Mosser & Packer, 2009; Packer et al., 2005; VanderWaal et al., 2009). This flexibility is a key feature of lion sociality that enables this species to exist across a wide range of habitat types and under varied ecological conditions (Mbizah et al., 2020; Patterson, 2007).

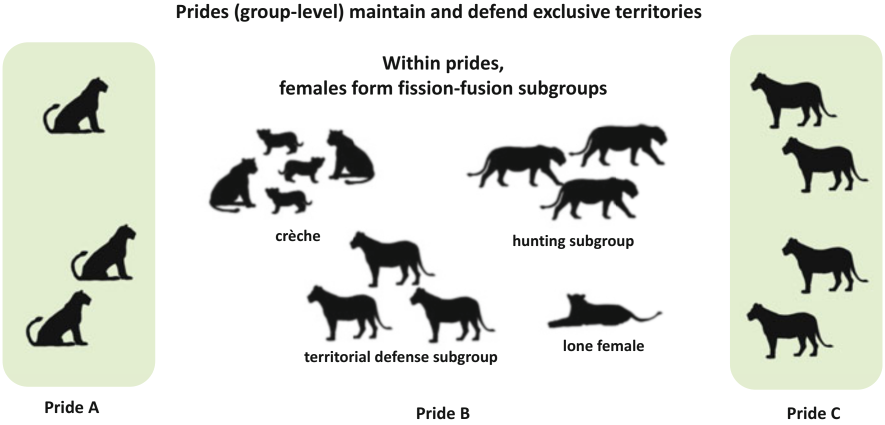

Fig. 2.2 Grouping and subgrouping patterns: The pride is the highest-level social grouping of female lions. Prides compete to maintain and defend exclusive territories. Within large prides, lionesses are seldomly found together but rather associate dynamically in subgroups. Subgroups include hunting parties, territorial defense associations, and cooperative crèches of cub-rearing females and dependent offspring. Silhouettes by Gabriella Palomo

Box 2.1. Sexual Dimorphism

Male lions are the only felids to develop conspicuous manes (Fig. 2.3a), a sexually dimorphic feature that contributes to their unique patterns of sociality. These manes, which can vary significantly in both length and hue, undergo strong selection and may act as an honest signal of fitness to mates and rivals (Patterson, 2007; West & Packer, 2002; Yamaguchi et al., 2004) (Fig. 2.3b). Darker and longer manes likely incur thermoregulatory stresses from the extra insulation (Kays & Patterson, 2002; Trethowan et al., 2017; West & Packer, 2002), increase the conspicuousness of males to rivals and prey due to their large size (Kays & Patterson, 2002; Schaller, 1972), and exact high energetic demands from growing and maintaining this physical feature (West & Packer, 2002; Fig. 2.3c).

In the Serengeti, older and/or healthier males experiencing better overall nutrition develop darker and heavier manes, while males that have been injured or are suffering food deprivation can only maintain short, blonde manes (West & Packer, 2002). Serengeti females prefer to mate with dark maned males, while males prefer to fight against lighter maned males. This enables females to select healthy and more aggressive mates and males to lower the potential costs of fighting (West & Packer, 2002).

However, the morphology of manes can vary substantially across lions' range. Lions inhabiting higher, cooler latitudes are characterized by extensive

(continued)

Box 2.1 (continued)
manes, whereas those residing in hotter, dryer regions display small or nearly absent manes (Gnoske et al., 2006; Kays & Patterson, 2002; Yamaguchi et al., 2004). Male lions inhabiting the dry, arid environment of Tsavo, Kenya lack manes entirely (Gnoske et al., 2006; Kays & Patterson, 2002). Mane length and thickness are inversely correlated with temperature (Patterson et al., 2006), such that this variation may be due to the higher environmentally imposed costs of maintaining a mane in hot, arid climates compared to cooler or wetter habitats (Gnoske et al., 2006; Kays & Patterson, 2002; Patterson et al., 2006).

2.2 Ultimate Drivers of Sociality: Patterns from the Serengeti Ecosystem

Social groups form when the costs incurred by group-living (e.g., heightened competition, disease transmission) are surpassed by the fitness gains experienced by a gregarious individual relative to a solitary individual. African lions form various types of groups and subgroups that perform specific functions, including resource defense (Mosser & Packer, 2009; Packer & Pusey, 1982), group hunting (Packer & Ruttan, 1988; Scheel & Packer, 1991; Stander, 1992a), and communal cub rearing (Packer & Pusey, 1994). The patterns of sociality that maximize the benefits of each function, however, can be at odds. The optimal number of females needed to defend cubs or protect a territory, for example, may differ from the size and composition of a group in which per capita food intake is highest (Packer et al., 1990). In some cases, such as protecting cubs post-parturition, remaining solitary appears to be the optimal strategy (Packer et al., 2001). As such, lions make complicated decisions about joining or leaving groups and subgroups to maximize individual fitness advantages (Schaller, 1972).

Lions of the eastern African Serengeti ecosystem are among the world's best-studied wild vertebrates (Packer, 2019; Schaller, 1972). Over 50 years of continuous behavioral and demographic monitoring programs have fundamentally shaped our understanding of the forces contributing to the evolution of gregarious behaviors of this unique social felid (Packer, 2019). In the following sections, we review evidence from the Serengeti that the defense of resources (i.e., territories for prides and females for coalitions) is the overarching driver in the evolution of lion sociality (Mosser & Packer, 2009; Packer et al., 2005; Packer & Pusey, 1982), while behaviors such as cooperative hunting and cub rearing reflect adaptations to social living and play a role of determining group size and composition at the subgroup level (Packer et al., 1990).

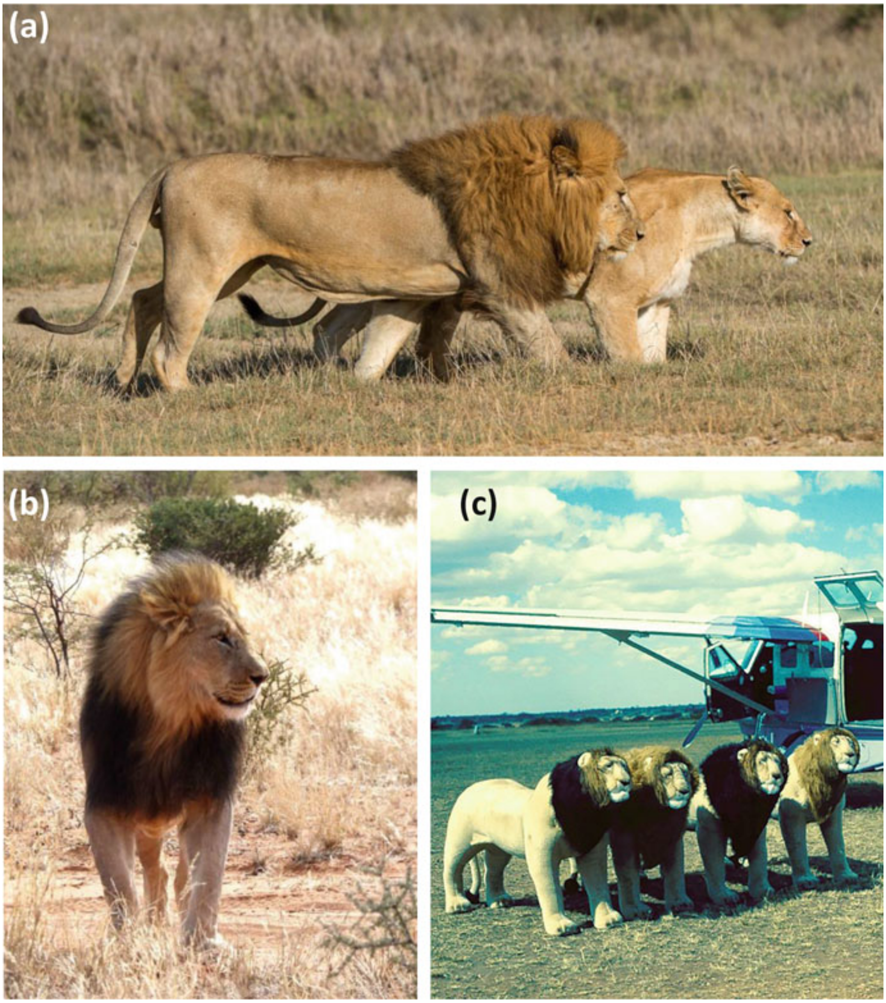

Fig. 2.3 The lion's mane: (**a**) Lions exhibit extreme sexual dimorphism, with (**b**) males growing and maintaining heavy manes that vary substantially in length and hue. (**c**) Experiments using dummy male lions with long dark, short dark, long blonde, and short blonde manes reveal that females significantly prefer males with long, dark manes while males avoided darker maned "competitors." These findings suggest that manes serve an important role in mate choice and male–male competition, acting as honest indicators of male fitness and reproductive potential. Image credits: (**a**) D. Rosengren, (**b**) M. S. Palmer, (**c**) C. Packer

2.2.1 Resource Defense

2.2.1.1 Defense of Territories

It is highly likely that the ability to monopolize high-quality territories in a heterogeneous landscape was the factor that initially favored sociality among females (Heinsohn, 1997; Heinsohn et al., 1996; Heinsohn & Packer, 1995; Mosser et al., 2015). Prides vigorously defend territories that contain resource patches, such as water sources, areas where prey are available and can easily be ambushed, and denning sites (Mosser et al., 2009, 2015; Packer et al., 2005) (Fig. 2.4). Gaining and

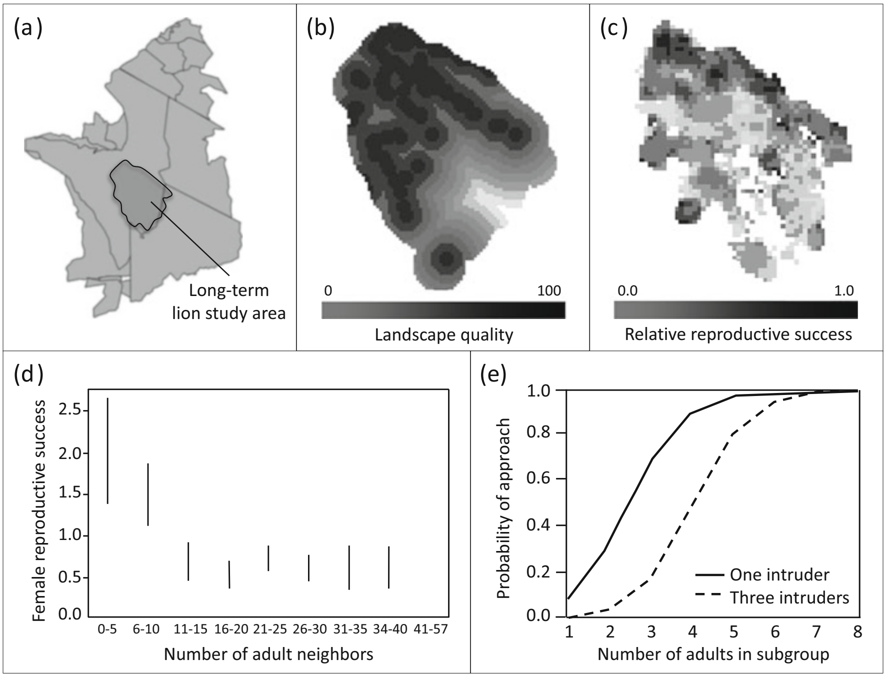

Fig. 2.4 Importance of territoriality as a driving factor in lion sociality and cooperation. Competition for high-quality territories and the threat of intrusion from rival neighbors directly affect female reproductive success. (**a**) The long-term (50-year) lion monitoring area in Serengeti National Park, Tanzania. (**b**) Relative landscape quality for the study area, based on distance to the nearest river confluence (scaled from 0 to 100). (**c**) Female relative reproductive success across the heterogeneous study area varies based on landscape quality within their territories. Reproductive success was calculated as the number of cubs per female that survive to at least 1 year, relative to the success of other prides each year (scaled from 0 to 1). (**d**) Lion density has a negative effect on reproductive success, with female lions that contended with more neighbors and, subsequentially, more frequent inter-pride encounters, suffering fitness consequences. (**e**) Lions have the cognitive ability to assess their odds of winning an encounter: the probability that a lioness would approach a speaker playing the calls of one or three intruders depends on the number of cooperating lions in a defensive subgroup. Data from Mosser and Packer (2009), Mosser et al., (2009), and McComb et al. (1994)

retaining control of a high-quality territory is vital, as females in these patches experience higher reproductive success than females in low-quality territories (Mosser & Packer, 2009) (Fig. 2.4). Good territories can support additional individuals at low cost to the territory owner (Macdonald, 1983), and larger groups in turn drive the formation of territorial exclusivity by excluding smaller groups and solitary agents from resource-rich hotspots (Mosser et al., 2015; Mosser & Packer, 2009; Packer et al., 2005). Prides hold a significant advantage over solitary females when it comes to holding and increasing territory size and quality: large prides dominate in competitive interactions while sharing the costs of territorial maintenance (Mosser & Packer, 2009). Solitaries are unable to maintain high-quality territories, rarely breed successfully, and experience higher rates of mortality compared to pride-living females (Mosser et al., 2009; Packer et al., 1990; Pusey & Packer, 1987). As such, there is strong selection pressure under these conditions to form large prides (Mosser & Packer, 2009).

The benefits of collective territory defense are amplified in patchy landscapes and at high lion densities, where competition for distributed limiting resources is intense (Mosser et al., 2009, 2015; Spong, 2002). Simulation studies suggest that resource heterogeneity is necessary for the evolution of lion group territoriality, with sociality increasing in the population as habitats become more heterogeneous (Mosser & Packer, 2009). Savannas are characteristically heterogeneous habitats and lion sociality is currently viewed as an adaptation for surviving in these variable landscapes (Box 2.4; Kleiman & Eisenberg, 1973; Mattern, 2000; Packer, 1986). In addition, lions can be found at higher population densities than many other large felids (Packer, 1986). In the Serengeti, for example, lions exist at a density of 15.3 lions per 100 km^2 and, as a consequence, potentially fatal competitive inter-group interactions occur once every ~5 days (Packer et al., 1990). Intense competition can also make it difficult for dispersing offspring to establish new territories (van de Waal et al., 2010), with dispersing females in densely populated areas experiencing significantly lower fitness than those that remain with their natal pride (Pusey & Packer, 1987). High costs of dispersal may have contributed to the development of the matrilineal associations we see today.

There is an upper limit to total pride size, above which the costs of group-living outweigh the benefits of resource defense (VanderWaal et al., 2009). Once this threshold is reached, within-group competition reduces per capita reproductive success to a point that forces subadult females to disperse (Pusey & Packer, 1987; VanderWaal et al., 2009). Serengeti prides are most likely to split when both intragroup competition is high and inter-group competition (i.e., number of neighboring prides) is low (VanderWaal et al., 2009).

In addition to selecting for large prides, territorial defense drives subgrouping patterns within prides (Packer et al., 1990). The fission-fusion dynamics operating in large prides mean that lions often encounter intruders while in smaller subgroups (Packer et al., 1990). In these scenarios, females roar to recruit nearby pride-mates to form larger and more competitive defensive subgroups (McComb et al., 1994). Lions in prides of four or fewer individuals tend to remain together rather than fission such that they are present in the largest possible group when encountering intruders (Packer et al., 1988). This display of extreme gregariousness is likely the safest course of action when it comes to resource defense despite potential costs incurred from within-group competition (Packer et al., 1988, 1990).

Territorial defense also incentivizes the evolution of cooperation and advanced cognitive abilities (Box 2.2) that can shift the competitive advantage and allow a defending pride to overcome the threat of intruders (McComb et al., 1994; Mosser & Packer, 2009; Spong & Creel, 2004). Experimental (McComb et al., 1994) and empirical (Mosser & Packer, 2009) evidence reveals that females actively cooperate when defending their territories from intruders, despite risking injury or death (Grinnell, 2002; Heinsohn, 1997; Heinsohn & Packer, 1995). Lions react to the calls of strangers that may pose a threat to their cubs or territory, but adjust their response based on whether intruders or defenders have the numerical advantage (Heinsohn et al., 1996; Heinsohn & Packer, 1995; McComb et al., 1993, 1994; Spong & Creel, 2004). Lions can assess their opponent's group size based on the number of roars detected and only engage with the intruders when their own subgroup size is larger (or when the resources being defended are of high value) (Heinsohn, 1997; Heinsohn & Packer, 1995; McComb et al., 1994).

In terms of cognitive complexity, lions condition their behavior during cooperative territorial defense based on their previous interaction history with specific companions (Heinsohn & Packer, 1995). Females show persistent individual differences in response during cooperative defense, occupying either "leader" or "laggard" (e.g., follower) roles. Leaders display conditional cooperation and score keeping, approaching a simulated intruder more slowly and more often look behind at her companion if the companion is a laggard (Heinsohn & Packer, 1995). The abilities to distinguish and remember the role other individuals play in cooperative events allow lions to adjust their decision-making during intra- and inter-group interactions, increasing their chances of a successful outcome at the individual and group level.

Box 2.2. Sociality and Cognition

The "social intelligence hypothesis" (SIH) proposes that social individuals benefit from cognitive abilities that facilitate social interactions (Byrne & Whiten, 1988). The resultant fitness advantage engenders an evolutionary link, whereby social complexity selectively favors cognitive complexity (Byrne & Whiten, 1988; Dunbar & Bever, 1998). Lions face selective pressures on cognition stemming from the need to navigate complex social as well as physical environments. In addition to cooperation displayed in territorial defense (Sect. 2.2.1.1), role specialization in group hunting (Box 2.3), and the ability for numerical assessment (Sect. 2.2.1.1), lions demonstrate a number of other cognitive abilities that benefit individuals when navigating social life (reviewed in Borrego, 2017):

(continued)

Box 2.2 (continued)

Innovation and cognition: A primary prediction of the SIH is that social species will outperform closely related asocial species on tests of general cognition. Compared to other asocial large carnivores such as leopards (*Panthera pardus*) and tigers (*Panthera tigris*), lions are indeed better at cognitive tasks that assess innovation and problem-solving (Borrego & Gaines, 2016) (Fig. 2.5).

Social facilitation: Although social learning has not been formally demonstrated in this species (Borrego, 2017), lions possess the cognitive abilities requisite for social facilitation, whereby the presence of conspecifics improves task performance (Zajonc, 1965). For example, observing a lion successfully complete a problem-solving task increased unsuccessful lions' motivation and reduced neophobia (e.g., fear of novel objects), potentially promoting increased problem-solving success (Borrego & Dowling, 2016).

Cooperative problem-solving: According to the "emotional reactivity hypothesis," social intolerance limits cooperation and, consequently, cognitive evolution (Hare & Tomasello, 2005). Therefore, social tolerance (e.g., lack of rank-related aggression) and behavioral mechanisms that promote group cohesion should favor the evolution of cognitive abilities associated with cooperation (Hare, 2007). For instance, it has been found that less tolerant species perform more poorly than socially tolerant species on cooperative tasks (Hare, 2007), rank-related aggression hinders cooperation in hierarchical species (Anderson, 2007), and the presence of intolerant individuals reduces cooperative success within social groups (Drea & Carter, 2009). Owing to their egalitarian social structure, lions are remarkably tolerant of other pride members. For example, conspecifics readily endure feeding in close proximity during experimental food sharing tasks (Borrego, 2020) and in the wild (Packer et al., 2011) without exhibiting apparent dominance hierarchies. In agreement with the emotional reactivity hypothesis, measures of social tolerance are positively correlated with a lion's ability to solve a cooperative problem (Borrego, 2020).

Overall, these findings highlight sociality as a potential evolutionary driver of cognitive complexity in lions, with their egalitarian social structure likely bolstering the evolution of cognition associated with cooperative interactions.

2.2.1.2 Defense of Prides

Sociality in male lions, on the other hand, can be attributed to numerical advantages in competition for exclusive access to prides (Bygott et al., 1979; Packer et al., 1988). Males' reproductive success depends on their ability to gain and maintain residence in a pride long enough to raise a cohort of cubs to independence (Borrego et al., 2018; Grinnell et al., 1995; Packer et al., 1988; Packer & Pusey, 1982). However, only a small proportion of Serengeti coalitions are successful in this

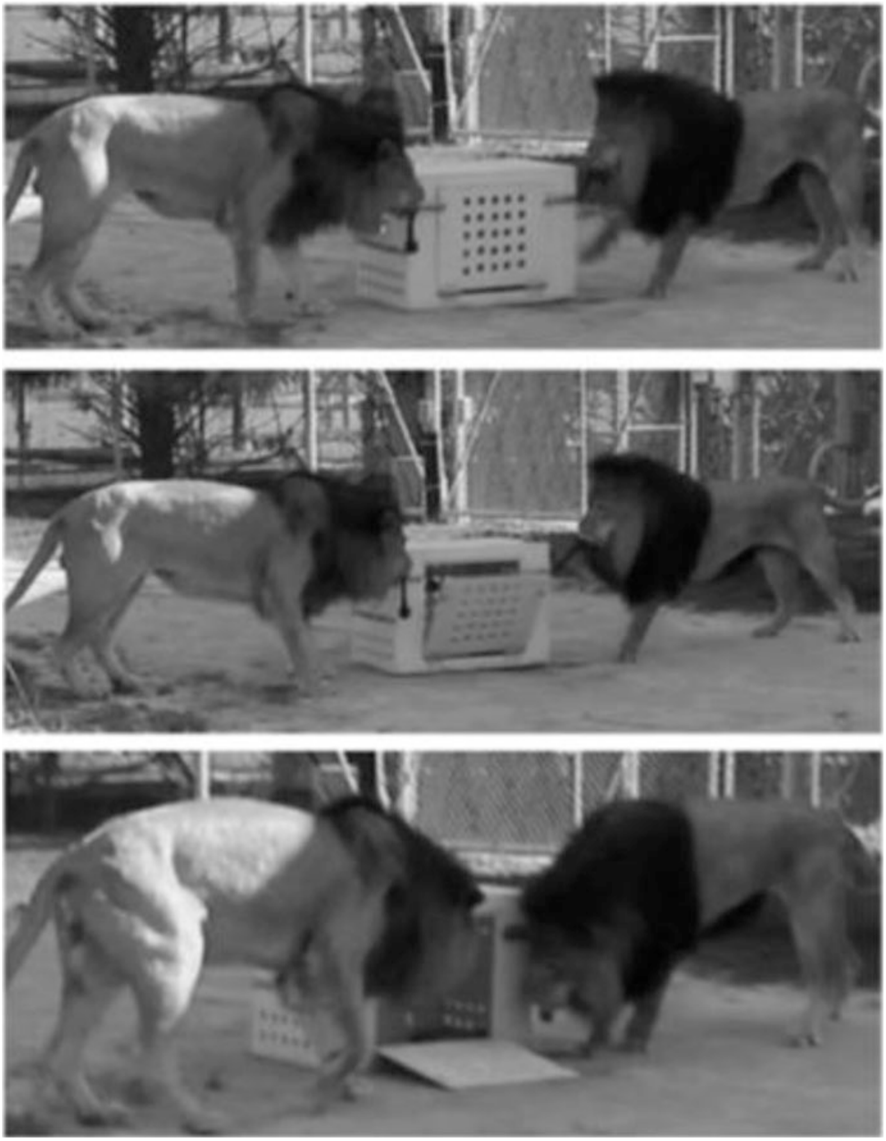

Fig. 2.5 Cooperation and cognition in lions. Two male lions solve a cooperative problem-solving task at Lion Country Safari, Florida. Lions must simultaneously pull ropes located on opposite sides of the box at a 180-degree angle to engage a spring latch and open the box door. Once the door was opened, lions gained access to a food reward. Images from Borrego (2020)

endeavor: only ~28% of nomadic coalitions become resident and even fewer manage to successfully raise even a single cohort of cubs (Borrego et al., 2018). Males that are evicted from a pride by a rival coalition rarely take over another pride, curtailing their reproductive lifespan and dramatically decreasing their fitness (Grinnell et al.,

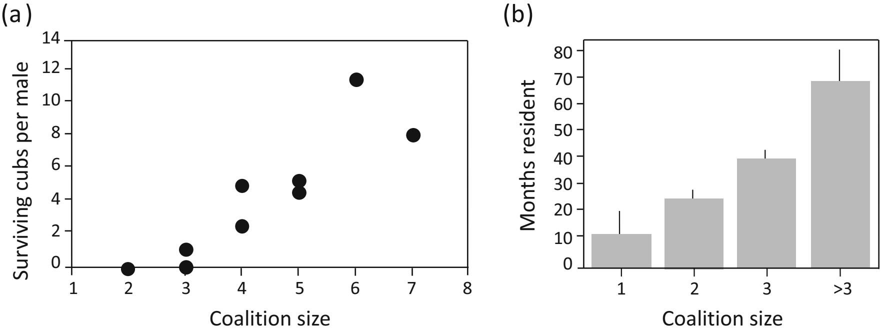

Fig. 2.6 Advantages of larger coalitions. For males, (**a**) increasing coalition size improves per capita reproductive success, (**b**) a consequence in large part of the increased amount of time that males are able to hold tenure over a pride. Data from Grinnell (2002)

1995; Grinnell & McComb, 1996; Packer et al., 1988). Larger coalitions enjoy a competitive advantage compared to solitary males or smaller coalitions and are more likely to gain tenure, retain their tenure for longer, and sire more surviving offspring (Borrego et al., 2018; Bygott et al., 1979; Packer et al., 1988) (Fig. 2.6). In some cases, large coalitions can even be associated with multiple adjacent prides simultaneously, increasing their reproductive advantage (Bygott et al., 1979). While larger coalition size increases individual member competition for females, overall, each additional coalition member increases individual reproductive success by 0.64 surviving cubs per male (Packer et al., 1988).

Whereas female prides are composed of closely related individuals, male coalitions can contain related or unrelated members. Typically, males that disperse in small cohorts (i.e., 1–2 brothers or cousins) form coalitions with unrelated males they encounter during their nomadic phase (Packer, Gilbert, et al., 1991; Spong et al., 2002). Nearly half of all coalition pairs and trios contain unrelated companions (Bygott et al., 1979; Packer, Gilbert, et al., 1991). Paradoxically, all coalitions larger than three males consist entirely of relatives (i.e., a large cohort dispersing from a single pride; Packer, Gilbert, et al., 1991). If bigger is better, why do males not form the largest coalition size possible with unrelated males? The between-group competitive advantage of large coalitions comes with a within-group cost: the individual reproductive success of individual members becomes increasingly skewed with increasing coalition size (Packer, Gilbert, et al., 1991; Packer, Pusey, et al., 1991). Thus, males only benefit from remaining non-breeders in large coalitions if they are enhancing the reproductive success of their kin (Packer, Gilbert, et al., 1991).

Coalition members are also highly cooperative, with males working together to take over prides, defend their pride(s) from other coalitions, and hunt large prey. Cooperation within coalitions appears to be based on mutual dependencies (Grinnell et al., 1995). For example, failing to respond to challenges by strange males imposes an extremely high risk: if a pride is lost to intruders, males may forfeit their only chance at reproductive success (Grinnell et al., 1995). Similarly, if a coalition member defects on his partner during a confrontation with other males, the partner may be injured or killed, which significantly disadvantages the remaining male(s) in future conflicts (Grinnell, 2002; Grinnell et al., 1995). Accordingly, males do not condition their cooperation on the relatedness nor behavior of companions and there are very few instances of defection or “cheating.”

2.2.2 Other Benefits of Group Formation

Early explanations for the evolution of sociality in lions focused on the potential fitness benefits of group hunting, and cooperative cub rearing and cub defense (Schaller, 1972). As intensive study of the Serengeti lion population later revealed, none of these drivers on their own outweigh the advantages of an ancestral solitary existence, but they do contribute to subgrouping decisions within the larger social unit (Mosser & Packer, 2009; Packer, 1986; Packer et al., 1990).

2.2.2.1 Obtaining Food

Hunting is a risky endeavor in which lions regularly pursue prey animals twice their size, regularly facing injury or death during prey capture (Van Valkenburgh & White, 2021). Schaller and Lowther (1969) speculated that hunting in groups enabled greater capture success, the ability to kill larger prey, and division of labor, and that these advantages ultimately selected for group-living. Supporting this theory, Schaller (1972) reported that Serengeti lions had higher capture rates when two or more lionesses hunted together: whereas a single female must attempt six hunts to ensure a single success, a group of females needs only attempt three hunts. When prey are scarce enough that only a few hunts can be attempted per day, a run of bad luck could be fatal to a solitary female (Packer, 1986). Large groups of females (5–7) were also observed hunting large and highly dangerous buffalo (*Syncerus caffer*), whereas smaller groups (1–4) primarily killed smaller, more easily captured warthog (*Phacochoerus africanus*) (Packer et al., 1990). There are no records of solitary females attempting to take down a buffalo, presumably due to both the low chance of success and potentially fatal risks (Scheel & Packer, 1991).

Despite these advantages, group hunting would only drive the evolution of sociality if the per capita rate of food intake in a group exceeds that of a solitary. This is not the case for Serengeti lions (Caraco & Wolf, 1975; Packer, 1986; Packer et al., 1990). Larger hunting groups do not make more captures per hunting attempt than smaller groups or solitaries (Gittleman, 1986; Packer & Ruttan, 1988). By banding together rather than acting as individuals, lions limit their search efficiency for heterogeneously distributed clumps of resources (i.e., herds of prey animals) and thereby reduce overall prey encounter rates (Fryxell et al., 2007). Even though larger hunting groups can acquire bigger carcasses, individuals must then divide the spoils among more companions. Solitary hunters, on the other hand, may take smaller prey but do not need to share food, and thus gain overall larger meals (Packer, 1986; Packer et al., 1990). In fact, lone females have significantly higher daily per capita food intake when food is scarce compared to hunting groups of two to four females; during periods of prey abundance, per capita daily food-intake rate does not vary across group sizes (Packer et al., 1990).

Consequently, subgroups formed by Serengeti lions do not conform to sizes predicted by optimal foraging theory (Mosser & Packer, 2009; Packer et al., 1990, 2005; VanderWaal et al., 2009). As lions do not adjust their grouping patterns to maximize food intake, other motivating factors (such as the probability of encountering rival lions; see above) are likely of outsized importance in driving gregariousness and pride size.

Subgrouping patterns and cooperative interactions, however, are optimized to increase hunting success (Box 2.3). During hunts, lions often alter their propensity to cooperate based on the species of prey pursued. Females predominantly choose to participate in group hunts of larger, dangerous prey where their involvement could increase hunting success but refrain from joining pursuits of more easily captured species (Scheel & Packer, 1991) (Fig. 2.7). These frequent decisions to opt out of group hunts underscore that cooperative hunting is not a key component, but rather a by-product, of lion sociality (Packer et al., 1990; Scheel & Packer, 1991).

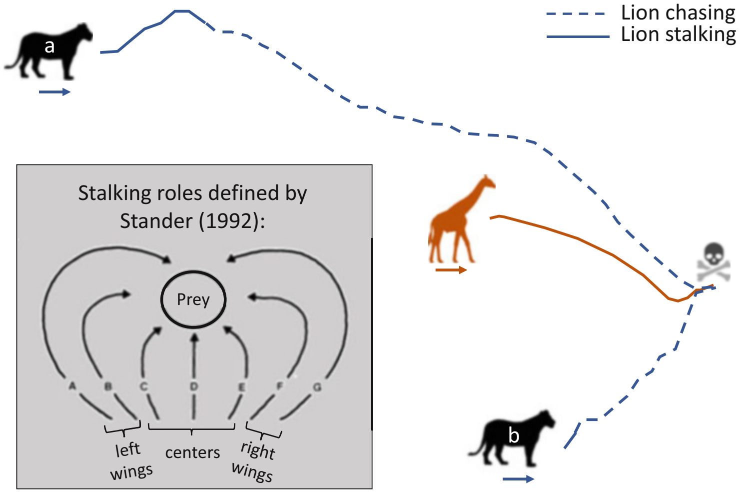

Fig. 2.7 Cooperative hunting strategies in lions. Hunting strategy of two lionesses stalking, chasing, and killing a juvenile giraffe in Khutse Game Reserve, Botswana (Borrego & Packer, unpublished data). The site where the lions successfully took down the giraffe is represented by the skull and cross bones. Lioness “a” is occupying a “left wing” position and lioness “b” is occupying a “right wing” position as defined by Stander (1992a) (inset). Silhouettes by Gabriella Palomo

Box 2.3. Cooperative Hunting

Lions adjust the complexity of their cooperative strategies depending on the type of prey pursued (Scheel & Packer, 1991; Stander, 1992a, 1992b). Boesch and Boesch (1989) describe four levels of complexity that can occur during group hunts: (1) *similarity*: different individuals perform similar actions, (2) *synchrony*: each individual times its actions in response to others' actions, (3) *coordination*: individuals relate their actions in time and space to another's actions, and (4) *collaboration*: individuals perform different complementary actions. Similarity and synchrony are achieved by simply "acting apart together," where individuals tolerate the activities of their companions while independently working toward a common goal (Noë, 2006). Despite being the simplest forms of cooperation, these tactics are often sufficient for hunting even large and dangerous animals. In a typical buffalo capture, for instance, additional lions "pile on" after the first lion has initiated an attack. Coordination and collaboration are more complex strategies, requiring individuals to base their own behavior on that of their companions. Role specialization within a hunt is often cited as evidence of coordination and is presumed to occur whenever individuals consistently perform the same tasks (Anderson & Franks, 2001).

Historically, coordination and collaboration were thought to be the norm for group-hunting lions; however, recent research suggests that these tactics are rarely used and vary depending on social and environmental circumstances. Current evidence for complex hunting strategies in lions is restricted to a single population in Etosha National Park, Namibia (Stander, 1992a). Etosha lions specialize on large, fleet-footed prey that they pursue across open, flat terrain that offers little opportunity for ambush hunting (Stander, 1992a, 1992b). Coordination and collaboration are thought to be favored when prey capture is sufficiently difficult, and accordingly, Etosha lions display the highest levels of cooperative hunting complexity. In this population, individual lions prefer to occupy distinct hunting roles and compensate for variation in each other's behavior (Stander, 1992a) (Fig. 2.7). These strategies result in an enormous advantage in terms of per capita food intake: singletons in Etosha are only successful 2.3% of the time whereas cooperative hunters enjoy a 73% success rate (Stander, 1992a, 1992b).

When prey is easier to capture, cooperation breaks down and lions even benefit from "cheating" their companions. Individuals can avoid risk and conserve energy by refusing to participate in a hunt but later scavenging from their companions' kills (Packer & Ruttan, 1988). In the Serengeti, cheating is more common during hunts of easily captured species such as warthogs where the success rate of solitary individuals is high (i.e., prey could easily be captured without help; Scheel & Packer, 1991). Under the difficult hunting conditions of Etosha, all group members always participated with no

(continued)

Box 2.3 (continued)
documented cheating (Stander, 1992a). This suggests that cooperation is only advantageous when the hunting success of solitary lions is low. Once this condition is met, the complexity of cooperative strategies varies according to prey characteristics, with a simple pile-on strategy typically favored for large but less swift prey compared to a complex division of roles when pursuing more nimble prey species.

Another proposed benefit of lion sociality is defending carcasses from interference competition by inter- or conspecifics (reviewed in Packer, 1986). While interspecific competition at carcasses has been reported in other systems (Cooper, 1991), loss of meat to other large carnivores in the Serengeti is exceedingly rare (Packer et al., 1990). The predominant lion competitor in this system is the spotted hyena (*Crocuta crocuta*) (Kruuk, 1972; Schaller, 1972), yet no discernable relationship exists between lion group size at a carcass and the probability of losing the carcass to hyenas (Kissui & Packer, 2004; Packer, 1986). As it is more probable that lions lose more meat to fellow group members than they do to hyenas, defending carcasses from interspecific competitors is likely not the ultimate driver of grouping patterns (Kissui & Packer, 2004).

2.2.2.2 Reproduction: Crèche Formation, Cub Rearing, and Cub Defense

Lion mothers form highly stable communal crèches, or nursery groups, in which they pool and cooperatively rear similar-aged offspring (Packer, 1986; Packer et al., 1988; Packer & Pusey, 1983a, 1994). As a result of synchronous mating driven by infanticide, pride mothers tend to give birth around the same time (Packer & Pusey, 1983a, 1983b). Cubs join the crèche when they are 4–6 weeks old and the crèche persists for 1.5–2 years, until cubs become independent and mothers resume mating (Packer & Pusey, 1987).

While it has been proposed that crèches provide nutritional advantages to cubs and mothers, little evidence supports this theory (Packer et al., 1990; Packer & Pusey, 1994). Crèche females preferentially nurse their own cubs and cubs reared communally do not ultimately receive more milk than those reared alone; rather, cubs in large crèches are often undernourished (Packer et al., 1988, 1990; Packer & Pusey, 1994). Mothers also experienced reduced food intake in large crèches due to food sharing among more individuals, with those living in maternal subgroups of 3–4 consuming less per capita than solitary mothers or mother pairs (Packer, 1986; Packer et al., 1990).

Cooperative defense of cubs is most probably the primary benefit of gregariousness for lion mothers (Packer & Pusey, 1983a, 1994). Infanticide by incoming males imposes a significant fitness cost, accounting for 27% of cub mortality (Packer et al.,

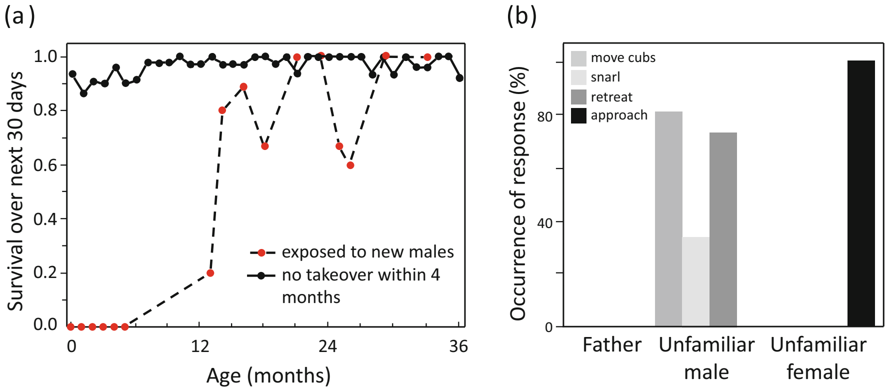

Fig. 2.8 Sociality benefits female reproductive success. Cooperation and gregarious behaviors improve reproductive fitness of female lions. (**a**) Incoming infanticidal males pose a significant threat to the survival of young cubs: all cubs <6 months old died after exposure to male takeovers while survival rates of unexposed cubs are far higher. (**b**) When subject to playbacks of resident males (fathers), unfamiliar males, and unfamiliar females, mothers took defensive action to protect their cubs against unknown incoming males. Data from McComb et al. (1993), Packer (2000)

Table 2.1 Offspring survival increases with female subgroup size. Number of instances in which cubs survived or were lost during aggressive encounters between non-resident males and pride females. No resident (defending) males were present during these encounters

Number of defending females	Some cubs survive	All cubs die
≥2	5	0
1	1	5

Data from Packer et al. (1990)

1988; Packer & Pusey, 1983a; Pusey & Packer, 1987; Fig. 2.8; Table 2.1). Mothers frequently risk injury or death to defend their cubs against infanticidal males (McComb et al., 1994; Packer & Pusey, 1983a, 1983b, 1994), but by forming crèches, they can act cooperatively to defend their offspring (Packer & Pusey, 1994; Fig. 2.8). Crèches' mothers are further able to reduce their appeal to incoming males by roaring in a chorus, as males are more reluctant to approach multiple roaring females compared to females roaring alone (Grinnell & McComb, 1996). However, this numerical advantage can break down as larger prides become increasingly attractive targets for male take-over (McComb et al., 1994).

Nevertheless, protection against infanticide cannot account for the evolution of gregariousness in lions overall (Packer et al., 1990; Packer & Pusey, 1994). Non-mother females within a pride do not participate in the crèche and most small prides still form as large a group as possible regardless of whether offspring are present, suggesting that additional forces initially drove the formation of sociality (Packer et al., 1990).

2.3 Proximate Drivers of Sociality

2.3.1 Plastic Variation in Sociality Across Africa

While African lions have been studied extensively in highly productive eutrophic savannas, as a species, they inhabit a wide variety of ecosystems with heterogeneous rainfall, productivity, habitat complexity, and prey availability (e.g., East, 1984; Fig. 2.9). These variable ecological conditions alter the costs and benefits of sociality and lions plastically adjust their grouping patterns and cooperative behaviors to maximize fitness under local environmental conditions (Cooper, 1991; Hanby et al., 1995; Mbizah et al., 2020; Meena, 2009). Below, we provide a broader perspective on African lion sociality, examining how the social patterns discussed above are shaped by proximate drivers, including competition, resource availability, and abiotic factors.

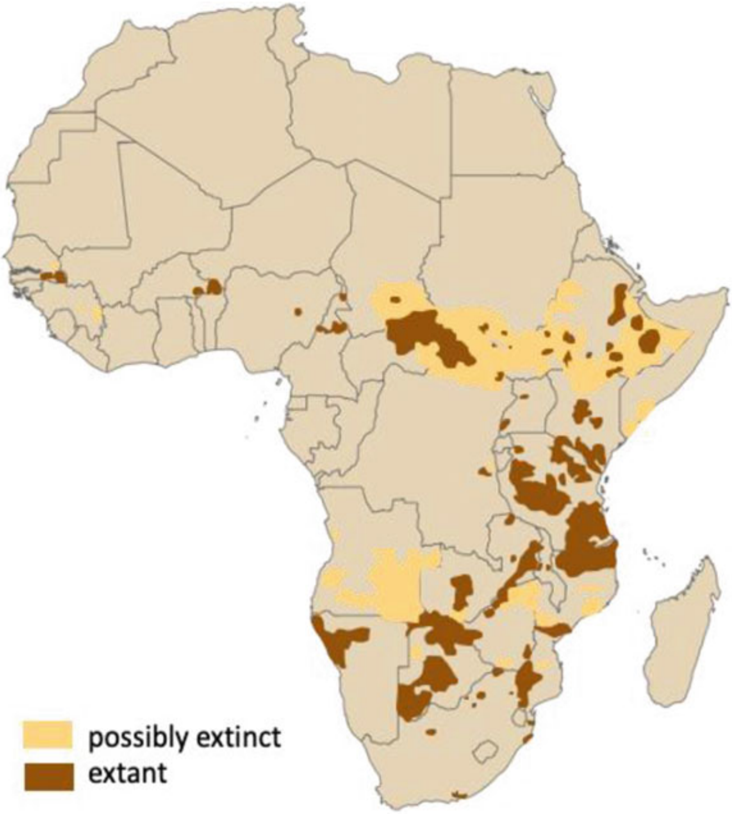

Fig. 2.9 Current lion distribution across Africa. Map adapted from Bauer et al. (2015)

2.3.2 *Intraspecific Competition*

2.3.2.1 Pride Size and Structure

As outlined above, intraspecific competition for territories and the resources they contain is a prominent force driving lion sociality. Across Africa, lion density is positively correlated with rainfall, soil nutrients, and annual temperatures, with populations being smallest in desert and semi-desert areas and largest in moist tropical savannas (Packer et al., 2013). As such, smaller prides and solitaries are more common in arid areas while prides are larger in productive areas where there are high levels of competition (Kissui et al., 2009; Kotze et al., 2018; Mosser et al., 2009). However, increasing numbers of lions in neighboring prides can negatively influence reproductive rates and ultimately limit overall pride size (Kotze et al., 2018; Miller & Funston, 2014; Mosser & Packer, 2009).

Local population density also shapes dispersal decisions and the formation of new prides. Both male and female subadults have been documented dispersing earlier and at higher rates when uncontested areas are available due to low population density (Dolrenry, 2013). In Amboseli, Kenya, lions of both sexes disperse at half the age and twice the rate of Serengeti lions (Dolrenry, 2013). Furthermore, the composition of the lion population is important for determining degree of intraspecific competition and its consequences on dispersal. Where there are high densities of males, and consequentially, high turnover of resident coalitions, we see increased incidence of direct infanticide and the forced early dispersal of subadults, which can lead to delayed infanticide if individuals do not have the experience or body size to compete with established coalitions or prides (Elliot, Valeix, et al., 2014).

2.3.2.2 Territorial Defense and Breeding Subgroups

In high density areas with substantial risk of encountering competitors, Serengeti lions form larger defensive subgroups and are quick to recruit nearby pride-mates when threatened (McComb et al., 1994). In the neighboring Ngorongoro Conservation Area, lions live at higher overall densities than in the Serengeti. Compared to Serengeti lions, Ngorongoro lions suffer greater mortality from fighting and approach intruders more quickly even when the odds of winning are low (Heinsohn, 1997). This increase in aggression may reflect the greater difficulty of defending a territory when the level of competition is high (Heinsohn, 1997). Alternatively, Ngorongoro females entering territorial disputes may anticipate being joined more quickly and consistently by nearby companions given that prides are not distributed as widely across the landscape (C. Packer, pers. obs.).

There are a few notable examples of interannual changes in lion density that may seasonally impact lion social structure. In southern African wetlands, such as the Okavango Delta, Botswana (Kotze et al., 2018), Kafue National Park, Zambia (Midlane, 2013), and Gorongosa National Park, Mozambique (Bouley et al., 2018), annual flooding is the primary driver of ecological change. For portions of the year, preferred dry-season habitat is inundated and lions are increasingly confined to increasingly small islands of dry land, exacerbating intraspecific competition and altering the relationships within and between prides. During these periods, home range overlap between adjacent territories increases substantially and subgroup sizes become larger in areas where competition is highest (Kotze et al., 2018). In addition to territorial defense subgroups, this also includes crèches of mothers with dependent offspring in accordance with findings from Serengeti that cub protection is the primary reason for association between adult females with cubs (Kotze et al., 2018).

2.3.3 Interspecific Competition

Kleptoparasitism by competitors such as hyenas can influence optimal lion feeding group size. While this may not occur often under conditions where prey is plentiful (Kissui & Packer, 2004), interspecies competition can be exacerbated when prey are scarce or differentially vulnerable to each predator species, or under conditions where competitor group sizes are relatively large or formidable compared to lion group sizes. In the semi-arid Chobe National Park (Cooper, 1991) and dry southern Kalahari (Mills, 1990), hyenas can drive females and subadult lions off carcasses, causing prides to lose almost 20% of the edible portion of their kills. Rates of food-stealing are higher for smaller prides and are exacerbated in the absence of adult male lions, even in otherwise productive eastern African savannas (e.g., Ngorongoro Crater; Höner et al., 2002). These acts of kleptoparasitism necessitate that lions hunt more frequently, expending more energy to obtain comparable amounts of food (Cooper, 1991). In these situations, the optimal (i.e., highest food intake per capita) foraging group size may be larger to account for protecting carcasses from interference competition.

2.3.4 Resource Availability

2.3.4.1 Pride Size and Structure

The "resource dispersion hypothesis" predicts that social groups are beneficial for resource defense when resources are heterogeneously distributed in time and space, and that optimal size of a social group depends on resource patchiness and richness of patches (Johnson et al., 2002; Macdonald & Johnson, 2015). Accordingly, pride size in the Serengeti increases as resources become more plentiful and larger prides control more resource-rich patches (Mosser et al., 2009, 2015; VanderWaal et al., 2009). In areas where prey are scarce, prides tend to be very small (Stander, 1991). For example, in Hwange National Park, Zimbabwe, a semi-arid savanna with limited dry-season surface water, the number of prey herds visiting waterholes (a proxy for patch richness) limits the maximum lion group size an area can support (Valeix et al., 2012). More broadly, a meta-analysis from ten distinct habitats in Tanzania, South Africa, and Uganda found that lion group size is correlated with lean season prey biomass, that is, the minimum amount of food the environment can provide across annual fluctuations in prey availability (Van Orsdol et al., 1985). However, when and where resources are not limiting, such as in productive wetland ecosystems (e.g., Okavango Delta, Botswana; Kotze et al., 2018) or fenced protected areas stocked with prey (e.g., South Africa; Hunter, 1998; Kilian & Bothma, 2003; Trinkel et al., 2010), lion pride sizes increase quickly until they become limited by other social and ecological factors.

2.3.4.2 Hunting Subgroups

Where diverse prey options are available, foraging theory predicts that lions should adjust their hunting group sizes based on prey pursued (Scheel, 1993). This can be seen in eastern and southern Africa, where larger subgroups form to hunt larger prey (Kotze et al., 2018; Scheel, 1993). When available prey options are severely limited, lions take this pattern to the extreme. This is exemplified in Botswana, where seasonal and overall declines in preferred medium-sized herbivores created periods where only dangerous megaherbivores such as giraffe (*Giraffa camelopardalis*) and elephant (*Loxodonta africana*) are available as potential meals (Kotze et al., 2018; Power & Compion, 2015). In Chobe National Park, for example, elephants represent >90% of the herbivore community during the dry seasons (Power & Compion, 2015). While elephants are rarely hunted by other lion populations, Chobe lions form exceedingly large hunting groups of up to 22 actively participating individuals to take advantage of this formidable resource (Power & Compion, 2015). On the other hand, where group sizes are constrained by other social and ecological factors, even solitary females can take down adult giraffe and ostrich (*Struthio camelus*) when drought has removed preferred prey (Dolrenry, 2013).

In addition to prey size, the difficulty of prey capture can influence hunting group size. Lions in Etosha National Park, Namibia, specialize on fleet and difficult-to-capture prey and, in contrast to Serengeti lions, capture success rates increase with hunting group size (Stander, 1992a, 1992b). As a result, all group members always participated in hunts with no defection or cheating (Stander, 1992a). Furthermore, unlike eastern African savanna lions, Etosha lions hunt most frequently in the group size associated with highest food intake (Stander, 1992a).

Prey availability also affects connections within and between hunting subgroups. During periods of scarcity, lions in Serengeti (Packer et al., 1990) and Hwange National Park, Zimbabwe (Mbizah et al., 2020), associate less with pride members, a strategy proposed to reduce competition, increase prey encounter rates, and ultimately boost individual food intake (Fryxell et al., 2007). In Hwange, increasing prey abundance caused lions to switch from associating equally but distantly with other pride members to forming highly modular subgroups (i.e., strong connections within but fewer connections between subgroups), suggesting that changing resource levels shape pride cohesion as well as subgroup formation (Mbizah et al., 2020). On the other hand, connections between female prides and male coalitions may weaken when diverse prey options are available. High local densities of buffalo can be found in many southern African systems such as the Kruger National Park, South Africa, which are preferred by males while females predominantly hunt smaller wildebeest and zebra (Funston et al., 1998). As such, resident males hunt frequently and these sex-specific differences in prey preference enable pride males to spend more time away from pride females, facilitating changes in lion social structure (Funston et al., 1998, 2001).

2.3.5 Habitat Structure and Complexity

2.3.5.1 Pride Size and Structure

Habitat structure and landscape characteristics are additional extrinsic determinants of lion social organization (Celesia et al., 2010; Mosser et al., 2009). Lions living in open habitats are vulnerable to detection by competitors and therefore form larger defensive groups and subgroups (Lamprecht, 1981), as well as being more visible to potential prey, necessitating formation of cooperative hunting parties (Davies et al., 2016; Loarie et al., 2013). In landscapes with thicker concealing vegetation, solitary individuals and smaller female prides and male coalitions occur with far greater frequency (e.g., Tsavo region, Kenya: Yeakel et al., 2009; Madikwe Game Reserve, South Africa: Trinkel et al., 2010; Addo Elephant Park, South Africa: Davies et al., 2016). The benefits of sociality may not outweigh the costs of forming and maintaining larger prides in habitats that allow for secrecy and stealth.

2.3.5.2 Territorial Defense and Breeding Subgroups

A cross-habitat review of published literature found that resident males tend to be strongly associated with pride females in open “plains-like” ecosystems than in more dense habitats (Funston et al., 1998). Funston et al. (1998) proposed three hypotheses to explain this variability in coalition-pride associations: (1) prey capture is difficult for male lions in open areas, necessitating that they rely more on females for food, (2) it is more difficult for males to detect intruders in dense habitat, forcing them to spend more time away from females to patrol the area, and (3) males closely associate with females when interspecific competition is high, as defending kills from spotted hyenas is vital to provisioning cubs. Female reproductive strategies and social patterns might also be affected by habitat cover. Dense vegetation allows mothers to better conceal their cubs, potentially negating their reliance on forming maternal crèches (Davies et al., 2016). As with tigers and other large felids inhabiting complex environments that allow for cryptic activity and ambush hunting

(Box 2.4), concealing vegetation may reduce some of the advantages of group formation and cooperation and enable dissolution of lion social structures.

Box 2.4. Insights into the Evolution of Lion Sociality: Comparison with Other Big Cats

Of all the large felids, lions are the only species where both females and males display complex social behaviors (Bertram, 1975; Yamaguchi et al., 2004). Comparison between lions and solitary felids has provided key insights into the conditions that may have generated lion sociality from the ancestral asocial state, as well as highlighting situations in which lions may return to a more solitary lifestyle (Packer, 1986).

Lions are typically found in savannas and habitats characterized by high levels of heterogeneity (Hanby et al., 1995). These landscapes are thought to be fundamental to the evolution of group-living lions, with simulation studies suggesting that the social genotype is never favored in a homogenous landscape (Mosser et al., 2015). However, the leopard (*P. pardus*)—one of the lions' closest living relatives—is solitary despite inhabiting the same ecological systems. Interspecific interactions with lions have been proposed as factor limiting the evolution of leopard sociality, as groups of leopards living sympatrically with groups of lions would face considerable interference competition (Mosser et al., 2015; Packer et al., 2009). Similar patterns of intraguild competition may have originally hindered social evolution in lions themselves, as lion sociality only arose after the disappearance of the even larger and purportedly social saber-toothed cats and cave hyenas (Carbone et al., 2009; Werdelin et al., 2010).

Lion abundance and the type of available resources also drive and permit the development of lion sociality, respectively. Where lions exist at high population densities, large food items allow multiple individuals (including those not involved with the hunt) to congregate on a single kill. Felids that take large prey but live at lower densities, such as leopards or mountain lions (*Puma concolor*), are unlikely to lose meat to unrelated conspecifics (Packer, 1986). Leopards additionally cache their food in trees, keeping it safe from competitors without the need to defend their kills (Balme et al., 2017; Rubenstein, 2009). Species that specialize on smaller prey, such as cheetah (*Acinonyx jubatus*), may find intraspecific scavenging less rewarding and rarely congregate at each other's kills (Packer, 1986). In both cases, these species would lose more meat to conspecifics if they formed groups and this loss might not be outweighed by other advantages of sociality (Packer, 1986).

Many large felids, including lions, hunt by ambushing their prey. This strategy typically requires stealth and cryptic behavior that often favors an asocial lifestyle (Kleiman & Eisenberg, 1973). In less productive environments where prey are more difficult to find or under circumstances where

(continued)

Box 2.4 (continued)
habitat complexity increases the advantages of individual ambush hunters, large felids such as tigers, mountain lions, and jaguars (*Panthera onca*) retain a solitary existence (Bekoff & Daniels, 1984). In productive but open habitats, group hunting and cooperation provide a critical advantage to lions when taking down prey (Stander, 1991).

2.3.5.3 Hunting Subgroups

As “sit-and-wait” predators, lions experience highest hunting success in areas with good cover where prey cannot easily detect an approaching predator (Hopcraft et al., 2005) and are limited in their ability to maneuver during escape (Davies et al., 2016). Whereas female lions in open savanna systems benefit from group hunting, those in the densely vegetated and concealing habitats are highly successful hunting alone (Davies et al., 2016). Males are particularly conspicuous to prey in savanna and desert habitats due to their large size and prominent manes (Loarie et al., 2013; Scheel & Packer, 1991; Stander, 1992b). They, therefore, tend to refrain from hunting when possible and spend more time with prides to feed from female-killed carcasses (Funston et al., 1998). However, males in densely vegetated habitats are typically successful hunters and can operate largely independent of females (Davies et al., 2016; Loarie et al., 2013).

2.4 Lion Sociality in Human-Dominated Landscapes

Intensifying anthropogenic pressures are reshaping lion social behavior as these animals attempt to survive in increasingly human-dominated landscapes (Kissui, 2008). Lions’ enormous capacity for behavioral flexibility allows them to persist outside of protected areas or even thrive under enforced management and conservation protections. Much research is still needed to understand how intricate social dynamics are affected under these conditions. At present, we can mostly speculate on how lion communication, cooperation, and intraspecific interactions are affected by human activity and what the cascading consequences (e.g., genetic diversity) of these changes may be. Below, we discuss what is currently known regarding patterns of lion sociality within human-dominated and highly managed landscapes.

2.4.1 Inside vs. Outside Protected Areas

Lions living outside of protected areas are exposed to a multitude of anthropogenic threats that have significantly altered their population and social dynamics (Frank et al., 2008). In these situations, lions face significant competition with humans for space and resources (e.g., prey biomass) as well as suffering direct and indirect persecution (Bauer et al., 2008; Loveridge et al., 2010). Given that protected area establishment is often biased to preserve locations of naturally high biodiversity, human activity outside of protected areas undoubtedly exacerbates challenges faced by already low-density populations attempting to persist in resource-scarce landscapes.

Lions living outside of protected areas are frequently observed in small groups or as singletons rather than in large prides. In human-dominated landscapes across Kenya, females and males are almost exclusively solitary or in pairs (Samburu: Bhalla, 2017; Amboseli: Dolrenry, 2013; Tsavo: Kays & Patterson, 2002). Smaller groups may be an adaptation to human persecution, allowing lions to avoid attracting human attention and therefore move through settled areas with less conflict (Dolrenry, 2013; Suraci et al., 2019). Alternatively, this may represent an extreme case of the low-density lion behavior observed in natural habitats, i.e., resulting from lower prey density, reduced competition for space, and lower densities of potential mates and competitors as discussed above. Understanding how existence in human-dominated landscapes alters lion subgrouping dynamics represents a vital area of future research. For example, there is some indication that cubs living outside protected areas learn to hunt and survive alone earlier than those within parks and reserves (Bhalla, 2017), but there is much to uncover regarding how this early maturation alters pressures to form crèches and foraging groups.

2.4.1.1 Trophy Hunting

Trophy hunting, defined as selective hunting for sport or recreation, is currently conducted in 23 African countries (Lindsey et al., 2007; Macdonald et al., 2017; Packer et al., 2011). Trophy hunters often target prime-aged males (3–7 years old) (Whitman et al., 2004, 2007), leading to variable male tenure length and frequent social perturbation (Yamazaki, 1996). Excessive offtake of tenured males is associated with an increase in infanticide (direct and delayed) resulting from competing males more easily ousting a resident coalition weakened by the loss of a member (s) (Elliot, Valeix, et al., 2014; Packer et al., 2011) and, in some cases, can result in population collapse (Whitman et al., 2004, 2007). While less common, removal of females also has consequences for pride social structure as territory defense and per capita reproductive output are highest in larger prides. For example, high levels of culling in the Venetia Limpopo Reserve, South Africa, decreased the lion population to a degree where lions existed only as solitary individuals (Snyman et al., 2014).

Excessive hunting of males has distinct implications for subgrouping patterns. While male:female ratios are closer to 1:1 in un-hunted systems, females can be 4–6 times more prevalent in areas where males are selectively hunted (Botswana, Cooper, 1991; Zambia, Yamazaki, 1996; Zimbabwe, Loveridge et al., 2007). Under conditions of extreme male depletion, male coalitions are far smaller (Davidson et al., 2011; Macdonald & Loveridge, 2010) and more likely to take on additional companions during tenure of a pride (Yamazaki, 1996). Male ranges often contract and may not cover the entire range of a female pride, but instead overlap with multiple pride territories (Yamazaki, 1996). Under such circumstances, copulation occurs frequently between males and females from different prides (Yamazaki, 1996).

2.4.1.2 Persecution

Lions outside of protected areas are also more exposed to persecution in the form of illegal hunting, snaring, and poisoning (Macdonald et al., 2017; Snyman et al., 2014). Lions are often directly targeted in retaliation for killing livestock and people (Ogada et al., 2003), while other incidences represent lion "by-catch" from bushmeat poaching operations (Midlane, 2013; Mwape, 2020). Significantly more lions die every year from these causes than from trophy hunting (Macdonald et al., 2017). Deaths resulting from persecution are more indiscriminate with regard to lion age and sex, causing different perturbations of social structure than those due to selective hunting (Woodroffe & Frank, 2005). Overall, poaching creates low-density situations in which lions form smaller prides or spend more time alone (Bauer, 2003; Dolrenry, 2013; Oriol-Cotterill et al., 2015). It may be the case that the need to avoid human attention combined with potentially low resources and low densities of competitors can reduce the drivers of sociality to a point where lion social structure fragments (Snyman et al., 2014).

2.4.2 Living in Managed Wildlife Areas

While lion populations are declining across Africa, conservation and tourism are driving efforts to restore select populations back to their historic range. A noteworthy case of this phenomenon is lion repatriation to small (<1000 km^2) fenced reserves, where lion populations exist in closed systems and are largely unable to self-regulate (Miller et al., 2013; Miller & Funston, 2014). As a result, populations must be heavily managed by methods such as limiting births (e.g., using contraception or performing hysterectomies), culling, and translocating individuals between reserves (Kilian & Bothma, 2003; McEvoy et al., 2019; Miller & Funston, 2014).

During the reintroduction process, lion social structure undergoes major disruptions both before and after release. Young lions are typically removed from their natal prides and often forced to bond with unfamiliar individuals prior to release into their new habitats (Kettles & Slotow, 2009; Miller et al., 2013). Joining of individuals from different families and locations to form a new pride is highly atypical under natural circumstances (Packer et al., 1990). As a result, artificial groups tend to remain unstable or fragment (McEvoy et al., 2021; Smuts, 1978).

Many small, fenced reserves reintroduce only 1–2 prides and a single coalition, creating conditions of reduced competition that can exacerbate pride dissolution

(McEvoy et al., 2021). Neighboring prides quickly become "known," while artificial removal of subadult dispersers and fencing limit further exposure to new individuals (Druce et al., 2004; Slotow & Hunter, 2009). Furthermore, prey abundance is maintained year-round, minimizing the need for lions to venture in search of food in ways that may expose them to unknown prides (McEvoy et al., 2021; Miller & Funston, 2014). Without the threat of territorial take-over, hostile encounters, or infanticide, key drivers for gregariousness are lacking, causing many prides to dissolve (Miller et al., 2013; Miller & Funston, 2014). However, a review of South African reserves suggests that these behaviors can be restored by increasing the threat of competition. As the number of prides and coalitions within a reserve increases, lions start forming larger groups and demonstrate higher levels of social cohesion than in less complex population structures (McEvoy et al. 2021).

These unique conditions affect the structure of lion breeding groups with consequences for pride population growth. Lion reproductive output was higher in small, fenced reserves compared to many larger systems (McEvoy, 2019; Miller & Funston, 2014). Mothers started giving birth at a younger age (Lehmann, 2007; Miller & Funston, 2014) and overall cub survival was substantially higher (87%) than for lion populations in open protected areas such as the Serengeti (Miller & Funston, 2014). When reserves contained only a single pride, lioness interbirth interval was shorter and cubs reached independence at a younger age (McEvoy, 2019). Lacking external threats from other lions, fewer crèches formed and males spent less time with their prides defending their cubs, preferring instead to pursue additional mating opportunities (McEvoy, 2019). Without periodic male takeovers, infanticide was largely absent from this system (Miller & Funston, 2014) such that females lacked birth synchrony (Lehmann, 2007; McEvoy, 2019), further contributing to the formation of smaller breeding groups (McEvoy, 2019). These trends toward asociality could again be reversed, in this case by increasing the number of adult female neighbors and male coalitions (McEvoy, 2019).

2.5 Conclusions: Current Unknowns and Future Directions

We are continuing to build a more nuanced understanding of behavioral ecology and social plasticity of lions where they are found across eastern and southern Africa. However, there exist several key gaps in our knowledge of lion sociality and cooperative behavior.

2.5.1 Geographic Bias

Currently, we have scant knowledge regarding lion social dynamics in central and western Africa, which contain approximately 25% of the Africa lion population (Bauer et al., 2015). In these areas, lions persist predominantly outside of protected areas and occur at extremely low densities due to low-standing prey biomass and high levels of persecution (Bauer, 2003; Sogbohossou, 2011; Sogbohossou et al., 2014). As we might anticipate from the case studies illustrated above, central and western African lions of both sexes lead small-group or solitary existences; while there is high territory overlap, there appears to be little interaction between individual lions (Bauer, 2003).

2.5.2 Behaviors Maintaining Social Bonds

There is still much to learn about species-wide variation in gregariousness among members in prides and subgroups. Basic information on the amount of time that individuals, subgroups, and pride members as a whole spend together under different conditions would reveal key information on the maintenance and degree of social behaviors. Long-term studies of known lions could be used to undercover other useful information about individual variation in social behaviors (e.g., bold vs. shy, leader vs. laggard) and the implications of interpersonal differences on social cohesion (Elliot, Valeix, et al., 2014; Heinsohn & Packer, 1995)

More complicated questions can also be asked about the prevalence of behaviors contributing to gregariousness and cooperation. For example, roaring (long distance lion calls) in Serengeti lions is essential for communicating among distantly separated pride members and serves as a warning to intruding females and nomadic males. We know little about the use of roaring as a social tie in other populations. Another area for future exploration is uncovering the social or ecological drivers that interact to promote cooperation during territorial defense or group hunting and the different forms these cooperative behaviors can take (e.g., what favors a cognitive complex strategy compared to a simple strategy; Box 2.3).

2.5.3 Consequences of Variation in Social Behavior

How lions interact with each other determines their impact on the broader environment. This issue is particularly important in managed landscapes, where altered social conditions can cause breakdown of natural predator–prey relationships and rapid population growth (McEvoy, 2019). Weak connections between individuals in a pride coupled with complex vegetation landscapes that enable solo hunters to operate effectively can result in more individually hunting lions, increasing the overall predation pressure on large herbivore prey (McEvoy, 2019). In some instances, this may lead to local prey extinction events known as “predator pits” (Palmer et al., In review). This is an extreme example, but one that demonstrates how an in-depth understanding of lion sociality can be used to predict impacts on their ecological communities.

2.5.4 Future Directions

Lions exhibit impressive social flexibility, and thereby offer a unique system for investigating questions regarding the conditions under which social groups form, how they are maintained, and when they break down. Advances in technology, such as GPS collars, accelerometers, and camera traps, are enhancing our ability to investigate lion social behavior, enabling a more detailed understanding of the circumstances that favor extreme gregariousness and those circumstances under which sociality breaks down. Additionally, as long-term data are acquired across the lion's range, cross-habitat comparisons are further enhancing our understanding of the factors that drive plasticity in the lion's one-of-a-kind social system.

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Chapter 3
The Role of Food and Mates in Shaping Asiatic Lion Societies

Stotra Chakrabarti, Kausik Banerjee, and Y. V. Jhala

Abstract Asiatic lions, once widespread from Persia to eastern India, are now confined as a single population in the Gir forests and the adjoining agropastoral human-dominated landscape of Gujarat, western India. These lions inhabit forested habitats with small and medium sized prey that are found at relatively uniform seasonal densities. In this chapter, we present information on the historic and current distribution of Asiatic lions, and their evolutionary origins. We further delve into the effect of prey size and availability, coupled with habitat characteristics on hunting strategies, prey acquisition, male and female group sizes, and territoriality. From our long-term observations of lion behavior, we comment on the possible drivers of sociality in this unique population. Additionally, based on a cross population analysis from lions in east Africa and Gir, we discuss the causes and consequences of sexual segregation in Asiatic lions, and highlight the uniqueness of their social and mating strategies. We end with the prospects of potential research in this landscape, as well as the need for comparative studies on lion behavior across populations that inhabit different eco-regions.

Keywords Behavioral plasticity · Carnivore behavior · Gir · Mating strategies · Optimal foraging · Sexual segregation

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Artistic rendering by Britney Danials. Original photo credit: Stotra Chakrabarti

Vignette

I was sitting on the hood of our 4 × 4, squinting hard at the nearby thicket, trying to locate the source of the loud high-frequency beeps from the radio receiver. The late-night chill in the air had turned my olive-green jacket into my warmest companion; I lacked the compact fur of our companions, lions. For the past 5 days, we (a team of 4) have been tracking Jodha, our newly radio-tagged Asiatic lioness, and her pride—a group of two lionesses with two small cubs—to learn more about their daily lives. While such continuous focal follows were quite the grind, they offered us with incredible information about how individuals of this unique population of lions went about their daily routine and navigated a landscape that is frequently full of people.

Since we fitted Jodha with a radiotransmitter a couple of months ago, we learned about her favorite hideouts - shady respites where she snoozed during the heat of the day. We witnessed how she often left her cubs under the watchful eyes of their older sibling for some much needed "me time," while she scoped good ambush points for *procuring food. Her small cubs rely on her milk, and will be dependent on her for the next two years. However, her older daughter, Saumya, who's on the cusp of adulthood, helps by babysitting the cubs during her hunting forays. Asiatic lion prides, like Jodha's, are typically small and cohesive with 2–3 lionesses and their cubs.*

I look at my watch—we have lost visuals for over 2 hours now. Jodha's group has vanished into a sea of very long and extremely itchy vegetation covering a semi-dry catchment of a dam; water mostly used for seasonal irrigation. The catchment is one of her favorite hunting grounds because wild herbivores often use it for fresh water, and the banks have the perfect hiding spots for a predator. Lions are sit-and-wait opportunistic hunters, and we are gradually learning that such ambush sites can create the crucial difference between starvation and a full tummy! Jodha hasn't caught anything in the past three days and their last meal was not a big one—she is hungry. While the moonlight and the radio-beeps helped us maintain good visuals on the group throughout the night, we have now lost them in the vegetation although she could not be more than 20 feet away—the radio-beeps were strong!

The eastern horizon was gently lighting up with brilliant crimson hues while Bhiku, one of our most experienced lion trackers with the sharpest of eyes pointed at a herd of nilgai advancing toward the water. We slowly inched our vehicle away toward the edge of the embankment, and decided to observe from atop a "machan"—a raised bamboo structure that farmers use at night to guard their crops against wild deer and antelopes. This elevated position helped us stay away from a potential hunt yet gifted us with visuals that we had not anticipated! We could see exactly where Jodha and Saumya lay observing the moving herd, while the 2 cubs played with each other.

What unfolded next was one of the rare instances of cooperative and coordinated hunts that we have witnessed in our years of tracking lions. Jodha was quick to leave the scene, half crouched, positioned herself near the far bank of the catchment, while Saumya circled around the herd. To our surprise, Saumya broke cover and charged! The herd scattered into smaller groups but Saumya kept pursuing a subgroup of 2 mothers and their calves. Within seconds, the scene erupted with a deafening growl while we stood in awe on top of the machan witnessing a tawny blaze grabbing and struggling with one of the nilgais. Saumya had precisely cordoned the herd to Jodha's ambush quarters, and she did what she did best. Dinner has been served!

The chapter on Asiatic lions recounts long-term information gathered across years of tracking lion groups while we closely followed their triumphs and tragedies, to stitch a comprehensive picture of what it takes to be a group of these very special lions.

Stotra Chakrabarti

3.1 Introduction

3.1.1 Origin, Distribution, and Status

The origin of Asiatic lions (*Panthera leo leo*) can be traced back to a dispersal event from East Africa, nearly 118,000 years ago (Antunes et al., 2008). However, the current lions in India share stronger genetic affinities with the lions of North, West, and Central Africa compared to the Southern and East-African lions (Bertola et al., 2011). This might be owing to an extinction event in the Pleistocene, which (possibly) exterminated West and Central African lions, subsequent to which recolonization of lions occurred from a *refugia* in the Middle East (Bertola et al., 2011). However, mt-DNA-based analysis of modern and ancient lion samples suggests that migration of lions into Asia began around 21,000 years before present and continued until late Holocene (Barnett et al., 2014). While Barnett et al. (2014) found that the maternal lineage of Indian lions aligns with the clade/group of North, West, and Central African lions, more recent analysis coupling nuclear markers with mt-DNA indicates Indian lions to form a distinct cluster with negligible overlap with extant African lions (Bertola et al., 2015). Based on such phylogenetic evidence, the IUCN delineates modern lions into only two sub-species: (1) *P. leo leo*—lions from India, Central and West Africa, and (2) *P. leo melanochaita*—lions from East and Southern Africa (Kitchener et al., 2017). While the phylogenetic affiliation of the Asiatic lions seems to be contentious, in this chapter we focus on the lions that are now found only in the Asian system.

The former range of the modern Asiatic lion, traced from literature, cultural relics, fossil evidence, and hunting records suggests a widespread distribution covering Anatolia, Syria, the Middle East through Eastern India (Caldwell, 1938; Joslin, 1973; Kinnear, 1920). Lions in India were common in the Indo-Gangetic Basin in North and Central India, and until the mid-1800s were abundant in the states of northern and western India (Dalvi, 1969; Fenton, 1908; Pocock, 1930). However, by the late 1800s, lions were exterminated from most of their range because of hunting and habitat loss (Divyabhanusinh, 2005). By the 1880s, these lions were restricted to a single free-ranging population in the Saurashtra peninsula of Gujarat, western India (Dalvi, 1969; Jhala et al., 2019). Some lions continued to survive in pockets of Iran and Iraq but soon became extinct. By 1888–1890, hunting and further fragmentation of forested patches and loss of habitat due to agricultural intensification and pastoralism in the Saurashtra region finally restricted the Asiatic lions to the Gir forests—a patch of dry-deciduous thorn forest of ~1800 km^2 (Divyabhanusinh, 2005; Jhala et al., 2019).

Based on microsatellite analysis, Driscoll et al. (2002) detected two relatively recent genetic bottlenecks in Asiatic lions, a major event about 2680 (range 1081–4279) years ago and a minor event ~180 years ago. The major bottleneck corresponds to the separation of the Kathiawar/Saurashtra Peninsula surrounding the Gir forest from mainland India by a rising sea level of the Gulf of Khambhat (Gupta, 1972), which resulted in the isolation and inbreeding of the Gir lions. By the time the

Gulf water receded, and the peninsula became continuous with the mainland, most of the lions from the mainland had been exterminated. Subsequently, at the onset of the nineteenth century, owing to severe hunting mainly for trophies, lions became further restricted only to the Gir forests, and their numbers dwindled to less than 50 (Edwards & Fraser, 1907; Kinnear, 1920; Pocock, 1930), causing the second (minor) bottleneck.

Because of timely protection measures adopted by the former rulers/*Nawabs* of the Gir region, the lions survived (Divyabhanusinh, 2005) and increased to about 287 by 1936 (Dalvi, 1969). Subsequently, the Government of Independent India enforced a ban on lion trophy hunting in 1955 and declared the Gir forests a Wildlife Sanctuary in 1965. The lion population has increased steadily with protection and habitat management by the state-run Gujarat Forest Department (Singh & Kamboj, 1996), and has reached a figure approximately 700 in the 2020 lion census (Gujarat Forest Department, 2020). The sub-species was also downlisted from the "Critically Endangered" category of the IUCN Red List in the 1990s (Nowell & Jackson, 1996) to "Endangered" in 2008 (Breitenmoser et al., 2008).

Lions have done extremely well under the management and protection of the forest department, facilitated by the positive attitudes from the local communities—leading to a one-of-a-kind conservation success story where the population and range of a large carnivore have steadily been restored in the Anthropocene, in close proximity with humans (Jhala et al., 2019). Lions now range over 15,000 km^2 of human-dominated landscape comprising the Gir Protected Area (Gir PA; 1800 km^2), Girnar Wildlife Sanctuary (180 km^2), and $>$13,000 km^2 of area, which is outside the formal boundaries of protected areas, while sharing space with a crowded human population (Jhala et al., 2019, Fig. 3.1). While their range has increased constantly and optimistically, this single free-ranging population has only one source of ~300 lions that live within the Gir National Park and Wildlife Sanctuary (lion density = 15/100 km^2), connected to several small sink populations of $<$50 lions each, in the agropastoral system (lion density = 2/100 km^2) (Banerjee, 2012; Jhala et al., 2019). Crucial for the long-term persistence of these sink populations is connectivity with the Gir PA source that provides new animals through immigration, as shown through data based on radiotelemetry (Jhala et al., 2014, 2019). Lions in India thus exist in a metapopulation framework with small sink populations dispersed across the human-dominated agropastoral landscape that are connected through corridors with the source population within Gir PA (Banerjee, 2012; Banerjee et al., 2010). Such connectivity, although crucial, is fast becoming tenuous with modern linear infrastructure catering to the aspirational need of a growing human economy.

Lions share space with humans across (almost) the entirety of their range in India, excluding the Gir National Park, which is ~250 km^2 of inviolate space nestled within the Gir Wildlife Sanctuary (Gir WLS). Within the PA, lions interact primarily with the forest dwelling pastoralist community of *Maldharis,* who live in 70 forest settlements (*nesses*) within the Gir WLS. Outside the PA, lion–human interactions range across urban, peri-urban, and rural settings.

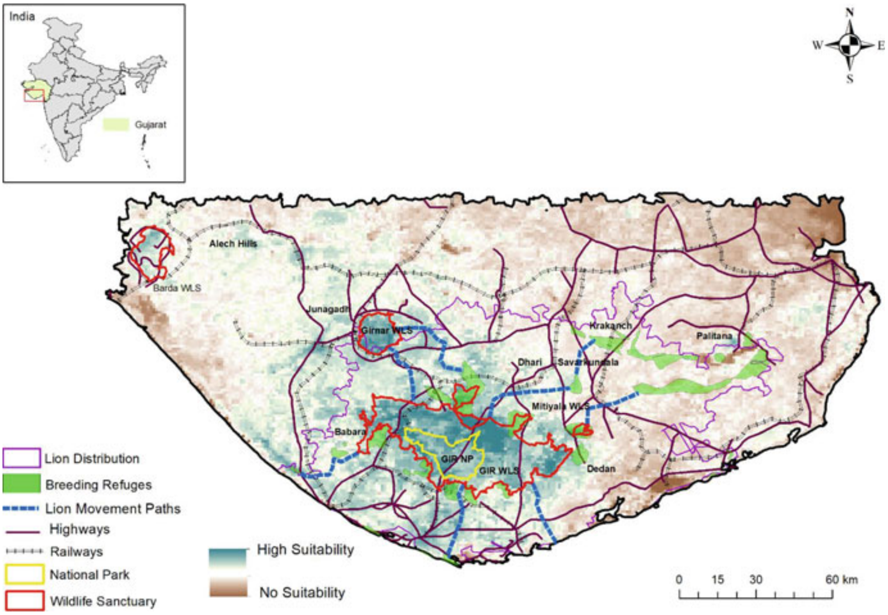

Fig. 3.1 Asiatic lion distribution: Habitat suitability map showing the current distribution of Asiatic lions in Gujarat, India. Habitat suitability for lions was derived from analysis of lion locations collected through radiotelemetry and long-term monitoring. Breeding refuges are habitats (>4 km^2) that currently hold breeding lion populations outside the Gir PA. Map from Jhala et al. (2019)

3.1.2 Morphology

Asiatic lions, akin to all extant lions, are sexually dimorphic with adult males crowning a mane that starts developing around a male’s first birthday (8–12 month of age), attaining near-complete growth by the age of 5–6 years (young adult) (Fig. 3.2). Females lack manes and are considerably smaller in size (average shoulder height = 94.5 cm) compared to males (average shoulder height = 101.4 cm). Females are also lighter (average body weight = 116.5 kg) than males (average body weight = 160.1 kg) (Jhala et al., 2019).

Asiatic lions can be visibly distinguished from African lions in having: (1) a typical loose flap of skin under their bellies—known as the “belly-fold,” which is rare in African lions. This belly-fold is prominent in all adults and believed to have evolved owing to a “founder effect” with some of the individuals of the small founding population exhibiting this trait, which later became pervasive owing to inbreeding (O’Brien, 2003), (2) sparser and scrawnier manes that never cover the males’ ears, exhibiting a prominent *mohawk* atop the sagittal/dorsal crest, and (3) a relatively elongated snout with a sloping forehead; making Asiatic lions look sleeker and longer in their side-face profiles in comparison with the African lions (Fig. 3.3). While it is often argued that Asiatic lions are smaller in size and mass than African

Fig. 3.2 Mane growth in male Asiatic lions: Photographs showing the serial growth of mane in male Asiatic lions across different age classes. (**a**) Older cub (10 months old with the first signs of facial hair and neck beard), (**b**) juvenile (1.5 years old with more profuse facial hair and longer neck beard), (**c**) sub-adult (3–3.5 years old with a thicker mane around the neck and strands over the head), and (**d**) young adult (6 years old with near-complete mane growth, covering the sides of the faces, the dorsal/sagittal crest and the neck). Photos by Stotra Chakrabarti

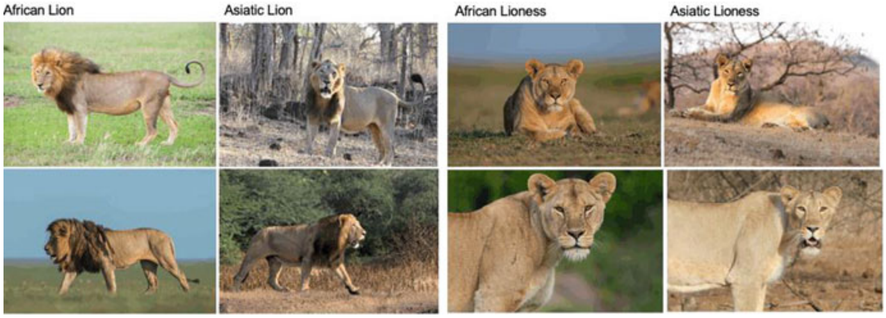

Fig. 3.3 Difference in appearance between African and Asiatic lions: Photographs showing male African and Asiatic lions (*left panel*), and female African and Asiatic lions (*right panel*). Note the sparse manes in Asiatic lions, as well as the prominent belly-fold. Photo credits: African lion photos by Daniel Rosengren, Asiatic lion photos by Stotra Chakrabarti

lions, we found no such evidence while comparing sex-specific height and weights of African and Asiatic lions (data in Smuts et al., 1980 versus data in Jhala et al., (2019).

One of the plausible reasons why Asiatic male lions have shorter and sparser manes is the high ambient temperature in Gir compared to areas in Africa (https://en.climate-data.org/). Ambient temperatures are reported to have a strong influence on mane growth in lions acting as a limiting factor to mane size through thermoregulatory constraints (Patterson et al., 2006). Thus, it is likely owing to the higher heat stress of carrying a thick mane, Asiatic male lions typically sprout sparser manes.

3.1.3 Habitat

Lions in Gir are found in a myriad of habitats that includes dry-deciduous forest with open-thorn and savanna patches characterized by Teak-*Ziziphus* and *Acacia-Ziziphus-Prosopis* plant communities, and grasslands. However, telemetry and long-term behavioral monitoring of known individuals indicate that lions within Gir PA prefer thick vegetation and riparian areas (Jhala et al., 2009, 2019, Fig. 3.4). Within the agropastoral landscape outside of the protected areas, lion ranges were composed of agricultural and thorn forests (Banerjee, 2012), with core areas distant from villages and townships having more forest and broken terrain (Jhala et al., 2019). Availability of such habitats (refuges) is patchy and dispersed in the agropastoral landscape; lion ranges were, therefore, larger in the landscape compared to those within the protected areas (Jhala et al., 2019). Lions in this human-dominated landscape have often been observed to venture into villages and townships at night to hunt livestock. However, during the day, with the advent of human activities, lions seek concealment within thicker vegetation. Even small patches of vegetation (5–7 ha) are used for daytime respite. However, adult lionesses in the landscape outside the PA require relatively human-devoid areas >4 km^2 as core breeding patches (Banerjee, 2012).

Fig. 3.4 Gir habitat: Photographs showing (**a**, **b**) Gir PA in the summer/winter versus monsoon, (**c**) Riparian areas such as dry stream-beds with trees like *Syzigium* spp. and *Mitragyna* spp. are mesic habitats even during the driest periods and offer ample shade for lions. Photos by Stotra Chakrabarti

3.1.4 Diet and Predation Ecology

Lions inside the PA primarily subsist on wild herbivores such as chital (*Axis axis*, modal prey, body weight 30–65 kg), sambar (*Rusa unicolor*), wild pig (*Sus scrofa*), and nilgai (*Boselaphus tragocamelus*), while their major prey biomass outside the PA is comprised of domestic livestock (Chakrabarti et al., 2016, Jhala et al., 2019, Fig. 3.5).

Lions employed diverse strategies for obtaining food. Within the PA where lions typically hunted wild herbivores, they primarily resorted to stalk-and-ambushing prey. Single lions hunted by opportunistic stalking, followed by an ambush. When lions hunted in groups (quite rarely), some individuals "flushed" prey while other/s attacked/made the hunt. Younger animals typically stalked and flushed/cordoned prey in the direction of experienced older lioness(es) who lay in ambush and made most of the kills in a group. While the thick vegetation cover in Gir often precluded our observations of complete hunts, most of the kills that could be observed were made by single lions. Coordinated hunts using a flush-ambush strategy (although rare) consisted of hunting prey species such as nilgai and wild pigs that are quite formidable to tackle. However, owing to low sample size of hunting observations, we are not certain whether the roles of flushers and hunters are preserved/specialized

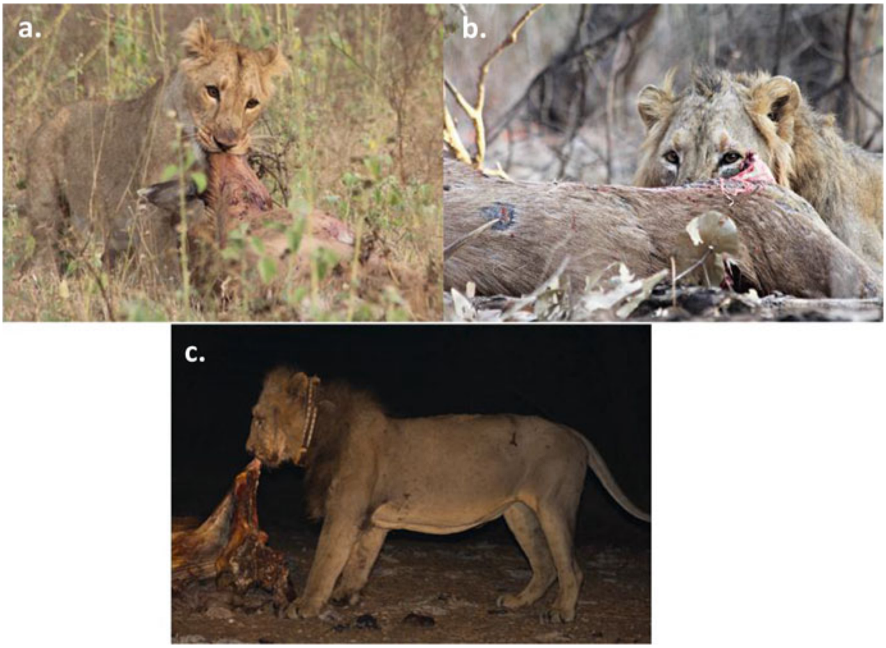

Fig. 3.5 Lion food habits: Photographs showing lions feeding on wild herbivores such as (**a**) Nilgai, and (**b**) Sambar within the Gir PA, and (**c**) scavenging on dead livestock at cattle dumps outside the PA. Photos by: (**a**, **b**) Stotra Chakrabarti, (**c**) Yogendra Shah

within a pride (as found in Namibia, Stander, 1992a, 1992b), or individuals improvise/change as per need of the moment.

Lions applied a different technique while hunting livestock accompanied by *Maldhari* herdsmen within forest habitats. For such hunts, lion(s) typically waited in ambush around routes taken by livestock and charged at them when the livestock herd was nearby. We have observed multiple individuals (especially male groups) waiting in ambush together around these grazing routes. Such sudden charges created a lot of chaos and confusion among the grazing herd. Domestic water buffalo (*Bubalus bubalis*) like their wild counterparts usually group together as a defense against predators while the *Maldhari* herdsmen rush to protect the more prized buffalos. Most *Maldharis* graze mixed herds with unproductive and younger cattle also constituting a good proportion of the herd. Domestic cattle, unlike buffalos, typically scamper when charged by lions and are often killed during these hunts. The *Maldharis* thus protect their prized buffalos by keeping a *buffer/sacrificial* population of unproductive cattle in their herds.

Often during such attacks, multiple livestock were killed (average 1.3 individuals killed/hunt), and the number of kills was weakly correlated with the number of lions reported by the herders (Banerjee et al., 2013). A majority of the livestock depredation by lions (inside the PA) occurred within forests when livestock were taken out for grazing, and rarely did lions raid livestock that were corralled within the *nesses*. Females with dependent cubs were responsible for 54.4% of the attacks; single male or male groups were responsible for 19.1% of the attacks and mixed groups of lions (mostly adult lionesses accompanied by juveniles/sub-adults) made 26.4% of the kills (Banerjee et al., 2013). Lions in the study area were found to raid livestock in proportion to the prevailing adult sex ratio in the population (Banerjee et al., 2013). Thus, all lions were equally likely to predate livestock. We did not record any leopard (*P. pardus*) attacks on grazing herds.

Data from day-night follows of radio-collared lions suggest a higher overall success rate in killing livestock (predation success = 58%) as compared to wild herbivores (predation success = 22%) (Chakrabarti & Jhala, unpublished). These day-night follows also revealed that among the total consumption of livestock by lions, only 35% was from predation while the rest was appropriated from scavenging events (Banerjee, 2012; Jhala et al., 2019). Such abundant scavenging opportunities for lions arise from the typical lack of consumption of cattle by the people of Saurashtra owing to prevailing socio-cultural and religious practices. Consequently, several charitable cattle camps (locally known as *Gaushalas* and *Panjrapoles*) that house old and unproductive cattle are distributed across the landscape outside the PAs, where these livestock frequently die in large numbers owing to disease and old age. Livestock carcasses are usually dumped at specific locations outside these *gaushalas* and villages, away from human habitation. We have observed lions in this landscape to make frequent "bee-line movements" to these carcass dumps to avail free buffets. If no carcasses are available at such dumps, then lions enter villages at night looking for stray feral cattle that yard within these villages/townships for safety. Most owned and productive livestock are kept within enclosed areas at night and are not available for lions to predate on. Lions in the landscape thus typically kill feral cattle that are left to fend for themselves and not corralled for the night.

Predation on prized productive livestock is low owing to the combined practices of stall feeding, keeping mixed herds, and corralling of livestock at night (Banerjee, 2012). However, recent data trends from the government compensation scheme suggest that human-lion conflict in terms of livestock depredation is getting severe as lion population and range increases concomitant with human population growth in the Saurashtra landscape (Jhala et al., 2019). Farmers in this agropastoral landscape are still tolerant toward lions in their neighborhoods, because coupled with the socio-cultural pride of the people in the last lions of Asia, lion presence also acts as effective insurance against crop damage from wild herbivores such as nilgai and wild pigs (Jhala et al., 2019).

3.2 Social Behavior: The Effect of Resources on Group-Living

Social behavior refers to the degree of association between individuals of a population and their relative spacing patterns (Gittleman, 1989). The underlying principle of any society is the tendency of individuals to form conspecific groups with temporary, semi-permanent, or permanent membership. Since sociality among carnivores does not exhibit a serial evolutionary trend across taxa, it may have originated independently in different families (Gittleman, 1989). This hints toward a convergent evolution of adaptive behavioral responses to similar eco-environments (Silk, 2007). Sociality evolves when the net benefits of association with conspecifics outweigh the costs (Krause et al., 2002).

Lions are the only social felids that live in functional units/groups called *prides* where individuals cooperate to appropriate and defend resources such as food, territory, mates, and offspring (Jhala et al., 2019; Packer, 2019; Schaller, 1972). However, to optimize the benefits of resource access and defense against costs of sharing, rarely are all individuals of a group found together—instead, lion societies are characterized by fission-fusion processes (Chakrabarti et al., 2021; Packer et al., 2005; Schaller, 1972). While our understanding of lion biology primarily revolves around long-term studies from the extremely productive Serengeti-Ngorongoro savanna ecosystem (Packer, 2019; Schaller, 1972), rarely do lions elsewhere have access to abundant large-bodied prey species as found in this ecosystem (Chakrabarti et al., 2021). Since sociality is often mediated through resource availability, the Gir lion model provides a unique opportunity to understand the drivers of group-living in light of small modal prey size (compared to the African system) and disparate energetic demands of lions within and outside the PA. In the following sections, we highlight the fundamental entities of Asiatic lion societies and discuss the causes and consequences of their sociality being essentially different from their Serengeti-Ngorongoro counterparts.

3.2.1 Prides: Lion Queens

3.2.1.1 Life History

At the center of the Asiatic lion society is a group of matrilineally related adult females and their cubs. These social units/prides can range in size from a lone lioness and her cubs to 7–8 lionesses (>2 years of age) and their dependent offspring. However, a typical pride of Gir lionesses is small with only 2–3 adults (Chakrabarti et al., 2021; Jhala et al., 2019) who cooperate to obtain food, defend territorial boundaries, and raise cubs. Females form subgroups that remain scattered within the pride's territory. However, such subgroups are formed only when pride sizes are relatively large; small prides remain together. Lionesses have their first litters between the age of 4–5 years with an average litter size of 2.3 (Banerjee & Jhala, 2012; Chakrabarti & Jhala, 2019). Pride-mates rear cubs communally, nursing each other's cubs. Such maternal crèches are possible only when prides have synchronous litters (cohorts that are born within a few months of each other). Such synchronous litters have been observed in <30% of the litters in Gir (Chakrabarti et al., 2020; Chakrabarti & Jhala, 2019). Cubs are weaned at the age of 5–6 months but remain dependent on their natal pride for about 2–3 years. Sub-adult lionesses (2–3 years of age) are either recruited into their natal pride or leave with their cohort-mates/siblings. Recruitment versus eviction of sub-adult lionesses depends upon natal pride size and ensuing competition, and timing of male take-overs. Male take-overs are discussed in subsequent sections.

The proportion of cubs surviving until 2–3 years is positively correlated with pride size in Gir ($r = 0.48$, data in Banerjee & Jhala, 2012 and Chakrabarti & Jhala, 2019). Thus, it appears that female group size has a net positive effect on cub recruitment with lionesses living in groups having higher success than solitary females; larger groups recruit more offspring than smaller ones. However, this trend should be interpreted with caution because of the confounding effects of artificial provisioning/supplemental feeding of some lion prides by the Forest Department and local communities. Such supplemental feeding is typically directed toward prides that reside in the tourism circuit of the Gir Wildlife Sanctuary to aid management interventions (e.g., regular health checks) and for ease of tourist viewing (Jhala et al., 2019). Supplemental provisioning can artificially boost cub survival by relieving lionesses from nutritional stress, which is common among females with dependent cubs (Packer et al., 1990).

3.2.1.2 Territoriality

Pride females have relatively stable and exclusive territories of just under 30 km^2 inside the PA while ranging over much larger territories (170 km^2) outside the PA (Chakrabarti & Jhala, 2019; Jhala et al., 2019). Such a stark contrast in ranging between prides within and outside the PA is attributable to the dispersion of habitat patches in the agropastoral landscape, wherein individuals must move over larger areas to optimize resource needs (Jhala et al., 2019). Longitudinal data from multiple prides within the PA suggest that pride territories remain fairly preserved over years and generations, with minimal to no shift in territorial core areas (Chakrabarti & Jhala, 2019). Adjacent pride territories are defended fiercely by their respective owners, with very little overlap (~8%, Fig. 3.6) in their home ranges (Chakrabarti & Jhala, 2019).

Gir lionesses primarily rely on olfactory markers (urine sprays, scrapes on the ground and tree barks) to designate and maintain territorial boundaries, unlike frequent long-distance roars as found in many African populations (Bertram, 1975; McComb et al., 1994; Schaller, 1972). Plausible explanation of olfactory cues being preferred over vocalizations by Gir lionesses to maintain territorial boundaries is perhaps the higher availability of shrubs and trees that act as "scent-posts" as compared to grassland systems of Africa. Further, the wooded system of Gir might also inhibit long-distance vocal communication to be as effective as in the grasslands of Africa where such roars can travel for kilometers without much interference. Additionally, Gir lionesses do not roar as frequently as compared to their open-grassland inhabiting counterparts in Africa (perhaps) to reduce unwanted attention from adult males (Chakrabarti et al., 2021; Grinnell & McComb, 1996, 2001, please see Sect. 3.3 of this chapter for more details). Based on field observations of intensively monitored female prides, outcomes of territorial confrontations between adjacent prides are governed by subgroup size of confronting females, with larger subgroups having a competitive advantage over smaller ones (S. Chakrabarti, pers. obs.). Similar results have been reported from African lion systems (Heinsohn & Packer 1995; McComb et al., 1994), probably suggesting effective territorial defense to be one of the benefits (and causes) of group-living in lions (Mosser et al., 2015; Packer et al., 1990).

Data from the Serengeti ecosystem show that owing to significant habitat heterogeneity in the savanna landscape, resource competition favors the formation of large prides that can defend "prized" territories with access to abundant prey and ambush sites (waterholes and river confluences) (Mosser et al., 2015). Thus, larger prides have higher resource securities leading to higher reproduction and retention of the F1 generation, and longer tenures (Mosser et al., 2015). However, since the Gir PA is primarily a dry-deciduous forest, it is arguably less heterogeneous with a uniform high density of small-medium prey (Jhala et al., 2019). A relatively high and uniform abundance of small prey coupled with a high density of lions favor small prides that range over smaller territories, modulated through unit prey size and density. Consequently, within the PA, pride sizes are relatively less variable (Chakrabarti, 2018).

Gir lionesses exhibit intra-sexual social cohesiveness and pride size that optimize cub rearing through alloparental care and protection against threats (from rivals), while reducing the costs of sharing small prey—relatively small but cohesive groups ranging within small/ compact territories. The agropastoral landscape outside the PA, however, presents a heterogeneous matrix with large swaths of agricultural fields and human settlements, with small pockets of "resource rich" lion habitats sprinkled across. These pockets are primarily characterized by *Prosopis-Acacia*

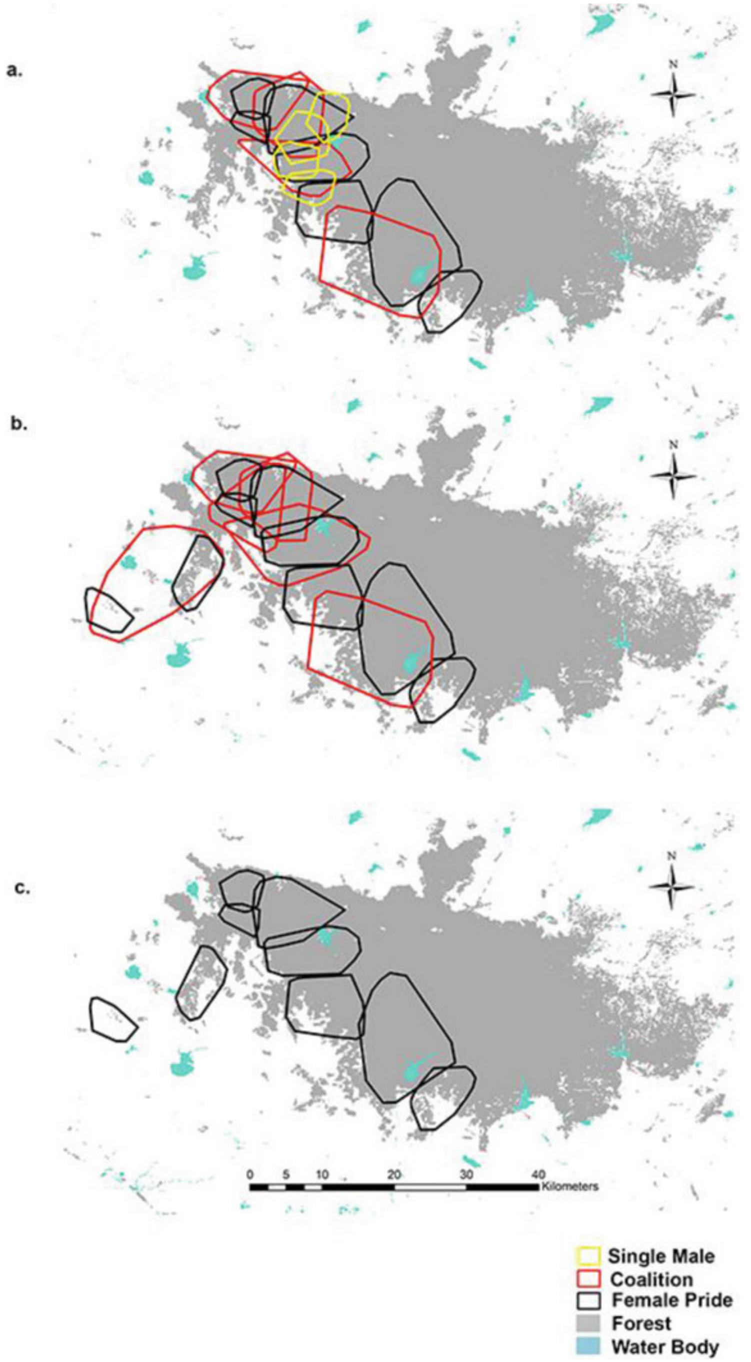

Fig. 3.6 Space use by male and female groups of lions in Gir: Spatial overlap of home ranges (95% minimum convex polygon) of male coalitions and female prides in Gir between: (**a**) 2012 and 2014, (**b**) 2014 and 2017, and (**c**) all monitored female prides from 2012 to 2019. Male space use was

thorn forests surrounding riverine habitats and erosion embankments that not only provide crucial cover for resting and concealing cubs, but also provide proximity to anthropogenic medium-to-large prey resources in the form of livestock and carcass dumps. While human settlements along with their livestock and carcass dumping sites form rich resources for food at night, lions need these (highly limited) forested patches and erosion embankments as daytime and breeding refuges. Thus, this matrix can be somewhat analogous to the Serengeti, and consequently prides in and around these small pockets can grow surprisingly large (6–8 adult lionesses and their dependent juveniles) that have been observed to congregate at large prey carcasses. Despotism in territorial retention and tenure among prides in this landscape can be expected, akin to the Serengeti-Ngorongoro ecosystem, but remains to be studied through long-term intensive monitoring.

3.2.2 Male Coalitions: Selfish Partners or Comrades in Arms?

3.2.2.1 Life History

Sub-adult male lions leave their natal prides between the ages of 2–3 years consequent to a territory take-over event where invading adult males challenge and oust the former resident males while evicting/killing all dependent young (Chakrabarti et al., 2020; Jhala et al., 2019). In addition to territorial take-overs, sub-adult males can also be aggressively expelled by pride females (their mothers/aunts/grandmothers/sisters) because the young males are bigger than the females by that age and often "bully" their way in to disproportionately access kills (Chakrabarti, 2018). Though the proximate cause for expulsion of young males by their kins may be competition for food, it ultimately results in avoiding inbreeding between closely related individuals in a pride (Bertram, 1975; Schaller, 1972). Subsequently, these young males enter a stage of nomadism and move away from their natal territories (average dispersal distance in Gir = 16 km, Jhala et al., 2019) in search of their own. During this phase, the young males conceal themselves by being silent (they don't roar) and even their urine carries no smell, unlike resident male spray/urine that smells to humans like *steamed rice* (S. Chakrabarti & Y. Jhala, pers. obs.). Such concealment is necessary because the young males cross multiple occupied territories while navigating the landscape, thereby becoming vulnerable to attacks from resident adult males.

◀

Fig. 3.6 (continued) found to be dynamic, with new coalitions ousting residents in 2014. Female pride territories remained more or less constant. Map from Chakrabarti and Jhala (2019)

3.2.2.2 Nomadism

During this nomadic phase, males form alliances with other males who are typically of similar age. Males in alliances/coalitions are bonded for life and rarely do males form new coalitions after the death of their previous partner(s); however, exceptions exist. Adult male group size in Gir ranges between 1 and 4 males, with pairs/2-male coalitions being the most prevalent (68% of all monitored coalitions) (Chakrabarti et al., 2020). Solitary males/singletons also hold territories and are more common than large coalitions (trios and quartets) (Chakrabarti et al., 2020). Thus, staying alone or forming groups are alternative life-history strategies for male lions; singletons are usually the males that did not get a chance to team up with others (see Sect. 3.2.2.6 for more details). Coalition males function as a unit, and cooperate while hunting, challenging resident males to take-over territories, and defending acquired territories from invaders. Asiatic male lion coalitions are small (largest coalition: four males) when compared to coalitions in the Serengeti-Ngorongoro ecosystem (largest coalition: nine males), probably reflecting the effect of unit (small) prey size and ensuing competition for food on coalition size, akin to the processes resulting in small pride sizes in Gir (Chakrabarti et al., 2020; Chakrabarti & Jhala, 2017).

Males form coalitions with related (siblings and cousins) and/or unrelated males, with 50% of the coalitions in Gir being composed of unrelated partners (Chakrabarti et al., 2020). However, unrelated males generally form pairs (>70% of observed pairs were unrelated), while large coalitions (trios and quartets) are always composed of siblings and cousins (Chakrabarti et al., 2020)

3.2.2.3 Territoriality and Land-Tenure System

If successful in challenging and evicting a resident coalition from its territory, the newly tenured coalition holds an average territory of 120 km^2 inside the Gir PA and >800 km^2 outside the PA for about 2–3 years (Chakrabarti & Jhala, 2019; Jhala et al., 2019). The contrasting territory sizes inside and outside the PA again depict the effect of patchy resources in the outside-PA landscape on range size of carnivores, in accordance with the Resource Dispersion Hypothesis (Macdonald, 1983), which predicts that territory size is contingent upon the dispersion of resources—larger territories will be used when resources are scattered over time and space.

Resident males interact with pride females primarily for mating and infrequently during large kills made by the lionesses or at traditional scavenging sites. Males with coalition partners can maintain territories almost thrice the size of those of solitary residents/singletons and remain in tenure twice as longer (Chakrabarti & Jhala, 2017, 2019). Teaming up with a partner is an optimal scenario for male lions in the Asiatic lion system because male territories can overlap with multiple female prides (2–4 prides). Consequently, male coalitions with large territories gain access to many females from multiple prides (Chakrabarti & Jhala, 2019). However, a specific male coalition's territory can overlap with pride ranges and the ranges of neighboring "rival" coalitions.

Thus, Asiatic male lions typify an intriguing land-tenure system for a territorial carnivore wherein ranges of multiple rival coalitions overlap (average overlap ~30% of territories, Fig. 3.6). These overlaps almost always coincide with female pride core areas (Fig. 3.7, Chakrabarti & Jhala, 2019). Thus, pride lands are seemingly shared between rival coalitions who start off as "nasty neighbors" at the beginning of their tenures with aggressive antagonistic encounters that are replaced eventually with amicable avoidance (Fig. 3.7). We found that the same rival coalitions who exhibit heightened aggression and conflict during territorial acquisition and adjustments, soon (within 4–6 months of sharing space and hostilities) coexist by avoiding each other and/or direct confrontations (Chakrabarti & Jhala, 2019). Shifting hostilities and resigned coexistence as "dear enemies," suggest a trade-off between maintaining exclusive territories (that entails risks of recurrent fights and costly injuries) and access to reproductive females. Such a strategy can become advantageous for males when mating opportunities are invariably low owing to small pride sizes and in a landscape like Gir where thicker vegetation (as compared to the open plains of Eastern Africa) provides ample cover for females to avoid detection/control by males (Chakrabarti et al., 2021).

Through this strategy, males arguably enhance direct mating opportunities by accommodating multiple pride ranges within shared territories. Male territorial behavior leads to a scenario where a single pride of females is shared between males from a "primary" coalition (that occupies most of the pride range) and multiple "peripheral" coalitions (whose territories overlap with a smaller part of the pride's range) (Figs. 3.6 and 3.7, Chakrabarti & Jhala, 2019). Male–female interactions and mating strategies are discussed in subsequent sections.

3.2.2.4 Despotism

Unlike other group-living terrestrial carnivores where strict dominance hierarchies exist, African lion social units are egalitarian (Packer et al., 2001). There are no reproductive or feeding hierarchies between female pride-mates, and competition for food and mates among male coalition partners are seemingly relaxed (Bygott et al., 1979; Schaller, 1972). However, information on such social strategies is based on Serengeti-Ngorongoro lion populations, where there is an abundance of large-bodied prey (such as blue wildebeest *Connochaetes taurinus*, zebra *Equus quagga*, and Cape buffalo *Syncerus caffer*), as well as many mating opportunities for males within large female prides.

The Gir system provides a different scenario in which not only are individuals reliant on small prey but also have fewer mating opportunities because of the low number of females in a typical pride (Chakrabarti & Jhala, 2017). This sets the stage for enhanced competition between coalition partners and consequently they acquire resources asymmetrically. In every coalition, a consistently dominant partner "reigns supreme" by acquiring 70% of all mating events (Fig. 3.8) and >45% more food

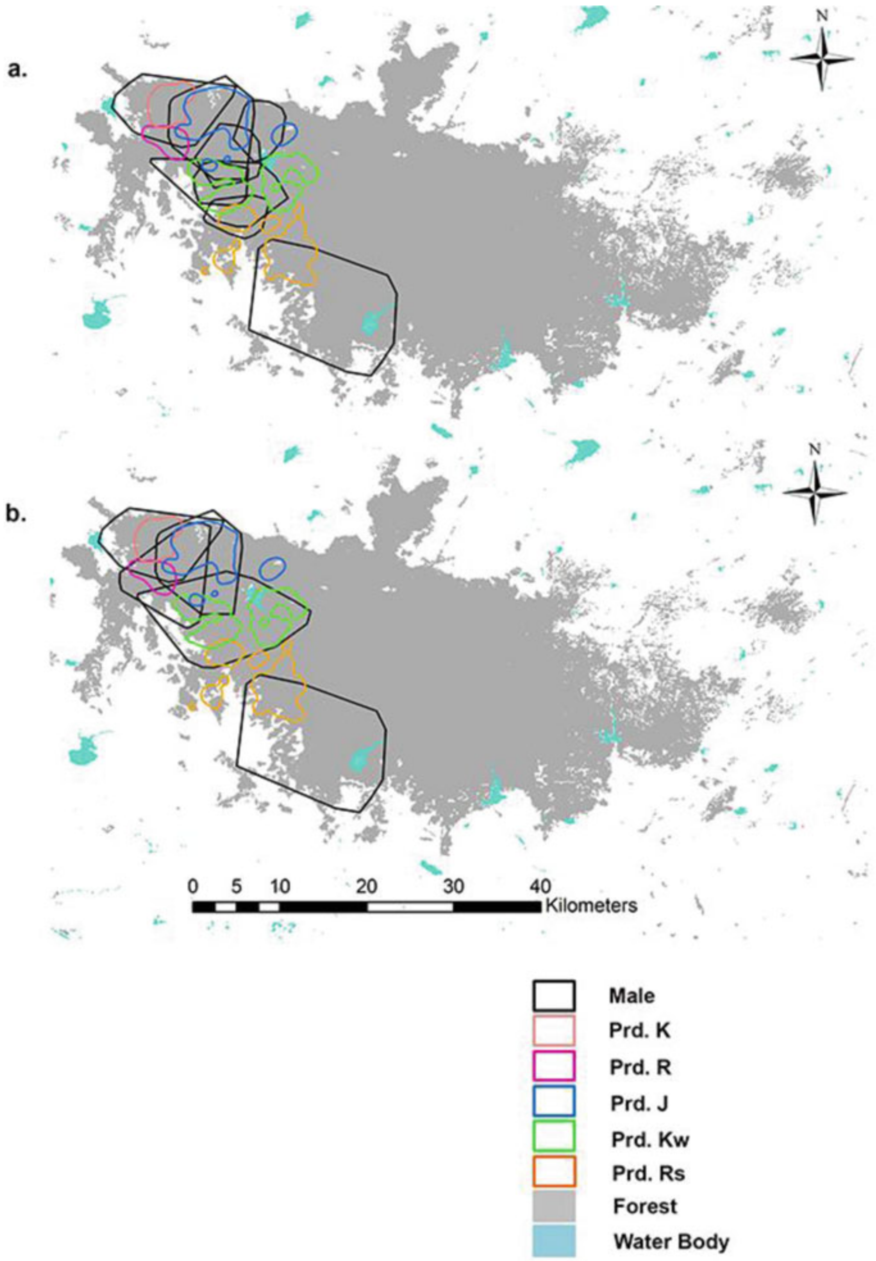

Fig. 3.7 Space sharing between prides and primary and peripheral male coalitions: spatial overlap between home ranges of male coalitions and 70% fixed Kernel core areas of female prides in Gir monitored during: (**a**) 2012–2014, and (**b**) 2014–2017. Adjacent male ranges overlapped at the female cores, but neighboring female core areas were almost exclusive. Map from Chakrabarti and Jhala (2019)

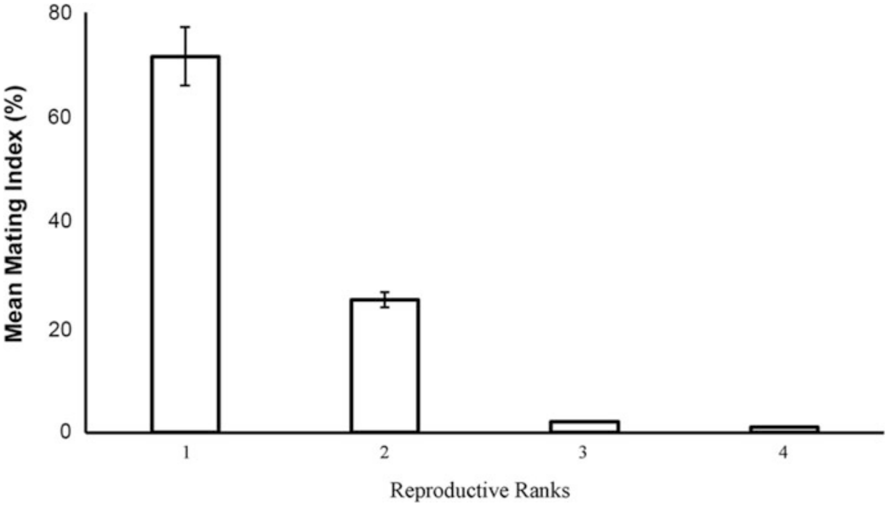

Fig. 3.8 Mating skew among coalition partners. Plot showing mean mating index (annual mating frequency calibrated by the total number of days each male was detected in the field averaged across same ranking males from different coalitions) of lions ranked in a descending order within each coalition. Error bars represent 95% CIs. Figure from Chakrabarti and Jhala (2017)

from kills shared with other partners (Chakrabarti & Jhala, 2017). In trios and quartets, this hierarchy is linear, with a male being dominant over every other partner except the male who is dominant over him (Chakrabarti & Jhala, 2017). Subordinate males can only acquire mating events when the dominant individual(s) is not around or is courting females. Further, subordinate males can be supplanted from courtships even when dominant partner/s arrives late to the scene (Chakrabarti & Jhala, 2017). Access to mates in the Gir system is thus based on social ranks, contrary to the "first come-first served" basis of mate acquisition by male lions in the Serengeti-Ngorongoro system where the first male to encounter a receptive female gains exclusive and uncontested access to mating (Packer & Pusey, 1982).

Skew in food sharing within coalitions is mediated by the size of the prey carcass, dominant male/s appetite, and the number of partners sharing a kill (Chakrabarti & Jhala, 2017). Male partners exhibit strict feeding hierarchies when the prey carcass is small, the dominant partner(s) is hungry and coalition size is large (Fig. 3.9, Chakrabarti & Jhala, 2017). This skew in food acquisition among partners is considerably relaxed when fewer and less hungry males are sharing a large kill (Chakrabarti & Jhala, 2017).

3.2.2.5 Kin-Selection

The decision to stay or leave a coalition for a subordinate male is contingent on the loss of opportunities incurred compared to all the dominant individuals and relative

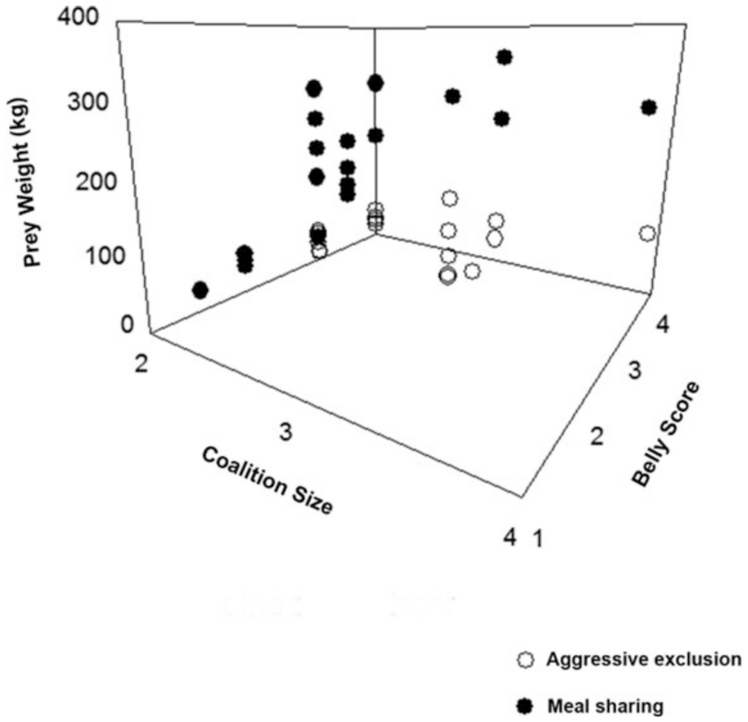

Fig. 3.9 Aggression between coalition partners at kills: Scatter plot showing how aggression among male coalition partners on a kill change with prey size, dominant partner appetite (quantified through belly scores, where 1 means fully gorged and 5 is completely starved), and number of male partners at the kill (coalition size). Aggression between males increases with lower prey size, greater number of partners, and larger appetite of the reproductively dominant males. **Empty circles**: *aggressive exclusion*, when feeding male(s) thwart the advance of at least one of his (their) partners through heightened aggression and does not allow him (them) to feed; and **filled circles:** *meal sharing*, mild aggression between partners (squabbles and occasional swats), but all partners feed on a kill simultaneously. Figure from Chakrabarti and Jhala (2017)

benefits achieved through independent control of a territory. We found that even with such autocracy within coalitions, the reproductive fitness of subordinates in pairs was higher than solitary resident males (Chakrabarti & Jhala, 2017). However, males at the bottom ranks of trios and quartets had very few mating chances similar to solitary males. Thus, the linear hierarchy within Gir lion coalitions affects large coalitions more stringently. Because of skewed direct fitness, trios and quarters are always made of related males; lower ranking subordinates typically acting as *non-breeding* helpers (Chakrabarti et al., 2020). The close genetic relatedness between these subordinates/non-breeding helpers and the dominant males in large coalitions offsets the reproductive suppression experienced by the former through kin-selected indirect fitness benefits (Fig. 3.10, Chakrabarti et al., 2020). This is in accordance with Hamilton's principle, which explains how in large groups owing to resource competition, some individuals are forced to forgo their reproductive rights yet

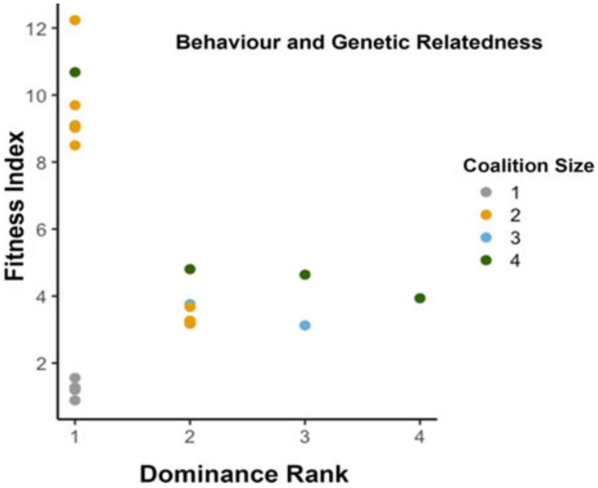

Fig. 3.10 Kin-selection within coalitions: Fitness index of individual males in coalitions plotted across different ranks and coalition sizes. Fitness index of a male = annual territory holding probability × (mating frequency of the male + r × mating frequency of another partner in the coalition). This was done for and between every individual in the coalition. r took the value of 0.25 if the partner pairs were full-siblings, 0.09 if they were half-siblings/cousins, and 0 if they were unrelated. Figure from Chakrabarti et al. (2020)

remain in the group by relying almost exclusively on indirect fitness benefits accrued through their relatedness/kinship with other (dominant) individuals in the group (Hamilton, 1964). Similar instances are present in other species such as wild turkeys (*Meleagris gallopavo*), where related males band together to form display coalitions at traditional lekking sites (Krakauer, 2005). These display coalitions are more successful in courting females than solitary males. However, akin to lions, the subordinates accomplish minimal/no breeding opportunities but derive indirect fitness benefits by being related to the dominant bird(s), who get many mating chances (Krakauer, 2005).

As discussed earlier, unrelated coalitions are fairly common in Gir but they are almost always constituted of two males (Chakrabarti et al., 2020). This is because it is only in pairs that each of the coalescing males has enough direct fitness paybacks from the relationship, which supersedes that of a solitary resident, making the partnership advantageous to both from a fitness standpoint without any kin-selected benefits (Chakrabarti et al., 2020). The mean fitness of individual males was not different among pairs, trios, and quartets in Gir although it varied greatly within large coalitions (>2 males), indicating higher inequality in per capita coalitionary benefits within large coalitions (Fig. 3.11a, b). However, the total fitness of a coalition (cumulative fitness across partners) was highest for large coalitions making them more advantageous as a unit (Chakrabarti et al., 2020).

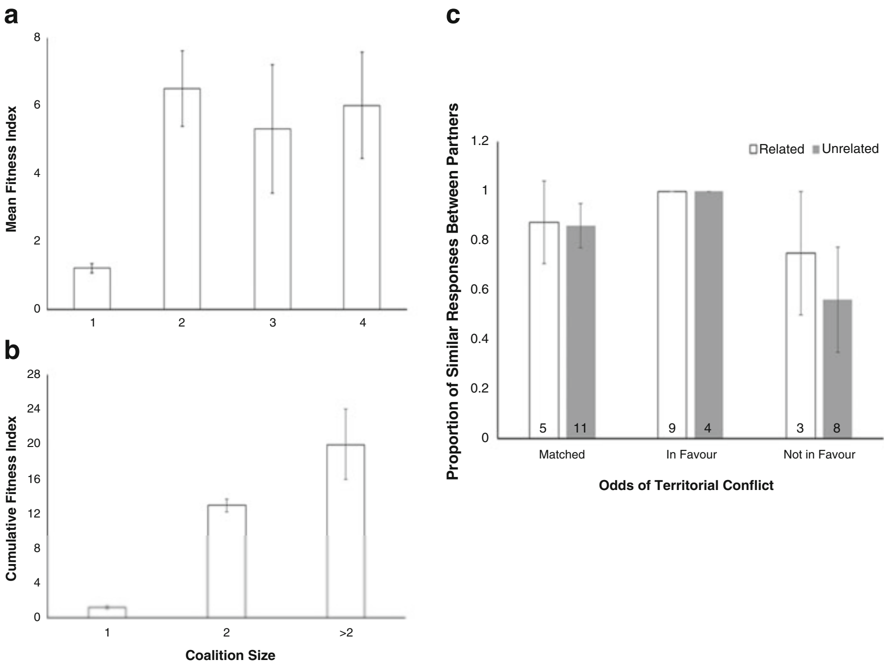

Fig. 3.11 Fitness and support within coalitions: (**a**) mean/average fitness index including genetic relatedness within respective coalition size, (**b**) cumulative fitness index, computed as the total fitness index of the respective partners in a coalition. Both metrics are represented as functions of coalition size, (**c**) proportion of similar paired responses between male coalition partners to scenarios of territorial conflict. Results are compared between related and unrelated pairs for situations when opponents were equally matched in numbers (odds matched), when odds were in favor (number of focal males > opposition number), and when odds were not in favor (number of focal males < opposition number). Estimated proportions in each of the three categories represent values averaged across individual coalitions. Numbers at the base of each bar represent respective sample sizes. Error bars represent SE. Figure from Chakrabarti et al. (2020)

3.2.2.6 Demographic Constraints on Coalition Formation

Although large coalitions have higher fitness as a group, they are rare in the Gir system due to the pronounced skew in resource acquisition within such coalitions, which obligates partners to be related as littermates and/or cousins/half-siblings (Chakrabarti et al., 2020). Based on probabilistic computations derived from demographic parameters such as litter size, litter sex ratio, cub survival, and synchroneity in cub birth events within a pride, we found that chances of related males reaching coalitionary age are consistently low (~7%) (Chakrabarti et al., 2020). Such unavailability of siblings and cousins results in the realized optimality of pairs in this system where male partners are typically unrelated, yet each accrues higher fitness than solitary lions (Chakrabarti et al., 2020). Based on behavioral observations, we found that unrelated partners are equally likely to support each other during conflicts with rival males, as are related partners (Fig. 3.11c). Thus, relatedness is not an absolute necessity for coalitions to form and operate, but makes the relationship advantageous as reflected by the higher cumulative fitness of coalitions with related males (large coalitions) (Chakrabarti et al., 2020).

Box 3.1: Cooperative Hunting Culture

Cooperative hunting, one of the aspects of lion sociality, has been studied in great detail in grasslands and open systems where fairly high visibility allows for direct observations (Stander, 1992a, 1992b). However, forested systems such as Gir impede complete observations of predation events. While we have information on pre- and post-hunting attributes from continuously monitored radio-tagged lions, data during the "*ambush-attack*" phase is scanty or restricted to a few groups because of logistical issues of following lions on hunts. Although such data are infrequent, each data point provides insights on group cohesion and inter-individual reliance during the acquisition of a primary resource, and thus makes for a rich discussion. One such group that was continuously monitored and provided us with observations on multiple complete predation events was a coalition/pair of prime-adult (6–7 years of age) male lions. This coalition inhabited a territory in the western part of the Gir WLS, and their range encompassed six *Maldhari nesses*. Each *ness* is typically constituted by a few families and their livestock, with 78% of the stock comprised of domestic water buffalos. The livestock are herded to forest pastures during the day and are corralled within thorn enclosures/bomas before dark (Banerjee et al., 2013). Lions hunt these livestock but herding practices of the *Maldharis*, honed over 200 years of coexistence with lions, have made them formidable protectors of their livestock, incurring very few losses to predation (Banerjee et al., 2013). This pair of male lions were exceptional in breaking through the *Maldharis'* protective defenses (Fig. 3.12). On the day of the hunt, the lions would choose a particular *ness* and scope the livestock (as they returned from the forest in the evening), typically from a vantage point/a nearby hill/behind thickets often unbeknown to the *Maldharis* and their livestock. The lions would wait until much later at night when human activities would subside, to get into a boma. Subsequently, they would kill/gravely injure one of the buffalo/cattle. During this event, while one male would make the kill, the other would stand guard against the buffalos that are known to charge menacingly. Subsequently, the lions would promptly jump out of the boma and disappear, leaving their dead/dying prey behind. However, the lions would never go too far from the *ness*; instead, would typically rest the following day under a tree or a shade nearby. The *Maldharis*, due to religious prohibitions, do not consume any part of dead livestock and would eventually dump the carcass at a specific site away from their *ness*. The lions would inevitably visit this dump site, reclaiming their hard-earned kill.

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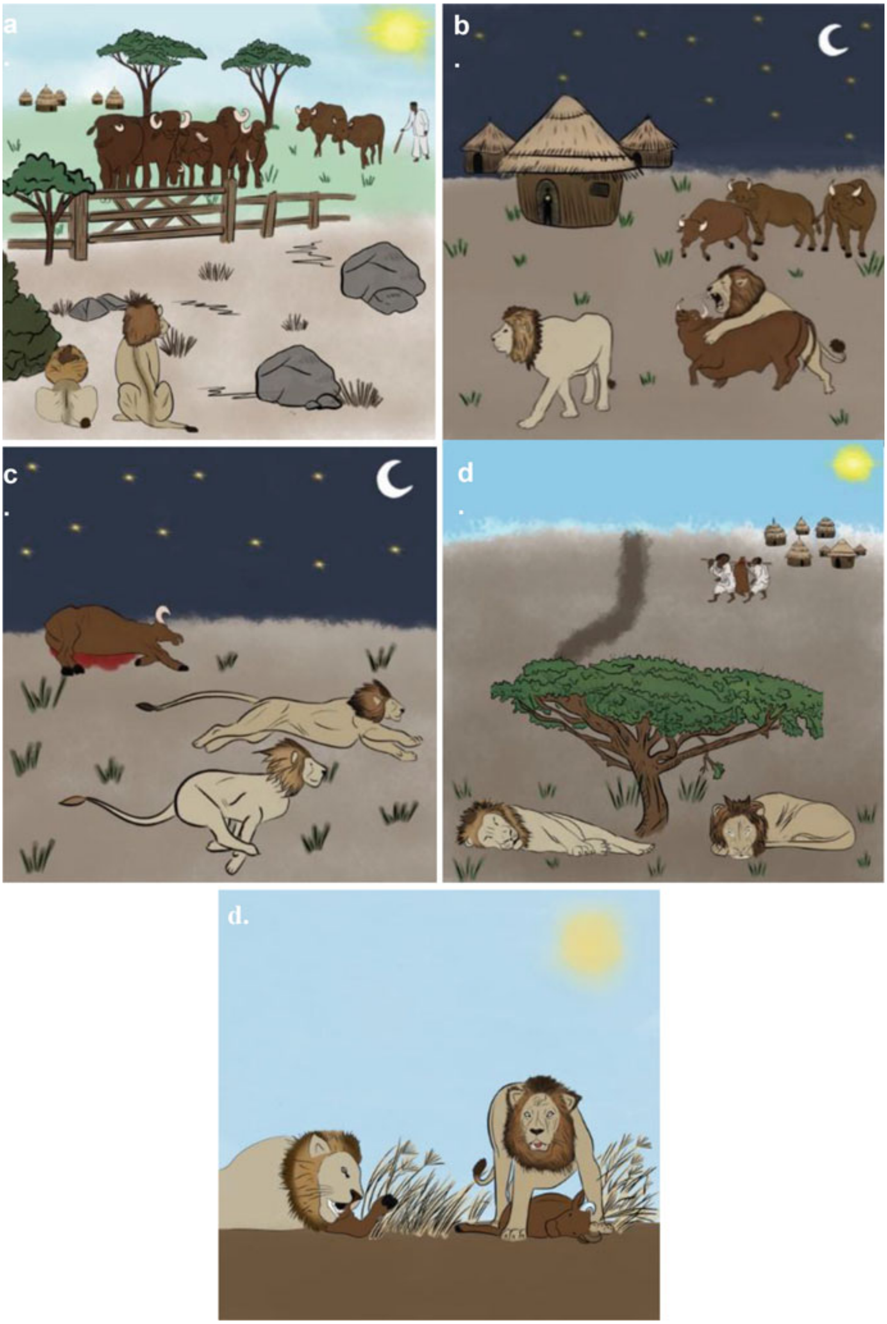


Fig. 3.12 Infographic representing observations on hunting specialization among Asiatic lions: (**a**) This particular coalition of two male lions would choose a ness where to hunt and then scope the returning livestock from afar, (**b**) late at night, the lions would enter a boma and kill a juvenile/calf, (**c**) the lions would be quick to get away, leaving their kill within the boma, and (**d**, **e**) the lions would however not go far, and will be resting under a tree/in a bush nearby, only to make a bee-line

Box 3.1 (continued)

We observed at least four such instances where this pair used the same strategy successfully at multiple *nesses*. We believe that the lions must have learned not to drag their kills out of the bomas after being chased/pelted by the *Maldharis* during their initial kills, because the commotion of the hunt invariably woke people up. However, they must have observed the *Maldharis* dumping the carcasses outside the next day and made the connection quickly. All they had to do was to wait for their kill to be presented to them!

These observations, although few and restricted to a particular coalition, provide us with crucial information on problem-solving and learning in this species. Lions are known to be better at tasks that require problem-solving and innovation than solitary felids such as leopards and tigers (*P. tigris*) (Borrego & Gaines, 2016). Observations on this particular coalition, as well as some male and female groups effectively tackling medium-large prey (such as nilgai and domestic buffalo in the agropastoral landscape) with support from group mates (K. Banerjee, pers. obs.) likely provides an opportunity to investigate foresight, expertise, and coordinated hunting strategies in Asiatic lions. Such expertise, if established with more data, has the potential to develop into *cultures* through socially transmitted learning. While individual and/or group-specific variations in behaviors are established in many taxa such as primates, cetaceans, and birds (Brakes et al., 2019, 2021), carnivores have typically not been considered until recently (Bump et al., 2022). Asiatic lions provide an interesting model where individual/group-level differences in hunting behavior and expertise can be studied especially at the interface of how lions navigate anthropogenic interactions, and whether there occur distinctive hunting cultures in this population.

Box 3.2: Insights from Rare Coalitions

The death of a coalition partner generally results in the surviving partner attempting to hold the territory on his own. However, males with “lost” comrades are evicted quickly because the lack of a partner significantly lowers fighting ability—a situation soon capitalized by invaders (Chakrabarti, 2018). Such eviction results in another (and typically final) phase of male nomadism wherein erstwhile territory-holders are yet again forced to navigate the landscape alone. We have witnessed at least two such occasions where evicted

(continued)

Fig. 3.12 (continued) to the site where the *Maldharis* would eventually dump the dead livestock. Illustrations by Stefani Westby

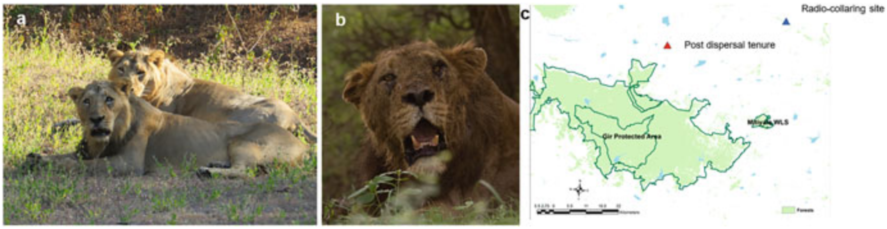


Fig. 3.13 Rare coalitions in Asiatic lions: (**a**) a father-son pair; father in the foreground (>10 years old) and the son in the background (~4 years old) (photo by Stotra Chakrabarti), (**b**) the radio-collared Chandgadh male who was a nomad when we collared him and later became territorial (photo by Yogendra Shah), (**c**) dispersal distance of the Chandgadh male, which moved nearly 40 km (displacement) from the site where he was collared (blue triangle) to where he finally settled down (red triangle) after partnering with an unrelated younger male, and established a new territory

Box 3.2 (continued)

males have dispersed and formed coalitions with younger males and have established territories elsewhere.

In one such incident, the protagonist was a very old male (>11 years) who was radio-tagged outside the PA near Chandgadh. The male was an older nomad, presumed to be an evicted male. During our study, this male moved ~40 km (displacement) from its original hideouts to reach the northern tip of the Gir PA (Fig. 3.13c). He then partnered with a younger male (~7–8 years old) to successfully evict the resident males to establish territory, and subsequently fathered cubs with a pride in that area (Banerjee, 2012). Another incident involves a nomadic prime-adult male (8–9 years of age) partnering with another younger territorial lone male (6–7 years of age) inside the Gir PA. The lone territorial male recruited this nomadic older male after much conflict and tension between them (fights, snarls, growls, simultaneous ground scraping at visible distances to each other), and subsequently with his help expanded the territory.

We have also observed one father-son pair in Gir during their attempts to take over a territory. When we first found this pair, they were nomads possibly due to the same eviction event—the father lost his territory while the son lost his natal pride. While we don't know for certain if this was how the situation had unfolded, we presumed so based on their genetic relatedness and age of the males (the older male >10 years—an age-class when territorial males typically lose tenures; younger male ~4 years, an age-class when young males are evicted from natal prides). Based on these rare observations, we submit that processes governing coalition formation can be complex and often regulated by immediate unforeseen events (Fig. 3.13).

3.3 Male–Female Associations: Cooperation and Conflict Among the Sexes

Lion social units demonstrate cooperation among same-sex individuals in accessing and safeguarding resources—prey, territory, and cubs. However, the level of interaction and cooperation between the sexes are more fluid and dynamic because adult males and females have subtly different resource needs and grouping patterns (males typically live in smaller coalitions than female prides), leading to males and females spending more time in same-sex subgroups (Chakrabarti et al., 2021; Packer et al., 2005; Schaller, 1972). Furthermore, the relative familiarity between females of a pride and between male partners within a coalition typically exceeds that between males and females because coalitions gain only (temporary) residence in an area, and interact with the females albeit briefly over the females' life span. This often results in the formation of female cliques. Males also spend more time patrolling and defending territorial boundaries from invaders than females do, keeping them away from pride females for considerable durations (Schaller, 1972). However, the sexes cooperate during territorial conflicts. In the Serengeti-Ngorongoro ecosystem, males actively support females during territorial confrontations with neighboring prides (Mosser et al., 2015; Mosser & Packer, 2009)—a scenario, which does not occur in Gir because invariably a coalition is co-resident in multiple adjacent prides and the males are typically absent when female prides confront each other (Chakrabarti et al., 2021). Furthermore, in the Serengeti-Ngorongoro ecosystem, males are likely to either help females while hunting very large prey such as Cape buffalo and giraffe *Giraffa camelopardali* or catch them by themselves and share with pride females (Schaller, 1972). Such a situation is absent in Gir, where prey is small, and females do not require male intervention (Chakrabarti et al., 2021).

Males however are considerably larger than females in all systems and parasitize female kills, and can even exclude females from feeding events altogether (Chakrabarti et al., 2021; Jhala et al., 2019; Schaller, 1972). Thus, female association with males comes with the costs of sharing/giving up food resources and can be pivotal in determining the frequency of inter-sexual interactions.

Below, we report the frequency of male–female associations in Gir and their social bearings under a comparative lens with that of lion populations in Serengeti and Ngorongoro, which feature a gradient of resources in terms of prey size and availability. Gir represents a system with small prey at relatively high and seasonally uniform densities; Serengeti alternates between high abundance of medium-large prey in the wet season and small scant prey during the dry months, while Ngorongoro has a year-round availability of large prey with a very high density of lions (Chakrabarti et al., 2021; Estes & Small, 1981; Hanby et al., 1995; Scheel & Packer, 1995). Through this comparison, we highlight the role of intra-sexual social factors and feeding ecology in governing social associations (other than mating interactions) between the sexes in lions.

3.3.1 Social Factors

Male–female associations increased across all three sites with an increase in male and female group size, but were low in large prides and when the territorial coalition covered multiple prides simultaneously (Chakrabarti et al., 2021). Consequent to lion socio-biology, adult males and females typically spend considerable durations in same-sex subgroups that are largely independent of pride or coalition size. Thus, when male coalition size is low, it becomes proximately impossible for them to physically associate with every female in a pride. Furthermore, large prides typically break down into many small female subgroups, creating a situation for the males to (perhaps) choose to be with only a few at a given time, further reducing overall associations. Such a time-space conundrum also appears for the males when they cover multiple female prides within their territory and can only associate with a select few at a time. Males are more likely to overcome these spatio-temporal constraints when the females fuse to form larger subgroups. Thus, male–female associations are largely contingent upon the fission-fusion connotations of lion sociality, and Gir with both small pride and coalition size coupled with co-residency of coalitions in multiple prides have the least frequent interactions between the sexes (Chakrabarti et al., 2021).

3.3.2 Resource Factors

The presence of a kill considerably increased the overall chances of observing a male in close proximity to females across systems (Chakrabarti et al., 2021). Males, besides mating, interact with females primarily to capitalize on feeding opportunities—mostly to scavenge from the kills made by the lionesses or sometimes facilitating the actual hunt. However, as discussed earlier, Gir lionesses do not require any help from males to hunt, and instead, have to be cautious to not lose their kills to male-kleptoparasitism. Such inter-sexual competition for food might substantiate the difference in time-activity budgets between the two sexes in Gir lions—the lionesses time their hunting peaks when males are least active (Chakrabarti et al., 2021; Jhala et al., 2019).

Quantification of direct observations of *joins-and-leaves* suggests that males join female subgroups more frequently, while lionesses are more likely to leave the males. (Chakrabarti et al., 2021). However, this averseness significantly reduces at large prey carcasses where both sexes were equally likely to join each other. This inter-sexual behavioral affinity is also mirrored in the trend of male–female associations across the three sites wherein Gir with the smallest available prey has the least overall male–female interactions, while the highest was recorded from Ngorongoro where lions feed on large prey (Fig. 3.14). However, the relative (positive) effect of kill size on male–female associations was different among the three systems—highest in Gir and lowest in Ngorongoro, with Serengeti showing intermediate effect. Such disparate effects can potentially be explained through prevalent habitat differences between the systems (Chakrabarti et al., 2021). Gir is primarily a forested system unlike the open plains of Serengeti/Ngorongoro, which provides ample cover for the lionesses to remain concealed from the males while they hunt and feed. In contrast, the open grasslands of Serengeti/Ngorongoro offer very little cover, and the males can easily track down females on a kill. These habitat differences are compounded by the high abundance of scavengers and sympatric carnivores such as vultures and spotted hyenas (*Crocuta crocuta*) in the Tanzania sites that facilitate carcass detections by male lions (Schaller, 1972; Zuberbühler, 2008). The Gir system lacks a rich scavenger community with no spotted hyenas and a declining vulture population.

3.3.3 Proximity Between the Sexes and Roaring

The reluctance of lionesses in associating with resident males in Gir also shows up in their physical avoidance of the males. Comparative analysis of concurrent location data of males and females shows a greater spatial separation between them as compared to the African sites. On any given day, lionesses in Gir were found at a median distance of ~3 km away from their resident males (Chakrabarti et al., 2021). Furthermore, lionesses in prey-scant environments (such as Gir, and Serengeti in the dry season when the wildebeest and zebra emigrate from the plains) roar less frequently (Chakrabarti et al., 2021). We did not find any difference in roaring rates between males in different habitats and seasons. Long-range vocalizations or roars are often used by group members to locate each other, and males are known to find females based on roaring cues (Schaller, 1972). Year-round silent lionesses in Gir and "quieter" females during prey-scant seasons in Serengeti indicate that the lionesses tend to avoid detection by the males by not proclaiming their locations aloud. The physical separation between the sexes and low roaring rates of females in Gir likely suggest that the lionesses are not only reacting to immediate conditions such as size of the prey killed, but also planning their next meal.

In sum, from this comparative analysis across the three sites, lions feed on the largest prey in Ngorongoro and the smallest in Gir, and females associate with males the most in Ngorongoro and the least in Gir (Fig. 3.14). Feeding ecology not only affects immediate competition between the sexes and resultant separation, but it also mediates male–female associations through its effects on demographic parameters such as pride and coalition sizes. Small and uniformly distributed dense prey results in small male and female group sizes and territories in Gir, which in turn promote co-residency of males in multiple prides. The resulting synergistic effect of small female pride and subgroup size, small male coalition size and co-residence of males in adjacent prides further reduces the frequency of male–female interactions in Gir through a feedback mechanism.

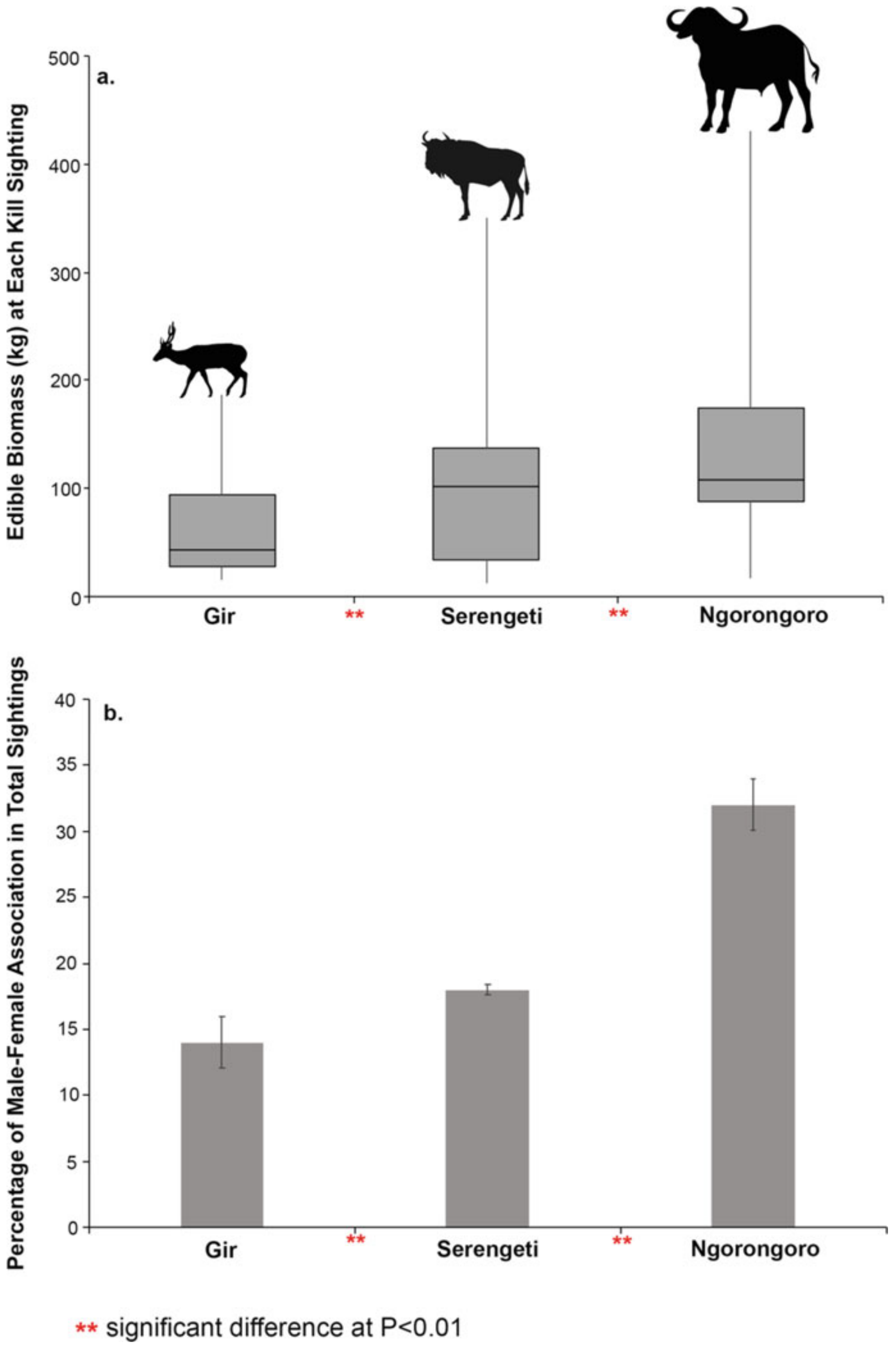


Fig. 3.14 Effect of prey biomass on male–female association in lions: (**a**) box-plots (box: inter-quartile range, horizontal line within box: median, whiskers: 10–90 percentile) showing edible biomass (kg) from lion prey carcasses in Gir ($n = 685$), Serengeti ($n = 3609$) and Ngorongoro ($n = 794$). Edible biomass = 5/8th estimated carcass weight, and (**b**) percentage of sightings with

3.4 Battle of the Sexes: Mating Strategies in Asiatic lions

Lions in Africa exhibit a "pride-centric" mating system wherein resident males have exclusive reproductive rights with their pride females and sire all the cubs born during their tenureship (Packer et al., 1991; Schaller, 1972). Reproductive monopoly is ensured by the resident males by maintaining exclusive territories and thwarting all invading and surreptitious males from gaining access to the pride. Consequently, by reducing chances of extra-pair paternity and preventing infanticide, the inclusive fitness of resident males is uncompromised. Sexually-selected infanticide is prevalent in lions where unrelated males kill any cub/dependent juvenile if not sired by them (Packer, 2019; Schaller, 1972). However, in the Gir system, owing to the factors described earlier, territories of multiple rival male coalitions overlap with that of a pride's range. This promotes the chances of female infidelity as well as females with dependent cubs encountering different rival coalitions. Below we summarize our findings of mating interactions in Asiatic lions and delve into their proximate and ultimate reasons and consequences.

3.4.1 Mating Interactions

Because of spatio-temporal segregation between the sexes, a lioness in estrus typically solicits male attention through frequent vocalizations. In fact, lionesses in Gir when observed roaring (frequently) were almost always seen with a courting male (consort) within 48 h. Roaring in lionesses thus largely serves as a "location marker" for the males in Gir, unlike for primarily maintaining social cohesion among pride-mates in African lions (McComb et al., 1994).

Gir lionesses perhaps do not require frequent long-range vocalizations to communicate with other pride females residing within a relatively small territory. Instead, they remain quiet to avoid unsolicited male attention. Even after being solicited, males often get vigorously thwarted by females during initial courting/consort hours. A typical mating event lasts for ~72 h but can continue for 120 h, with 40–60 copulations per day. However, copulation frequency peaks on the 2nd day of mating, and the mating event generally wanes out with the lioness separating from the male who often tries to prevent the female from leaving. Lionesses frequently rely on stealth to disappear while the males are asleep. We have observed courting males harassing separating females (Chakrabarti & Jhala, 2019), and in a few cases they have been aided by their coalition partners to prevent lionesses from leaving.

◄

Fig. 3.14 (continued) adult male(s) and female(s) seen together relative to the total number of observations in Gir ($n = 1092$), Serengeti (26,368) and Ngorongoro ($n = 4296$). Error bars are 95% CIs. Figure from Chakrabarti et al. (2021)

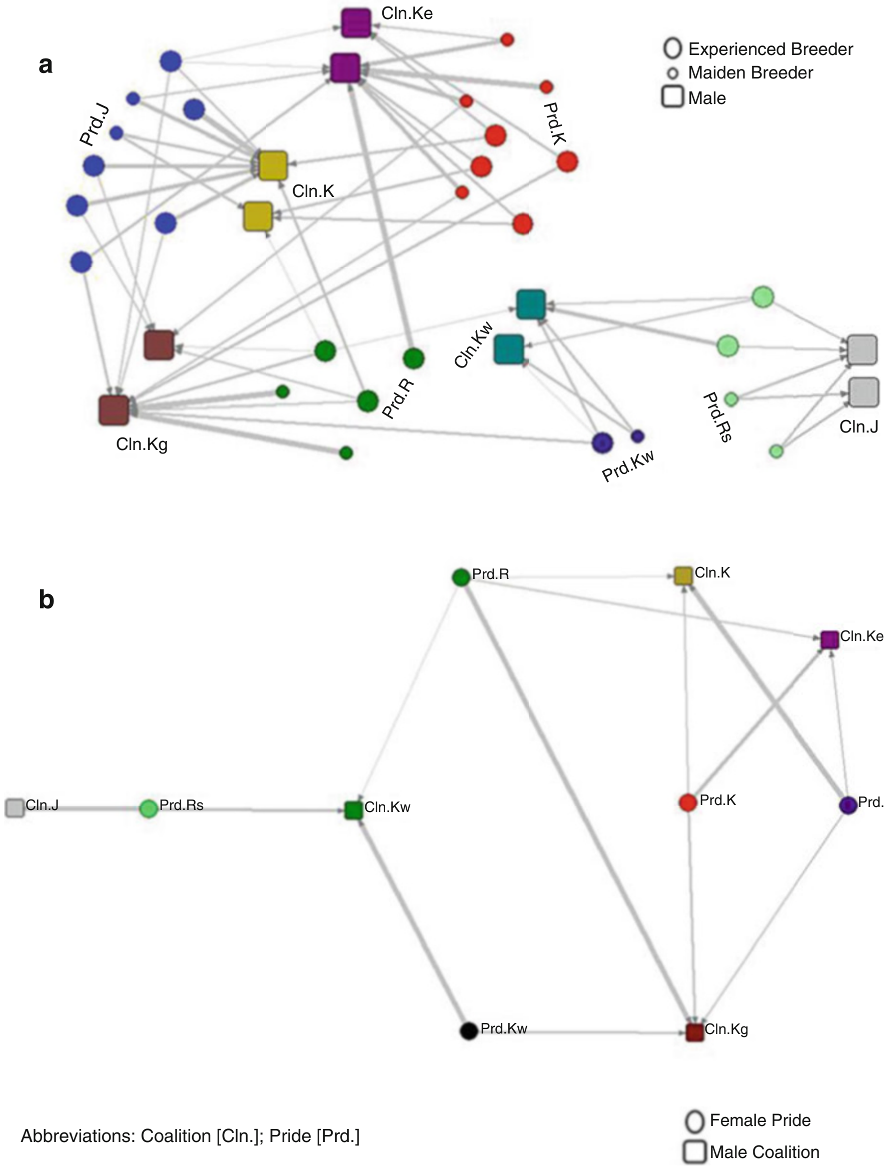
3.4.2 Mating Networks

Based on social networks created from mating interactions between males and females belonging to groups monitored intensively to avoid non-detection of mating events (see Chakrabarti & Jhala, 2017, 2019 and Chakrabarti et al., 2021 for methods), we found that Asiatic lions exhibit a complex mating network (Fig. 3.15). Overall, among all the mating events observed of lionesses belonging to a pride, the majority (64%) occurred with *primary* males, while the rest (36%) were distributed among multiple males from the *peripheral coalitions* of that pride. None of the prides were found to be exclusive to a particular coalition; instead, lionesses mated with multiple males from separate coalitions before conceiving. Moreover, there was a significant age/experience bias when it came to multi-male mating. We found that only 10% of the young/first-time breeding lionesses mated with males from other than their primary coalition, while experienced/older lionesses chose promiscuity more frequently and of all the observed extra-primary coalition mating, 90% involved experienced/older lionesses) (Fig. 3.15a).

In some cases, females were found to mate with multiple males from separate coalitions during the same estrus event (Chakrabarti & Jhala, 2019). If the extent of territorial overlap between a coalition and a pride can be considered as a proxy for spatial proximity, then experienced/older lionesses “preferred” to mate with peripheral males over their primary males (Chakrabarti & Jhala, 2019). This age-based promiscuity in lionesses likely originates from the cognitive prerequisites for effective female mate-choice. Exertion of female mate-choice incurs multiple constraints including the time and effort spent by females in searching for suitable partners (Clutton-Brock & McAuliffe, 2009). In lions and other species, the ability of an individual to gather and process information to successfully navigate these search costs (by processing olfactory and auditory cues, and/or by memory) arguably should increase with age and experience. It is likely that more matured and experienced lionesses are better at finding multiple suitors across different mating events/estruses, while first-time breeding lionesses stick to the males that they encounter the most (i.e. primary males) (Chakrabarti & Jhala, 2019).

3.4.3 Female Promiscuity as an Insurance Against Infanticide

Lions as a species exhibit sexually-selected infanticide, which can contribute to ~30% of cub mortality (Banerjee & Jhala, 2012; Chakrabarti & Jhala, 2019; Packer & Pusey, 1983; Schaller, 1972). In the Gir system, owing to the spatial nature of male and female territories, lionesses and their cubs inevitably interact with multiple rival males, each capable of killing “apparently” unrelated cubs. However, based on the observational data on adult male and cub interactions, we found same litters are tolerated and nurtured by rival males from different coalitions (Chakrabarti & Jhala,



Abbreviations: Coalition [Cln.]; Pride [Prd.]

Fig. 3.15 Mating networks of Asiatic lions: Social networks with: (**a**) nodes as individual males and females, the links between them are mating frequencies relative to the total mating events observed for that female. Shapes with similar colors represent individuals belonging to the same group; (**b**) nodes as coalitions and prides, with the links representing mating frequencies of a pride and the coalition relative to the total mating events observed of that pride. Arrow widths depict the relative frequency of mating events. Figure from Chakrabarti and Jhala (2019)

2019). However, these peaceful interactions between males and cubs occur only when the males have had mating interactions with the cubs' mothers and/or other females of the pride. Aggressive overtures and infanticide take place when unfamiliar males (invaders/strangers) encounter pride females and their cubs (Chakrabarti & Jhala, 2019). No aggression/infanticide from males belonging to multiple rival coalitions suggests that female promiscuity successfully convinces multiple males regarding cub paternity when the mothers and/or associated lionesses are familiar (via mating), but not when the females lack previous interactions with the males. Observed patterns lend evidence to the "kin-recognition hypothesis" where males do not recognize their offspring directly but rely on indirect cues to ascertain parentage (Widdig, 2007), which in this case is likely to be familiarity with mothers and associated lionesses. Alternatively, in a system where pride sizes are small and mating opportunities for a male are low, exacerbated through a despotic coalitionary structure, the costs of accidentally killing one's own cubs perhaps outweigh the benefits of exclusive parentage, thus effectively buffering infanticide from convinced and/or confused males. Females also implement mating as a way to "entice" unfamiliar males and divert them from vulnerable cubs as observed in a few cases where lionesses with young cubs expressed behavioral estrus (showing lordosis/ body bent backward and playfully soliciting copulations from invading/unknown males) while drawing them farther from hidden cubs (Chakrabarti & Jhala, 2019).

3.4.4 Female Reproductive Parameters

Long-term serial observations on individual females show that the mean conception/ pregnancy rate of Asiatic lionesses is 19% (Chakrabarti & Jhala, 2019). This means that an average Asiatic lioness requires 5–6 mating events (event: the full estrus where a lioness copulates several times with one or multiple males) to conceive. We measured conception rates as the number of pregnancies that we could ascertain visibly from the swollen bellies and teats of females (a stage that occurs late during a pregnancy) relative to the number of mating events (for detailed methods, please see Chakrabarti & Jhala, 2019). Such low conception rates might originate from low sperm count and a high frequency of sperm deformities found in male Asiatic lions (O'Brien, 2003). Alternatively, low conception rates might be a physiological adaptation of Asiatic lionesses, which permits them to mate with multiple males before conception (Chakrabarti & Jhala, 2019). Such a strategy would allow females not only to use multiple male mating as an insurance against cub infanticide but also has the potential to reduce costs of injuries, and loss of female mate-choice associated with encountering multiple coercive males. As discussed earlier, males often harass receptive females, and fighting such males can be costly for the females. A low conception rate can buffer the ultimate loss of female choice even when the lionesses sometimes have to give in and mate with coercive/harassing males (Chakrabarti & Jhala, 2019).

We present evidence that feeding ecology strongly mediates mating strategies in Asiatic lions that result from small male and female groups holding relatively small territories. While prey size and abundance mediate immediate male–female associations, the relatively thicker vegetation of Gir (compared to the East-African plains) likely provides ample concealment for sexual segregation to persist. Across habitats, lions are known to live far more gregariously in open habitats in response to higher chances of detection by competitors, as well as by potential prey that necessitates cooperation for territorial defense and hunting (Davies et al., 2016; Lamprecht, 1981). The forested system of Gir presents an intriguing scenario where prey size and distribution, coupled with habitat structure promote deviation of the lion mating system from the classical notions of this species' ecology as inferred from open grasslands systems in Africa.

While our research on mating strategies and sexual segregation was typically directed to lions inside the PA, the outside-PA landscape offers a significantly different habitat with more openness caused by agricultural-thorn-scrub matrix, as well as relatively abundant medium-large prey in the form of domestic livestock. This habitat is more comparable to the East-African plains, however, refuge patches that are crucial for concealment and cub rearing are extremely dispersed. While our radiotelemetry data suggest that lion land-tenure system in this landscape is perhaps similar to that within the Gir PA—female pride ranges are shared between multiple male coalitions (Banerjee, 2012)—we do not have intensive male–female interaction data to comment further.

3.5 Drivers of Sociality

Evolution of group-living in carnivores has been primarily attributed to (1) tackle large and dangerous prey, (2) defend resources and territories from conspecifics and competitors, and (3) supplement offspring survival and recruitment through group protection and alloparental care (Gittleman, 1989). From our observations of hunts typically being conducted by single individuals coupled with the lack of very large (and difficult to tackle) prey in the Gir landscape, it is unlikely that sociality in Asiatic lions is driven by the benefits of cooperative hunting. Examples of complex cooperative hunting strategies in lions primarily come from Etosha National Park in Namibia where predation success of solitary individuals in capturing large and fast prey in an open landscape is very low (Stander, 1992a, 1992b). Lions across Botswana are also known to use numerical strength in hunting dangerous and very large herbivores such as elephants (*Loxodonta africana*) and giraffe, which are the only prey available during certain seasons (Kotze et al., 2018; Power & Compion, 2015). In contrast, habitats with diverse prey size and ample opportunities/cover for ambush provide sufficient chances for single lions to capture small-medium prey (Scheel & Packer, 1991). Cooperative hunting is not the norm in such habitats; group members refuse to participate in hunts and instead rely on kills made by their pridemates (Packer & Ruttan, 1988). Gir with its undulating terrain and woody vegetation offers sufficient ambush opportunities for solitary lions to succeed. Thus, cooperative hunting is arguably not a necessity among pride members in Gir, and therefore is not a typical observation. Furthermore, while cooperative hunting, even in the simplest form where group members "pile on" a prey after an individual lion has initiated the attack (Scheel & Packer, 1991), can be advantageous in tackling large and dangerous prey, e.g. Cape buffalo and elephant, such herbivores are absent in Gir. Instead, most prey species are small or do not need additional help from group members to tackle.

From our data, it seems that cub recruitment is likely contingent upon female pride size. This might be owing to better defense of territories by larger groups and alloparental care. As mentioned earlier, larger subgroups of females have a competitive advantage over smaller ones during territorial confrontations and pride-mates have been observed to support each other's cubs and defend against threats. This trend mirrors the benefits of cooperation among female lions in Africa (Packer et al., 1990). However, to reiterate, this relationship between female pride size and successful cub recruitment in Gir should be interpreted with caution owing to the confounding effect of food subsidies in this landscape in the form of carcass dump sites and supplemental feeding (Jhala et al., 2019). Information on male lion behavior and life history suggests that resource acquisition and defense in the form of territorial ownership, retention and access to females are apparently the main benefits (and drivers) of coalition formation (Chakrabarti et al., 2021; Chakrabarti & Jhala, 2017, 2019). Coalitions fare better than singletons in all these aspects. However, coordinated and cooperative hunting is observed rarely in case of males barring a few exceptional instances (as discussed earlier), with majority of the hunts being carried out by single individuals.

Protection of kills can aid group formation, especially in habitats where lions frequently lose kills to competitor species such as spotted hyenas (Cooper, 1991; Höner et al., 2002). However, in areas such as Gir, which is typically devoid of such competitors, optimal lion group size can be low. Also, the thick vegetation of Gir provides ample cover for lions to hide their kills from scavengers, further reducing the need for numerical strength in safeguarding kills.

Therefore, although Asiatic lions have been observed to hunt cooperatively (especially to single out medium-large wild and domestic bovids from their herds), it is unlikely that the need for such cooperation is a driving factor behind their sociality. Instead, territorial acquisition and retention coupled with reproductive advantages are perhaps the ultimate drivers for sociality in both males and females, while cooperative hunting might be a potential secondary benefit. However, we acknowledge that our claims regarding social drivers in Asiatic lions need to be further substantiated with quantified research on predation success between solitary versus social units.

3.6 Conclusions and Future Research

Information from the Gir system when compared with that of studies from African plains suggests that lion social behavior can be highly variable leading to different strategies that are contingent upon ambient conditions. Our arguments pertaining to prey size and availability shaping male and female group sizes can also be translated to lion populations in West and Central Africa where the lack of large prey has resulted in small group sizes in both sexes (Bauer et al., 2003). A high degree of sexual segregation has also been reported in the woodlands in Kruger National Park, South Africa, where vegetation cover is dense and male lions are often found away from pride females (Funston et al., 1998). In such habitats, females likely have more options to conceal cubs and ambush prey, thus resulting in less need for male support and cooperative hunting. Extra-coalition paternity has also been reported from lion populations in Etosha (Lyke et al., 2013), where males are unable to maintain exclusive territories. Thus, eco-geographical variables, through their effects on social and prey attributes, mediate lion societies. Some lion populations are severely hunted for trophies and some are killed because of retaliation. This has the potential to significantly alter the social organization of lions by artificially changing the dynamics of male and female group sizes.

Asiatic lions typify a conservation success story with exemplary coexistence with humans. However, such proximity with humans and anthropogenic food subsidies, coupled with the outside-PA landscape changing rapidly owing to infrastructural development, can have significant changes to lion behavior and sociality. From our long-term monitoring of this population, we have understood that a key feature of Asiatic lion behavior lies in the long-term preservation of small and cohesive sex-separated social units. While group sizes are low, such groups (prides and coalitions) are crucial in maintaining the ecological and evolutionary potential of this sub-species. Anthropogenic food subsidies can disrupt “normal” group sizes by artificially inflating local population densities, biasing cub recruitment, sex ratio and turn-over, and relaxing the resource limitations imposed on large groups (Jhala et al., 2019). Such human-induced changes can have severe consequences for the current adaptations of the Asiatic lions to small prey and dispersed resources. Moreover, dump sites and areas where livestock carcasses are traditionally disposed or placed to artificially supplement/provision lions, attract scavengers including feral/stray dogs. These places not only increase the chances of intra- and inter-specific interactions, but can also promote disease spill-overs. Canine Distemper has caused lion deaths in epidemic proportions in the landscape in recent years (Jhala et al., 2019), and many such outbreak epicenters can be traced back to scavenging sites where stray dogs overlap with lions (S. Chakrabarti, pers. obs.). Infrastructural growth in the outside-PA landscape in the form of roads, railways, fences, and canals has also expanded dramatically in the past few years and has the potential to isolate small sink populations, thereby compromising movement from the source PA, causing extinctions. Thus, understanding and safeguarding the underlying mechanisms of lion sociality is not only key for their fundamental ecology but also for the long-term conservation of the species.

In this chapter, we have summarized our long-term individual identification-based information on Asiatic lion behavior at the interface of resource availability and distribution. However, comparison of behavioral trends especially with respect to male–female interactions from within and outside the PA can provide rich information on local adaptability and plasticity of lion behavior. While additional data on individual behavior (hunting, resource defense, mating, cub rearing) of lions inhabiting the landscape outside the PA is constrained by the logistics of monitoring animals over large/dispersed spaces, such information can be very helpful in providing a holistic understanding of Asiatic lion ecology and guiding their conservation in a landscape, which is rapidly turning hostile/lion-unfriendly. Our next steps in lion monitoring are to collect more behavioral information of lions outside the PA and substantiate the processes behind some of the social correlates that we have discussed in this chapter.

From our understanding, we believe lion behavior should be studied through a comparative lens across habitats, which probably would result in a spectrum of behaviors that have long been considered to be ubiquitous.

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Chapter 4

Wolves in a Human World: Social Dynamics of the Northern Hemisphere's Most Iconic Social Carnivore

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Abstract Wolves are one of the most studied wildlife species in the world, yet we only have an emerging picture of how humans affect wolf social dynamics. This chapter provides an overview of wolf social dynamics, including the fundamentals of how they live, breed, hunt, and survive, the advantages and disadvantages that coincide with group living, and how human pressures may affect their social behavior.

Wolves are a short-lived species with a fast-paced life history who display a high degree of behavioral flexibility. Their primary social unit is a multigenerational family group, also called a "pack." Group dynamics (e.g., number of individuals, age structure, composition, and cohesion) and foraging strategies (e.g., prey selection, hunting tactics, and scavenging behavior) vary widely and are generally context dependent. In other words, they differ between systems, seasons, prey type, size and density, the density of conspecifics and other competitors, habitat type and landscape

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characteristics, and levels of anthropogenic disturbance. Regardless of the system, group living provides a range of advantages to wolves, including territorial defense, breeding, hunting, and food defense. However, these must be balanced with inherent disadvantages of group living, such as intraspecific competition within the pack, e.g., competition for food.

Anthropogenic disturbance can directly and indirectly alter wolf behavior. For example, wolves alter their spatial and temporal movement patterns and space use within human-modified landscapes and in response to human disturbance, which can dampen their ecological role as apex predators. Humans also directly affect pack dynamics and social behavior by killing individuals, via both legal and illegal harvest. By reviewing recent research conducted on wolf populations living under different levels of protection, we suggest that wolf pack social structure appears to be comparatively more complex (i.e., include more age classes and complex relationships) in systems where anthropogenic mortality is low. In addition, high anthropogenic mortality across all age and sex classes may alter dispersal patterns and reduce pack cohesion and functionality, which may ultimately foster pack dissolution. In turn, this may increase pack turnover rates and reduce both individual lifespan and pack longevity, with potentially relevant ecological and conservation implications.

The consequences of anthropogenic disturbance on social dynamics is likely particularly important, as there are few wolf populations inhabiting landscapes free from humans and their impact. Wolves are often considered a resilient species, meaning you can hunt them and their numbers will quickly rebound. Indeed, wolves may appear numerically resilient, but their pack composition and social dynamics are likely more fragile. This is important because changes to pack size and composition can affect a pack's ability to successfully hunt prey, rear pups, and defend their territories, as well as their overall ecology, population dynamics, and cascading effects through an ecosystem.

Keywords Behavior · *Canis lupus* · Cooperation · Foraging · Gray wolf · Human-induced mortality · Hunting behavior · Pack · Predation · Sociality

Artistic rendering by Britney Danials. Original photo credit: Jacob W. Frank (center). Illustration credit: Britney Danials (bottom right and left)

The Mollies pack first came into sight in the morning, as I crested a large hill in Pelican Valley. The hill, the Pelican Valley 'observation point' or 'OP', became a short, temporary winter home over the course of my graduate study in Yellowstone National Park. The pack, about 17 strong, was harassing a large bull bison in the main part of the valley, each taking a turn lunging at the hind end of the behemoth. The bison, standing his ground on a patch of windswept bare ground amidst the snow covered landscape, would spin towards his attackers, swinging his great head and horns in an attempt to deter the wolves. It was an amazing struggle to watch; the winter-weakened bull attempting to defend himself from continual harassment, the wolves attempting to kill one of the most dangerous prey in North America. Risk was high for both sides, and life or death a potential outcome for either party. The scene played out over the course of the day and into the evening. The wolves intermittently attacking, then resting and waiting, never letting the bison relax or move on. The bull charging, swinging his head and kicking during attacks, then standing wearily *while some wolves rested and others circled, never a moment to rest, never a chance to escape. The next morning the bull was dead and the wolves were feeding. We never saw the kill, which surely happened during the night when the bull finally succumbed to exhaustion, or made a mistake like moving into the deep snow in an attempt to flee. Watching this event play out over the course of almost an entire day really drove home just how difficult it can be for wolves to make a living, and how important sociality is to their success.*

Wolves are a social carnivore that live, hunt, and survive in groups. This chapter provides a general overview of wolf social dynamics and the advantages and disadvantages of group living, and discusses how social behaviors may be affected by human disturbance. Hunting as a group is a key social strategy, thus we review what we currently know, and don't know, about wolf foraging behavior, and explore how hunting behavior and tactics vary between prey species and across habitats and systems. Wolves are one of the most widely-studied social carnivores in the world, and we know quite a bit about how wolves navigate human-dominated and human-modified landscapes. Yet, we only have an emerging picture of how humans affect wolf social dynamics. Here, we propose several novel hypotheses about how humans might affect wolf sociality and behavior, including how human-induced mortality may alter pack composition and potentially other social behaviors, such as dispersal. These hypotheses were derived by (i) reviewing most recent and relevant studies on wolf demography and social ecology, and (ii) contrasting wolf populations living under different levels of protection from human-induced mortality. There are few studied wolf populations that are not subject to some combination of legal and illegal harvest, thus comparisons were sparse. However, we suggest there is evidence to support the notion that human disturbance may disrupt the social behavior of wolves, and conclude that preserving the integrity of such social dynamics be incorporated into conservation and management paradigms. – Aimee Tallian

4.1 Introduction

Characterized by their tight social bonds and broad behavioral flexibility, gray wolves (*Canis lupus*) are an incredibly adaptable species (Packard, 2019). Wolves can utilize a diverse array of prey and other food resources and persist in a wide range of habitats and environmental conditions. This behavioral flexibility and opportunistic, generalist nature resulted in a historical species distribution that once spanned almost the entirety of the Northern Hemisphere (MacNulty, Stahler, Coulson, et al., 2020; Paquet & Carbyn, 2003). Wolves occurred everywhere large ungulate populations persisted and beyond, for example, into coastal ecosystems in the far north (Fuller et al., 2003).

Over the past several centuries, large-scale persecution and eradication efforts by humans severely constricted their range in North America, Europe, and Southeast Asia (Fritts et al., 2003; Ripple et al., 2014). However, natural recolonization and recovery efforts have seen populations rebound in some areas since the latter part of the twentieth century, including in human-dominated landscapes (Fig. 4.1; Boitani,

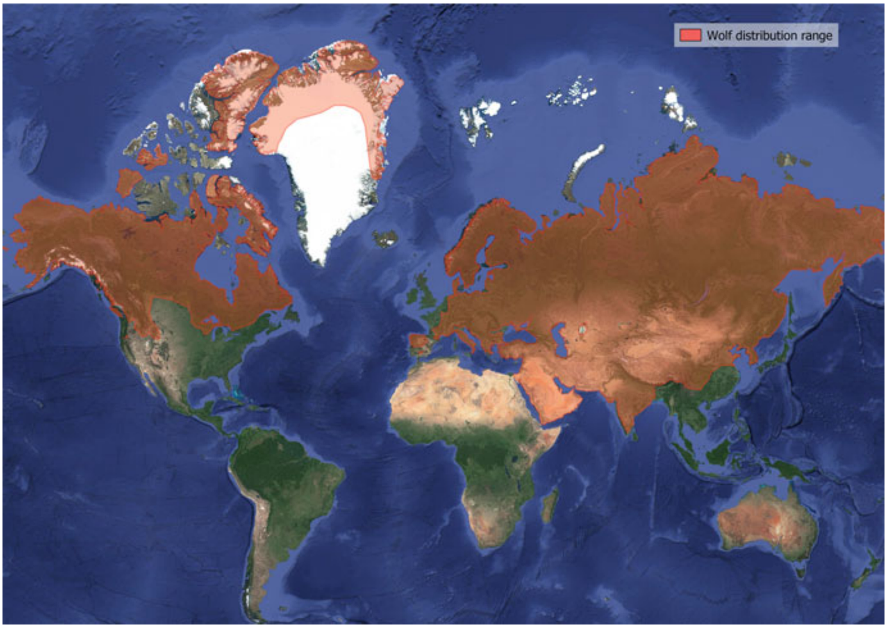

Fig. 4.1 The worldwide distribution of wolves (*Canis lupus*) shown in brown. Source of the data used in figure: IUCN (2019)

2003; Boyce, 2018; Chapron et al., 2014). Wolf numbers have rebounded over the last several decades in Scandinavia and heavily human-dominated Western and Southern Europe (Chapron et al., 2014; Wabakken et al., 2001). In northern Eurasia, including Russia and Finland, wolves persisted throughout the past several centuries (Pusenius et al., 2020), albeit with wide variation in local trends and densities. Declines occurred across the Middle East and Asia as well (Ambarli et al., 2016), although in general these wolf populations are currently considered stable (IUCN, 2020). In North America, wolves roam over most of Canada, Alaska, and several of the Northwestern and northerly Midwestern contiguous United States (Fig. 4.1). The wolf reintroduction in Yellowstone National Park in the mid-1990s is one of the most celebrated "experiments" in nature (Boyce, 2018). Wolves have also recently naturally returned to environments with a heavier human footprint than Yellowstone, such as some areas in the Canadian Banff National Park (Hebblewhite, White, et al., 2005). Concurrent with the timing of their recovery, wolves gradually came to be a quintessential image of northern wilderness, and arguably the most iconic social carnivore in the Northern Hemisphere (Fig. 4.2).

Compared to many other large social carnivores, wolves are a short-lived species with a fast-paced life history (MacNulty, Stahler, Coulson, et al., 2020), which likely affects most aspects of their behavior, including their social dynamics (Stahler, Smith, et al., 2020). Fast-paced species exhibit rapid growth, early maturity, high

Fig. 4.2 A gray wolf in Yellowstone National Park. Gray wolves have become a quintessential image of northern wilderness

fecundity, and short life spans and generation times (Gaillard et al., 2016). Wolves reach peak fitness and predatory ability at around 3–4 years old (MacNulty, Smith, Vucetich, et al., 2009; Sand et al., 2006b). Although individuals can live into their teenage years, wolves generally don't live past ~4–5 years in the wild (Mech, 1988). In Yellowstone, for example, survival declines after the age of ~6 (Cubaynes et al., 2014; MacNulty, Smith, Vucetich, et al., 2009), although mean age is often lower in harvested than unharvested wolf populations (Hayes et al., 1991). Most wolves first reproduce at 2 years of age (Fuller, 1989; Fuller et al., 2003; Peterson et al., 1984; Wikenros et al., 2021), although in some areas females do not breed until they are four (Mech et al., 1998, 2016; Mech & Seal, 1987), delivering on average 5–6 pups per litter (MacNulty, Smith, Vucetich, et al., 2009; Mech, 1970). Such short generation times allow for rapid population growth and evolutionary change (Bromham, 2011; Galtier et al., 2009), which facilitates quicker adaptation to environmental fluctuations (Gamelon et al., 2014). Thus, wolves' behavioral flexibility and fast-paced life history likely facilitated their historically wide range and marked adaptability across diverse habitats and facilitate current recovery in some areas.

4.2 The Social Unit: An Overview

The life of a wolf is generally centered around the pack, the species' primary social unit. Wolves are territorial, meaning they occupy a geographical area that they vigorously defend. In its most simple form, a pack is composed of a territorial breeding pair and their offspring, which generally includes a proportionate number of males and females (Stahler, Smith, et al., 2020). The dominant pair mates and breeds during winter, producing pups the following spring. Varied numbers and ages of offspring may remain with the pack across multiple years, overtime creating a multigenerational family unit that are typically 1st order (e.g., siblings, parent/offspring) and 2nd order (e.g., half-siblings, grandparent/grand-offspring) relatives (Stahler, Smith, et al., 2020). However, pack composition (e.g., age structure, sex ratio, kinship ties, and plural vs non plural mating) and pack size are dynamic and can vary within and between ecosystems in response to prey type and abundance, wolf density, and anthropogenic factors (Borg et al., 2015; Stahler, Smith, et al., 2020; Thurber et al., 1994). Packs tend to be more complex in both composition and behavior as they increase in size. For example, larger packs may have an additional, or subordinate, breeding pair (i.e., plural mating) and be less cohesive, or travel together less often, than smaller packs (Stahler, Smith, et al., 2020). It is a misconception that wolf packs are structured by a discrete hierarchical relationship (e.g., alpha male/female, beta, etc.), where all pack members are continuously competing to move up the social ladder (Schenkel, 1947). This long-lasting misconception arose from studies of wolves in captivity (Rabb et al., 1967; Zimen, 1975). In the wild, leadership positions are generally a dominance of parents over offspring (Mech, 1999).

The dominant male and female usually share leadership roles, e.g., initiating pack activities (Packard, 2003; Peterson et al., 2002), although recent evidence from Yellowstone suggests that the dominant female often "holds the highest leadership role" (Stahler, Smith, et al., 2020). Subordinate individuals are more likely to take leadership roles, or initiate pack activities, in larger packs that have a greater number of adults (Peterson et al., 2002; Stahler, Smith, et al., 2020). There is also a general division of labor within the pack, where the dominant female leads breeding and pup care and the dominant male the provisioning of food, while subordinates cooperate with care of young, hunting, and territorial defense (Cassidy et al., 2015, 2017; MacNulty et al., 2012; MacNulty, Smith, Mech, et al., 2009; Mech, 1999). Wolf packs tend to be more cohesive during winter (Benson & Patterson, 2015; Metz et al., 2011), and the breeding pair move tightly together before denning (Nordli, 2018). During summer, packs tend to be less cohesive, especially when packs are larger (Metz et al., 2011; Packard, 2003). This is often due to pack activities revolving around pup-rearing, where individuals or smaller groups (e.g., 2–4 individuals) of adults leave the den or rendezvous sites to hunt and bring back food, while other individuals remain with pups to care for them (Murie, 1944; Packard, 2003). Additionally, wolves tend to hunt smaller prey in summer, such as ungulate neonates (e.g., Mech, 1966; Metz et al., 2012; Murie, 1944; Sand et al., 2008), requiring fewer hunters to take down compared to larger prey.

A breeding pair is typically the core of any given pack (Mech, 1970; Smith et al., 1997), and the territorial establishment of a breeding pair is indicative of new pack formation. While this is often thought of as an independent solitary male and female coming together (Mech, 1970), the way in which new packs form is as diverse and varied as pack composition and behavior. In Yellowstone, for example, only 14% of new packs were established by a lone male and female. The majority of packs were formed by groups of individuals from different natal packs that came together (Stahler, Smith, et al., 2020). Stahler, Smith, et al. (2020) suggest this likely happens more often in areas where wolf density is high (e.g., Yellowstone), and/or the subsequent survival rates of solitary dispersers are low (Fuller et al., 2003; Jimenez et al., 2017; Smith et al., 2010), for example due to either human harvest or encounters with other established packs (Cassidy et al., 2015). Although less common, established packs may also split to form new packs, which usually happens when there are multiple breeding pairs within the group (Stahler, Smith, et al., 2020). While dominant breeders generally have a tenure between 1 and 8 years (Mech et al., 1998), a pair can establish a genetic lineage that persists for several decades within a territory, especially in unharvested wolf populations. For example, anecdotal evidence suggests that a family lineage persisted in Denali National Park for over 50 years (Haber, 1996). In Yellowstone, family lineages persist for an average of 10–12 years, although genetic evidence suggests that the Mollies pack family lineage has persisted for 25 years and counting (Stahler, Smith, et al., 2020).

4.3 The Advantages and Disadvantages of Group Living

Theory suggests that animals form groups when the benefit of living together exceeds the cost of maintaining distance with conspecifics (Markham et al., 2015). By living in groups and displaying cooperative social behaviors, individuals may increase their fitness, i.e., their ability to pass on genes to the next generation. For wolves, group living provides a range of advantages including territorial defense (Cassidy et al., 2015; Mech & Boitani, 2003), cooperative breeding (Clutton-Brock, 2002; Mech, 1970), cooperative hunting (MacNulty et al., 2012, 2014), and food defense (Vucetich et al., 2004). However, pack size may be regulated by intraspecific competition within the pack, e.g., competition for food (Peterson & Ciucci, 2003).

Living in large groups allows wolves to better defend themselves and their territory (Mech & Boitani, 2003). This is important because (1) territories provide access to key habitat and prey, and (2) in the absence of human harvest, intraspecific strife is often the primary source of wolf mortality (Cubaynes et al., 2014; Mech et al., 1998). In Yellowstone, the chances of winning an inter-territorial fight are 20% greater for the larger of the competing packs (Cassidy et al., 2015; Smith et al., 2015). This suggests that larger packs might be more advantageous in areas with high wolf density, as observed in the northern Rocky Mountains of the USA (Sells et al., 2022), where inter-territorial strife occurs more often (Stahler, Smith, et al., 2020). Interestingly, wolf packs can lose territory when they miss a year of reproduction or lose pups, likely because the smaller subsequent pack size limits territorial defense capability (Smith et al., 2015).

Pack size also affects wolf reproductive performance. For example, Stahler et al. (2013) demonstrated that pack size was the second most important driver of reproductive success for wolves in Yellowstone. Here, litter survival increased with pack size, while pup production peaked at eight pack members (Stahler et al., 2013). These authors suggested that decreased pup production in larger packs is likely indicative of high intra-pack competition affecting maternal body condition (Stahler et al., 2013). Interestingly, eight individuals was also found to be the optimal group size for disease recovery (e.g., sarcoptic mange; Almberg et al., 2015). As packs are usually family groups, the proximate drivers of pack size are the survival and the dispersal of pups. This means that the size of packs is rhythmed by birth, mortality, and dispersal events, with pack size usually higher in summer, right after parturition, than later in the year (i.e., winter; Fernández-Gil et al., 2020).

The extent to which prey size dictates wolf pack size remains an open debate. Some research supports the notion that larger packs may persist in areas where they hunt larger and more dangerous prey. For example, Barber-Meyer et al. (2016) suggested wolf packs in North America that preyed primarily on moose were larger than those preying on white-tailed deer (*Odocoileus virginianus*). Indeed, packs that prey on larger ungulates like moose and bison (*Bison bison*) tend to be the largest reported (Carbyn et al., 1993; Mech et al., 1998). However, other researchers suggest that foraging ability related to prey size is likely not the ultimate driver of pack size (Fuller et al., 2003), although it may play a more important role in less disturbed systems. Furthermore, it is difficult to determine whether heterogeneity in pack size arises from prey-specific foraging strategies or are the result of foraging efficiency, a classic conundrum of which came first (Mech et al., 2015).

Nudds (1978) theorized that packs that undergo drastic declines in ungulate prey abundance will dissolve into smaller, more efficient groups. This seems to be in line with the consistently small pack size (2–4) in low density wolf populations living with extirpated ungulate communities and thriving on human refuse, which was observed in Italy in the early 1970s and 1980s (Ciucci et al., 1997; Macdonald et al., 1980; Peterson & Ciucci, 2003), as well as a more recent study showing that wolf pack size declined with a proxy for prey availability (Sells et al., 2022). Furthermore, although larger wolf packs are better at hunting large prey (MacNulty et al., 2014), increased pack size does not necessarily mean increased per-capita food acquisition (Schmidt & Mech, 1997; Thurber & Peterson, 1993). Thus, competition for food likely influences dispersal events, playing a key role in pack size regulation (Peterson & Ciucci, 2003). Indeed, research shows that wolves in larger packs have less access to food biomass at the individual level (Zimmermann et al., 2015), and that wolves often persist in pack sizes larger than those considered optimal for foraging (Schmidt & Mech, 1997, Thurber & Peterson, 1993).

Yet, living in large packs may still prove useful for food acquisition, as large packs tend to be more effective at competing with scavengers (Hayes et al., 2000; Vucetich et al., 2004; Wilmers et al., 2003). For example, larger packs lose less food to scavengers, such a ravens (*Corvus corax*; Vucetich et al., 2004), which are known to preferentially associate with wolves as a foraging strategy (Stahler et al., 2002). It is unclear whether larger pack sizes also give an advantage in terms of carcass defense from dominant competitors, such as brown bears (*Ursus arctos*), but it is reasonable to assume so based on anecdotal observations and work with wild dogs (*Lycaon pictus*; Carbone et al., 1997). Notably, both wolf pack size and composition are heavily influenced by human disturbance, including legal and illegal wolf harvest, which we cover in more depth in the final section of the chapter, Sect. 4.7.

So, what is the optimal wolf pack size? There is no unique answer to this question, as sociality is adaptive and context dependent. Pack size is presumably a dynamic adaptation to mitigate intraspecific competition within the pack, while maximizing the benefits of territorial defense, cooperative breeding, and food acquisition under widely varied environmental circumstances (e.g., systems that vary in prey type, size, and density, density of conspecifics and other competitors, habitat type and landscape characteristics, and anthropogenic disturbance; Fig. 4.3). Thus, the size of wolf packs varies widely across study systems. Results by Fernández-Gil et al. (2020), which were updated with other studies (see Milleret, 2021), show a mean wolf pack size of 5.2 (SD = 2.3) across the Northern Hemisphere (N = 48 studies) (Figs. 4.4 and 4.5). Reported pack sizes tended to be higher in North

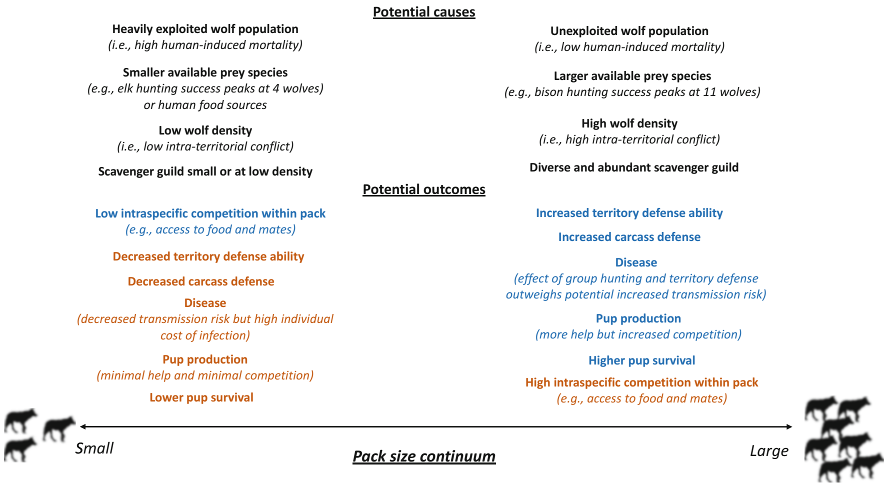

Fig. 4.3 The potential drivers and observed outcomes of wolf pack size. Outcomes are listed as potential benefits (blue) and costs (brown) of living in small and large packs, suggesting that there is a trade-off between the individual benefits of living in a large group and the cost of intraspecific competition. Note this means that some outcomes are actually maximized with medium-sized packs, e.g., pup production in Yellowstone is maximized when packs contain no more than 8 wolves (Stahler et al., 2013)

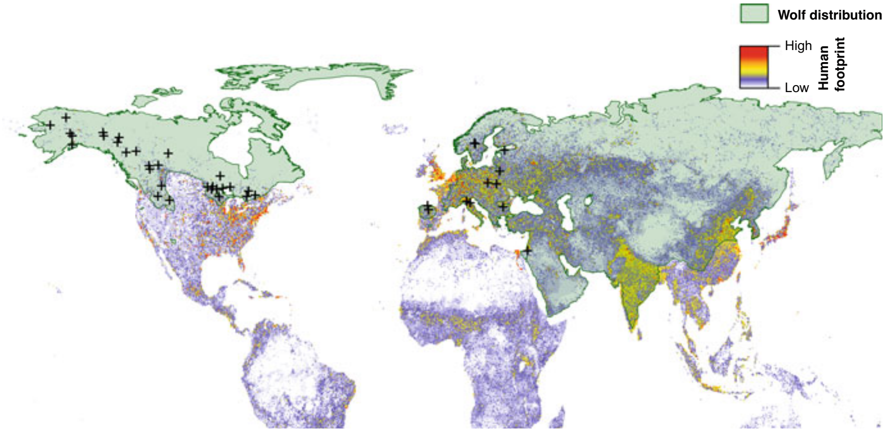

Fig. 4.4 The worldwide distribution of wolves shown in green overlaying an index of human footprint (Venter et al., 2018). The black plus signs (+) denote the study areas that provided the data for Fig. 4.5. Source of the wolf distribution data used in figure: IUCN (2019)

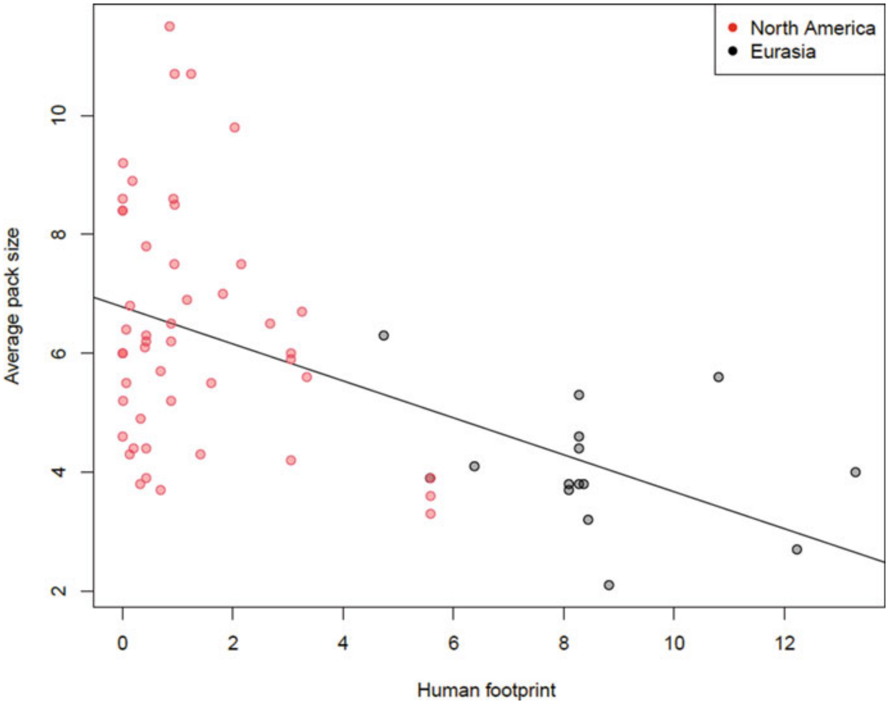

Fig. 4.5 Mean wolf pack size across study areas in North America and Eurasia during winter with respect to the human footprint index (Venter et al., 2018). Results from Fernández-Gil et al. (2020) were updated with other studies (see Fig. 4.4 and Milleret, 2021) to generate the graph ($N = 48$ studies)

America (Fig. 4.5), with the Druid pack of Yellowstone at 37 individuals the largest confirmed (Stahler, Smith, et al., 2020). Comparatively in Europe, the largest wolf packs observed in Scandinavia included 12 individuals (Svensson et al., 2021), and a rare sighting of 16 individuals was once observed on the Iberian Peninsula (Nakamura et al., 2021). However, wolves are an elusive species, and robust estimations of pack size and composition are challenging to obtain. Thus, the tracking method used (e.g., snow tracking, direct observation, genetic analysis, or GPS tracking) and seasonality and pack cohesion in relation with local environmental conditions (e.g., presence of snow, sightability, etc.) likely influence pack size estimations (Fernández-Gil et al., 2020), which is important to keep in mind when comparing results across systems. Environmental conditions, demographic events within the pack (e.g., death of individuals), the presence of neighboring packs, prey availability and characteristics, and the presence of other competing carnivores are just a few examples of the many complex and interacting factors driving wolf pack dynamics (Fig. 4.3).

4.4 Wolf Foraging Behavior: What We Know and What We Don't Know

4.4.1 Wolf Diet

Wolves are, first and foremost, predators. However, wolf diet can be broad, depending on the system and season, ranging from large wild ungulates and domestic livestock to smaller prey like beaver (*Castor canadensis, Castor fiber*), hares (*Lepus* spp.), and birds, to fish, sea otter (*Enhydra lutris*), and seals in coastal ecosystems (Mech et al., 2015; Newsome et al., 2016; Peterson & Ciucci, 2003). They have also been observed eating grass and fruit, provisioning berries to their young (Gable et al., 2017; Homkes et al., 2020), and subsisting off human refuse (Newsome et al., 2016; Peterson & Ciucci, 2003). Wolf diet composition varies substantially across biomes and between continents (Newsome et al., 2016) and can even vary locally. In the heterogeneous, human-modified landscapes of southern Europe, for example, even neighboring wolf packs display relatively large variation in main prey items (Ciucci, Artoni, et al., 2018; Nores et al., 2008). Yet, wolves primarily prey on ungulates, or hooved animals, and their ungulate species of choice varies according to their local prey community (Newsome et al., 2016).

4.4.2 Prey Selection

Theory predicts that predators select prey based on their relative abundance in the landscape and will "switch" between prey species as their relative abundances fluctuate (Murdoch, 1969; Murdoch & Oaten, 1975). Wolves follow this pattern, at least to some extent. For example, wolves in southern Scandinavia switched prey selection from moose (*Alces alces*) to roe deer (*Capreolus capreolus*), a smaller ungulate, once roe deer density was high enough (Sand et al., 2016). However, prey selection is based not only on species abundance, but also on prey accessibility (i.e., vulnerability to predation). Prey switching may be less pronounced, or not occur at all, when the alternative prey is dangerous or difficult to kill (Garrott et al., 2007). In Yellowstone, for example, wolves did not switch to bison as they became relatively more abundant than elk *Cervus elaphus* (Tallian, Smith, et al., 2017), likely due to the high risk of injury when hunting them (MacNulty et al., 2014). Interestingly, wolves increasingly incorporated bison into their diet as their abundance grew, but did so not by prey switching, but rather by modifying their foraging strategy from hunting to scavenging (Tallian, Smith, et al., 2017).

4.4.3 Scavenging and Scavengers

Wolves are adept scavengers, and scavenging as a foraging strategy occurs across much of their range (Peterson & Ciucci, 2003). Indeed, it is likely that wolves have been scavenging off human-hunted ungulate kills since Paleolithic times (Fritts et al., 2003). Today, they continue to scavenge from human-provided foods, including garbage (Newsome et al., 2016; Peterson & Ciucci, 2003), as well as scavenge from ungulates that die of natural causes (Tallian, Smith, et al., 2017), and kills made by other predators (e.g., mountain lion; *Puma concolor*; Stahler, Wilmers, et al., 2020). Their predation patterns are also intimately linked to the scavenger guild on the landscape. For example, wolves that coexist with brown bears in Scandinavia have depressed kill rates compared to allopatric wolves (Tallian, Ordiz, et al., 2017), which is the result of both interference and exploitation competition between the two species (Tallian et al., 2021). In Scandinavia, bears often use kills made by wolves, while the opposite was not documented (Ordiz et al., 2021; Ordiz, Krofel, et al., 2020). Together, these studies imply that bears likely limit wolf foraging ability, i.e., limit wolf access to food biomass. It is likely because wolves lose kill biomass to a range of scavengers, from ravens to bears, that wolves developed the strategy of eating fast and consuming their kills quickly (Vucetich et al., 2004).

4.4.4 Predator vs. Prey

Scavenging behavior aside, it seems likely that wolves are able to assess the cost–benefit ratio of hunting in a multi-prey system, selecting the prey species that provides the most profit (i.e., biomass intake) with the least risk of injury (Weaver, 1994). Elk seem to be the ideal prey for wolves; their medium size offers a decent trade-off in terms of hunting difficulty, injury risk, and biomass reward (Mech et al., 2015). This highlights that wolves face considerable hazards (i.e., risk of injury or even death) when hunting large and potentially dangerous prey (MacNulty, 2002; Mech et al., 2015; Mech & Peterson, 2003). Wolves and their ungulate prey are linked in an "arms race" (Dawkins & Krebs, 1979; Lima & Dill, 1990; Mitchell & Lima, 2002) that manifests at both the long-term evolutionary scale and the short term-behavioral scale. Wolves attempt to find, chase, subdue, and kill prey (MacNulty et al., 2007), while prey use physical and behavioral adaptations to mitigate risk at each one of these stages.

Tactics used by ungulates to avoid encounters and deflect attacks are numerous and varied (Caro, 2005) and include birth synchrony (Ims, 1990), the strategic use of certain habitats in time and space (Fortin et al., 2009; Kohl et al., 2019; Mao et al., 2005; Palmer et al., 2021), migration (Fryxell et al., 1988), elusive behavior such as constant movement (i.e., shell games; Harvey & Fortin, 2013, Simon et al., 2019), deploying defensive weaponry (Metz et al., 2018), grouping (Caro, 1994; Tallian, Smith, et al., 2017), and using aggressive behavior (MacNulty, 2002; Mech et al., 2015). Wolves must overcome a suite of defenses to have a successful hunt, and by and large, wolves are successful because they live and hunt in social groups. But they are by no means a "perfect" predator. In fact, most predation attempts fail, and hunting success varies between systems with different prey types and environmental conditions (Mech, 1966; Murie, 1944; Sand et al., 2006a). Depending on the system and prey, hunting success (i.e., the number of prey encounters that result in a kill) ranges between 1 and 56% (Mech et al., 2015). In general, it seems that the number of successful kills per encountered prey is generally higher with smaller, or less dangerous, prey (MacNulty, Stahler, & Smith, 2020), or when ungulates are naïve to newly recovered wolves (Sand et al., 2006a).

4.4.5 Coordination or Cooperation?

Theories on specific hunting strategies have varied through time, but no strong singular pattern appears consistently throughout the literature, either across or within a prey species (Mech et al., 2015). A key overarching question is, do wolves use higher-order complex strategies (i.e., foresight, understanding, and planning) when hunting prey (Mech, 2007)? The answer is unclear. While most biologists think that wolves use "some form of cooperative strategy," this has never been empirically tested and remains anecdotal (Mech et al., 2015; Peterson & Ciucci, 2003). Higher-order strategic hunting behavior may indeed occur, or, alternatively it might develop "naturally" as wolves learn how to play off one another to initiate a favorable response from prey. For example, models suggest that apparently complex and cooperative wolf hunting behavior, including chasing, encircling, relay hunting, and ambushing, can arise using very simple individual-based movement rules (Muro et al., 2011). Wolves are certainly capable of learning and understanding causal relationships and using these cognitive abilities to adapt to their environment (Lampe et al., 2017). It has been suggested that "these cognitive abilities extend to hunting strategy" (Gable et al., 2018). Mech (2007) stated that wolves are "intelligent animals and can use foresight, understanding, and planning when hunting their prey," and coordination when hunting is likely driven by visual rather than auditory cues (Mech, 2007).

Yet, coordination (e.g., not getting in each other's way) is different than cooperation (e.g., acting together to produce an optimal outcome). Cooperation or mutually beneficial interactions between conspecifics often stem from behaviors that benefit the individual, rather than only the group (Bergstrom et al., 2003). In the context of wolf hunting behavior, individual wolves "are expected to withhold hunting effort in the presence of competent companions who are likely to succeed by themselves" (MacNulty et al., 2012, p. 81). Mech first noticed this in 1970 when studying a pack of 15 wolves, observing that "seldom was the whole pack in on the kill; usually only 5 or 6 animals made contact with the prey" (Mech, 1970, p. 42). Known as "free-riders" (MacNulty et al., 2012), this is a key concept in the level of cooperation that occurs between wolves when hunting, and something we will return to again in Sect. 4.6. Regardless of which individuals were involved in a particular hunt, the outcome is that most pack members receive a meal, although feeding order (e.g., the dominant pair often feeds first) may limit access for some subordinate individuals (Mech et al., 2015, Peterson & Ciucci, 2003).

4.5 Wolf Hunting Tactics

Wolf hunting tactics are as plastic and diverse as the rest of their social behavior and can vary widely between systems and prey type. This is likely because the specific circumstances surrounding any given hunt are different, and the hunts themselves are dynamic operations rather than controlled actions. For example, interactions can occur in different habitats and terrain, under different weather and landscape conditions, with prey that have varied body conditions, group sizes, group composition, and vigilance levels, and with packs that vary in size, composition, cohesion, and individuals who vary in fitness, energetic conditions, and motivation (e.g., diseased, or levels of hunger).

4.5.1 Using the Landscape

It is critical to first acknowledge the role that the landscape plays in wolf hunting success. Terrain and landscape characteristics can leave wolves at either a predatory advantage or disadvantage, as it can affect each step in the predatory process (e.g., search efficiency, encounter rates, attack rates, capture success; MacNulty et al., 2007, Martin et al., 2018). Search efficiency, and thus encounter rates, may increase in open versus closed terrain (Hebblewhite, Merrill, et al., 2005) or when there are more human-made linear features on the landscape (e.g., roads, powerlines, trails, etc.) that allow wolves to move faster and further (Dickie et al., 2017). Attack and capture success may, alternatively, increase in closed habitats that offer fewer escape routes for prey (Hebblewhite, Merrill, et al., 2005; Kunkel & Pletscher, 2000), or under other conditions that inhibit prey escape or defense.

Deep snow, for example, often gives wolves a decisive advantage when hunting large ungulates (Peterson & Allen, 1974). Heavy snow-fall increases wolf predation on deer (Nelson & Mech, 1986), elk (Becker et al., 2009; Carbyn, 1983; Huggard, 1993), moose (Post et al., 1999), and bison (Mech et al., 2015; Smith et al., 2000; Tallian, 2017). Severe winters and high snow depths inhibit prey defensive strategies (Mech & Peterson, 2003) and decrease ungulate body condition (DelGiudice, 1998; Gaillard et al., 2000), leaving individuals weakened and therefore more vulnerable to predation. Interestingly, greater snow depths resulted in larger pack sizes and increased hunting success/kill rates in Isle Royale National Park (Post et al., 1999), and decreased chase distances during successful attacks when hunting large prey in Scandinavia (Wikenros et al., 2009). Unsurprisingly, in areas with less severe winters, snow penetrability and depth may play a more minor role (Hayes et al., 2000).

4.5.2 The Young, the Old, and the Weak

This brings us to the most widely accepted and observed wolf hunting tactic; targeting ungulates that are either young, old, or weak. Wolves tend to select fawns, calves, yearlings, and older senescent individuals, or animals that suffer from disease, injuries, abnormalities, or are in an otherwise weakened condition (MacNulty, Stahler, & Smith, 2020; Mech & Peterson, 2003). This includes selecting older, senescent animals (Metz et al., 2020; Wright et al., 2001) as well as juveniles with almost every ungulate species they hunt (e.g., Ciucci et al., 2020; Jędrzejewski et al., 2012; Lodberg-Holm et al., 2021; Metz et al., 2012; Nores et al., 2008; Sand et al., 2005), and targeting herds with calves when hunting larger prey, as observed with bison in Yellowstone (Tallian, 2017) and Wood Buffalo National Park, Canada (Carbyn & Trottier, 1987). Selection for young, old, and weak ungulates is indeed strong. For example, Hoy et al. (2021) found that within their primary prey species of moose in Isle Royale and elk in Yellowstone, wolves did not switch to less vulnerable age-sex classes (i.e., prime-aged adults) even when more vulnerable age-sex classes (i.e., calves and senescent adults) were rare.

Selecting vulnerable individuals is likely an adaptation to hunting relatively dangerous prey that are larger than themselves, which are difficult to successfully subdue. Ungulates kick, stomp, and gore to defend themselves (Caro, 2005), which becomes more dangerous for wolves as the relative size of their prey increases (Mukherjee & Heithaus, 2013). Yet, their nose may be their greatest ally in defending themselves; it is likely that wolves can smell the weakened condition of prey (R.O. Peterson pers. comm. in Mech et al., 2015). For example, domestic dogs (*Canis familiaris*) are capable of detecting cancer in humans via smell (Willis et al., 2004). Wolves' noses are likely even more sensitive to prey disease and body condition; thus, a keen sense of smell provides a wealth of communal information to all members of the pack. By attacking weaker and more vulnerable individuals, wolves are less likely to be injured or killed. However, because there are no hard and fast rules when it comes to hunting ungulates, even the strategy to target prey that are young and in weakened body condition is not consistently employed. For example, Metz et al. (2018) found that male elk that shed their antlers earlier in the year were preferentially killed by wolves, even though elk that cast their antlers early were in better nutritional condition than those that held them longer. This suggests that the cyclical loss of defensive weaponry, rather than weakened body condition, left prime-aged male elk more vulnerable to wolf predation (Metz et al., 2018). In other words, prey vulnerability can manifest in a variety of forms.

4.5.3 Move, Chase, Subdue

Wolves are classically considered a cursorial predator that is "kept fed by its feet" (Mech, 1970, p. 149). They are capable of moving long distances in short time frames (Wabakken et al., 2007) and generally move across the landscape in search of prey. Wolves commonly approach prey, such as bison, elk, and musk ox (*Ovibos moschatus*) in the open without any attempt at stalking (Mech et al., 2015). Correspondingly, chasing and subdueing is arguably the most common ungulate hunting technique, and the one that biologists have most often witnessed in the field (Mech et al., 2015). Thus, this type of hunt is often regarded as a "straightforward" hunt (Peterson & Ciucci, 2003).

Indeed, when ungulates run, wolves are more likely to attack (Mech, 1966; Tallian, Smith, et al., 2017). The pack pursues the ungulate attempting to catch up to it, slow it down, and subdue it, or get it to the ground. They usually do this by grabbing the animal's neck, nose, and/or hindquarters with their teeth and holding on, using their weight to slow the animal and drag it down (Mech, 1966). This may require multiple repeated chases and attacks before the individual succumbs (Wikenros et al., 2009). Here, wolves are at risk of being kicked and are often swung about as the animal attempts to shake them off (Mech et al., 2015), and, as one co-author observed, injuries are relatively common. The length of the chase, or how far wolves travel before they either succeed or give up, varies, but appears to be correlated with prey energetic condition, prey fat stores (Paquet, 1989), or anti-predator behavior and predator–prey life history (Wikenros et al., 2009). Chase length, or effort, may also be correlated with the energetic condition of the pack, and how long it has been since they last fed.

Some chases can be very long. For example, wolves were observed chasing a deer in Minnesota for over 20 km, although it was unknown whether that chase ended successfully for the deer or for the wolves (Mech & Korb, 1978). There is some evidence to indicate that wolves may "relay run" during long chases (Peterson & Ciucci, 2003). Here, the lead chaser would move to the rear of the group while another takes over. The previous leader will continue pursuit, but save energy by taking advantage of straightline short cuts through the twists and turns of the chase. There is varying degrees of evidence for this and seems mostly observed with caribou (*Rangifer tarandus*) (Kelsall, 1968; Olson, 1938), except see (Mech et al., 2015). Once again, it is debatable whether this tactic develops from a cooperative strategy, or simple behavioral rules that benefit the individual. For example, "free-riding" wolves that are contributing little toward the rear of the pack might stay in that position if the lead chaser perserveres, still gaining a meal at the end. However, if the lead chaser missteps or falls behind, it may be advantageous for the individual in the rear to step up and take the lead, or risk missing the meal.

4.5.4 Ambush, Chase, Subdue

As mentioned, wolves are generally considered cursorial rather than ambush predators, e.g., they move long distances over large areas in search of prey and approach prey quickly in the open once found, rather than waiting in areas where they are likely to encounter prey and using concealment to let prey approach them before attacking (Preisser et al., 2007; Schmitz, 2005). However, these are seemingly black and white definitions for behaviors that are dynamic and fluid in nature. Wolves also employ the element of surprise when hunting. They use cover to stalk their prey and even wield ambush stategies such as lying in wait for prey to approach them (Gable et al., 2018; Kelsall, 1968; Mech, 2007). Packs sometimes attempt to sneak up on prey groups, even in open terrain (Mech et al., 2015), and the presence of stalking cover may increase wolf hunting success (Kunkel & Pletscher, 2001). While ambush behavior seems to be correlated with smaller prey, such as hare and beaver (Gable et al., 2018; Kelsall, 1968), Mech (2007) observed wolves using a group combination of stalking and ambushing in a predation attempt on musk ox on Ellesmere Island, Canada. Under certain circumstances, the element of surprise likely accords a considerable advantage when hunting, for example mediating prey defensive movements (e.g., attacking before prey can group together with vulnerable young at the middle) or by closing chase distances before an attack (Mech, 2007; Mech et al., 2015).

Box 4.1. Panel Showing Different Hunting Tactics Used by Wolves with Different Sized Prey

(A) Larger packs are better able to hunt large prey; elk hunting success peaks at 4 wolves, while bison hunting success peaks at 11 wolves (MacNulty et al., 2012, 2014).

(continued)

Box 4.1 (continued)

(B) Smaller prey are generally more likely to flee, thus wolves give chase in an attempt to bring them down. However, larger prey, such as bison, are more likely to stand their ground, thus wolves encircle and continually harass.

(continued)

Box 4.1 (continued)

(C) A sequence showing wolves grabbing an elk by the hind quarters and neck, and grabbing a bison by the hind quarters, avoiding its dangerous head.

4.5.5 Prey Size Matters

Prey size may, in part, dictate the hunting tactic used by wolves (Fig. 4.6). For example, large and dangerous ungulates may take a long time to kill. In some cases, wolves may injure or wound an individual, and return later to finish the kill when the animal is in a weakened condition, which has been observed with moose and bison (Mech et al., 2015). In other instances, the "hunt" may last for hours, or even days (MacNulty, 2002). For example, with bull bison, wolves' largest and most dangerous prey (Carbyn et al., 1993; Mech et al., 2015; Mech & Peterson, 2003), wolves take turns to continually surround and harass an animal (Carbyn & Trottier, 1988; MacNulty, 2002). Continued harassment means the target is in a more or less constant state of defense and inihibits the abililty of the target individual to forage and rest. Wolves thereby weaken their quarry until they are able to overcome them or harass them until they "make a mistake" and move to part of the landscape that leaves them more vulnerable to attack (e.g., deep snow; Mech & Peterson, 2003).

4.5.6 Shell Games

Finally, wolves alter the area in which they hunt in a type of "shell game" with prey (Bergerud, 1985; Bergerud et al., 1984; Mitchell, 2009; Mitchell & Lima, 2002; Sih, 2005). Wolves continually move across the landscape in search of prey that are in weakened condition and/or prey that might be less wary, while prey move constantly to avoid spatial predictability. For example, wolves alternate the use of their territory, never staying in place for too long and revisiting areas after several days have passed, periodically checking on the vulnerability of different prey groups (Demma & Mech, 2009; Jedrzejewski et al., 2001; Mech et al., 2015; Weaver, 1994). The prey species also play this game. For example, Simon et al. (2019) found that bison engaged in complex proactive and reactive movement tactics with respect to the long-term distribution and immediate presence of wolves. Fine-scale landscape

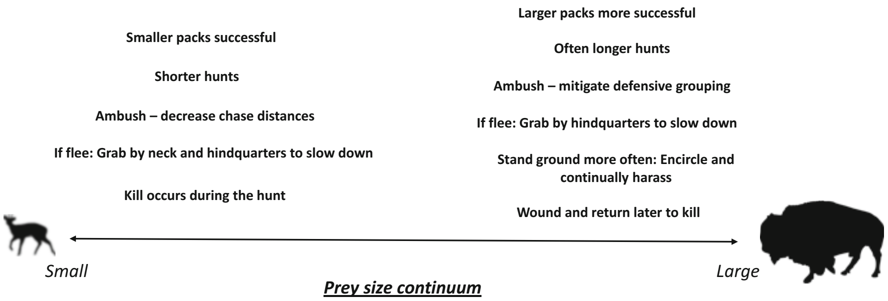

Fig. 4.6 Hypothetical relationship between wolf hunting behaviors and prey size. Wolf hunting tactics are plastic and this represents general patterns, rather than hard rules

structure can also generate contrasting spatial predation risk patterns, and refuge areas for sympatric ungulates, which has been shown with moose and roe deer in Scandinavia after the recolonization of wolves (Gervasi et al., 2013).

Research suggests that in the short-term (e.g., within days) absence of wolves, prey vigilance decreases and prey groups may become more dispersed, or move into riskier landscapes in search of food (Fortin et al., 2009; Osada et al., 2015; Tallian, 2017). For example, during the winter in Yellowstone's Pelican Valley, a comparably harsh environment for wintering bison, bison responded to extended wolf presence in the valley (wolves were absent for at least 7 days) by moving to safer "patches," or snow-free areas, on the landscape to feed (Tallian, 2017). In addition, preys' response to predation risk can vary across time, as well as space, as they balance daily needs such as food and water, with their fear of predation. For example, elk differentially respond to predation risk by wolves and cougars (*Puma concolor*) in Yellowstone by avoiding the nighttime, steep, and forested hunting activity pattern of cougars, and the crepuscular, open-grassland hunting activity pattern of wolves (Kohl et al., 2018, 2019). Similarly, in the Białowieża Primeval Forest in Poland, elk responded to lynx (*Lynx lynx*) olfactory cues by reducing site visitation duration and increasing their vigilance and reducing foraging (Wikenros, Kuijper, et al., 2015). Prey can thus minimize threats from multiple predators in the same system through nuanced behavioral shifts. However, Cusack et al. (2020) found only a weak spatial response by female elk to wolf predation risk in Yellowstone, suggesting that ungulate spatial response to wolves likely varies in strength. Importantly, the strength of ungulate spatial response to wolves varies with their nutritional condition, i.e., nutritionally stressed animals dampen their anti-predator behavior (Oates et al., 2019), which can confound interpretations of prey spatial response when not taken into account.

The hunting technique adopted by wolves likely depends on the ungulates themselves and their general defensive strategies, and the behavior the targeted prey displays upon being attacked. These include fleeing or running (e.g., commonly caribou, pronghorn, deer, and other small prey), using escape terrain (e.g., goat and sheep species), standing and fighting (e.g., bison, moose, and musk ox), or some combination of all three (e.g., elk may use all strategies within a single attack sequence; Mech et al., 2015). Wolves may be more likely to ambush smaller prey, who are more likely to flee, while they may use the wound and wait technique on larger, more dangerous prey such as moose and bison, which are more likely to stand their ground (Fig. 4.6). Yet, these techniques are not mutually exclusive, and many of them may be employed during a given hunt. Although no overarching common pattern arises within and between prey species, what seems clear is that wolves strive to take advantage of the situation that is presented to them, with varying degrees of success.

4.6 The Social Unit and Foraging: A Dynamic Adaptation

The pack provides a fundamental advantage for wolves when it comes to foraging. While solitary wolves are capable of hunting large prey (Mech et al., 1998; Thurber & Peterson, 1993), evidence from Yellowstone suggests that wolves had a 2% chance of successfully killing an elk when alone (MacNulty, Stahler, & Smith, 2020), a considerable disadvantage when considering an average local success rate of ~24% at the pack level (MacNulty, 2002). Wolves are indeed better at foraging in packs, but to what extent does group living and pack size contribute to hunting success?

4.6.1 Hunting Success

Research from Yellowstone suggests that wolves are most successful at hunting elk when at least four members of the pack are actively participating in the hunt (MacNulty et al., 2012). Note this refers to the number of individuals *actively* participating in the hunt at any given time, not the overall size of the pack. Interestingly, MacNulty et al. (2012) also found that hunting success, or the likelihood of capturing prey, actually declined as hunting group size increased beyond four hunters, likely because more individuals withheld effort in larger groups. However, wolf packs hunting bison, a considerably larger and more dangerous prey than elk, were most successful when at least 9–13 members were actively participating in the hunt, and evidence suggested that success may have continued to increase with hunting group size beyond that (MacNulty et al., 2014). Thus, free-riding, or withholding effort, is likely to occur more often in larger packs when more members are around to perform tasks, except when hunting larger and more dangerous prey that require greater effort and cooperation to subdue (Packer & Ruttan, 1988).

This brings up the concept of role specialization in the hunt, and what function it plays in hunting dynamics and success. Anecdotal evidence suggests individuals may vary their role and participation from hunt to hunt, helping to broadly spread risk and effort across the pack (Mech et al., 2015). Body size also makes a difference, and in general, larger wolves are more successful ungulate hunters (MacNulty, Smith, Mech, et al., 2009; Mech et al., 2015). Larger wolves are better at strength related tasks such as biting and pulling down prey, while smaller wolves tend to be better at movement-related tasks (e.g., running after prey; MacNulty, Smith, Mech, et al., 2009). Thus, larger body size likely increases a wolf's advantage when hunting larger prey, but could be less advantageous if hunting smaller, quicker prey. In general, males tend to be more successful at the strength-related tasks because they are often larger in size, while females are better at chasing (MacNulty, Smith, Mech, et al., 2009; MacNulty, Stahler, & Smith, 2020).

Individual wolf hunting success peaks around the age of 3–4, suggesting that wolves become less adept hunters as they age due to physiological senescence (MacNulty, Smith, Vucetich, et al., 2009). Similarly, young animals such as pups of the year and yearlings contribute little to hunting success, suggesting they are still in the learning stages (MacNulty, Smith, Vucetich, et al., 2009). Thus, the prime-aged males and females of the pack are most likely to take on lead roles in the hunting process. Research from Scandinavia shows that the age of the breeding male, rather than the size of the pack, affected the success of the hunt (Sand et al., 2006b). This could be because packs in Scandinavia primarily consist of a single breeding pair and their offspring (Chapron et al., 2016). Thus, pack sizes are small and made up of primarily young, inept hunters, so the age, size, and experience of the dominant adults play a more crucial role.

4.6.2 *Social Learning*

Can wolf packs become better at hunting a novel prey as they gain experience with it? Although this remains empirically uncertain, wolves are very much capable of learning (Lampe et al., 2017; Packard, 2003). It is likely that wolves learn together through trial and error and move and adapt to group strategies based on common goals, communal understanding, and body language (Mech, 2007). Similar to other large carnivores (Lowrey et al., 2016), anecdotal evidence suggests that some individuals and packs become "better" at hunting certain types of prey than others and continue to exploit those prey successfully while other packs do not. Long-lived wolf packs that retain pack members through time are therefore likely more successful at what they do, all else being equal, as those individuals simply have more practice at working together to overcome the barriers of anti-predator defenses and local landscape constraints (Mech, 2007). Thus, certain packs may become more adept at hunting certain types of prey, which may explain why neighboring packs sometimes select relatively different prey (e.g., Mech et al., 1998; Nores et al., 2008), as previously mentioned.

This raises the question: Do wolves become better hunters of specific prey over generational timeframes? In other words, do culture and generational learning contribute to wolf hunting success? This question is difficult to answer, as studying learning and cultural transmission across generational time frames in wild wolves is fraught with complication. Yet, many wolf biologists think there is some basis to this argument (Fritts et al., 1992). For example, Steve Fritts thinks that pups learn a "prey search image" from their parents and natal pack, which would help explain why some wolves inhabiting anthropogenic landscapes target livestock while others do not (Fritts et al., 1992). This implies that wolf packs may be able to learn to hunt novel prey, but that requires overcoming their predisposition to what they consider prey.

4.7 Humans and Wolf Ecology and Social Dynamics

Humans affect wolf demography and behavior via two primary pathways: (a) altered ecological conditions (i.e., modification of landscapes and climate) and (b) wolf harvest. Modification of landscapes can take multiple forms, ranging from heavily human-dominated and human-modified landscapes (e.g., urban areas) to landscapes that have relatively low human densities but are still human-modified (e.g., infrastructures, managed forestry, and agricultural areas). Similarly, wolf harvest, both legal and illegal (i.e., poaching), can occur across the entire gradient of human densities and landscape modifications, including in protected areas such as nature preserves. Below, we cover what is currently known about how these two pathways affect wolf behavior and social dynamics. While we acknowledge humans can impact wolf ecology in a variety of ways (e.g., human pressures can affect wolf genetics via inbreeding and hybridization with dogs), here we focus specifically on how humans affect wolf social dynamics and behavior.

4.7.1 Wolves in Human-Modified Landscapes

Wolves are apex predators that can limit the populations of both prey and mesopredator (i.e., medium-sized predator) species, either numerically and/or behaviorally (e.g., see Boyce, 2018 for a summary on these topics). However, the behavior and ecology of wolves can be fundamentally altered when they persist in human-dominated or human-modified landscapes (Fig. 4.7). For example, the ecological role of wolves may be dampened in heavily human-modified landscapes, which can alter ecosystem structure and function (Ordiz et al., 2013). This can be caused by a range of factors, including behavioral modifications that wolves employ to survive in close proximity to humans and in human-altered habitats (Ordiz et al., 2013, 2021), altered pack composition and social structure via human-induced

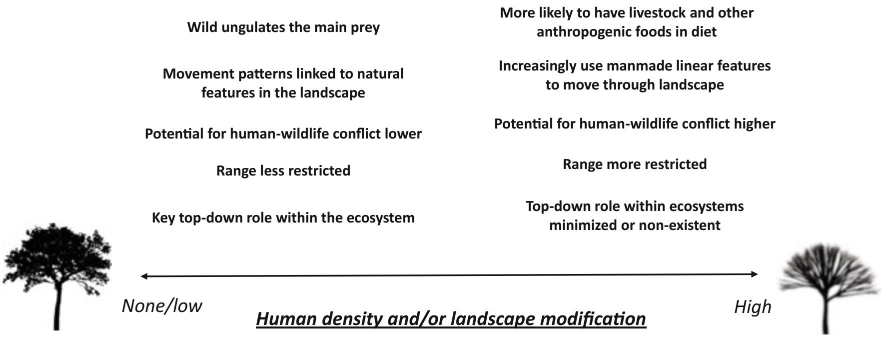

Fig. 4.7 The hypothesized relationship between wolf ecology and the level of human density and/or human landscape modification

mortality (which we cover in detail in Sect. 4.7.2), or generally altered ecological conditions whereby humans usurp top-down influence via enhanced primary production and predator and prey regulation (Darimont et al., 2015; Muhly et al., 2013).

Wolves in both human-dominated and human-modified landscapes adjust their daily activity patterns and habitat use (Ciucci et al., 1997; Mancinelli et al., 2019); in turn, this can spatially and temporally alter their ecological role as apex predators (Fritts et al., 2003; Ordiz et al., 2013, 2021). Human-related factors, such as human and road densities, affect wolf habitat selection at multiple spatial scales ranging from the landscape level, e.g., where wolves establish new territories, to more fine-scale movements and habitat choices within home ranges, e.g., where they select specific locations such as rendezvous sites (Ciucci, Boitani, et al., 2018; Ordiz et al., 2015; Ordiz, Uzal, et al., 2020; Sanz-Pérez et al., 2018; Thiel, 1985). Wolves spatially and temporally avoid humans, especially during daytime (Milleret et al., 2018), and hide in even more concealed spots after direct encounters with people (Wam et al., 2012). However, wolves also preferentially use roads (Newton et al., 2017; Zimmermann et al., 2014) and other manmade linear features (Latham et al., 2011) compared to natural pathways when available, which can alter prey encounter rates and predation patterns (Dickie et al., 2017; Whittington et al., 2011), although this is seemingly not consistent across all systems (e.g., wolves avoid roads in Finland; Kaartinen et al., 2005). Similarly, in boreal realms, human modifications to local snow conditions, e.g., snow compaction via winter activities such as snowmobiling, altered wolf movement patterns, hunting behavior, and hunting success (Paquet et al., 2010). Finally, in human-dominated landscapes, core wolf areas tend to be located in the more inaccessible parts of their home range, e.g., in Italy they primarily occur in the higher elevation and more forested regions (Mancinelli et al., 2018).

In these heavily human-dominated landscapes, wolves prey more often on widespread livestock and utilize other anthropogenic food resources, such as garbage, comparatively reducing predation pressure on wild ungulates, i.e., a "shield effect" (Zimen & Boitani, 1975; Zlatanova et al., 2014). The use of readily available anthropogenic foods (e.g., large livestock carrion) is even observed in areas where wild prey abundance is high, which reduces the role of wolves as predators, and also likely affects the top-down cascading effects of predation (Ciucci et al., 2020). Likewise, wide availability of unprotected livestock increases the occurrence of depredations by wolves, which both alters predator–prey interactions, as well as fuels conflicts with livestock stakeholders (Marino et al., 2016; Recio et al., 2020). Wolf-livestock conflict, in turn, becomes a main reason for retaliatory killing and/or lethal management of wolves in human-dominated landscapes (Fritts et al., 1992). At the landscape scale, this may limit wolf expansion and the transboundary connection of wolf populations, as exemplified in Spain (Quevedo et al., 2018). Furthermore, killing wolves can have undesired management effects, leading to increased livestock depredations, which is likely a consequence of breaking pack social structure (e.g., Fernández-Gil et al., 2016). Similarly, in other European countries that are witnessing the return of wolves after decades of absence (Chapron et al., 2014), road traffic strikes and illegal mortality may limit further population expansion (e.g., in Northern Europe; Sunde et al., 2021).

The story of wolves recovering in Scandinavia, a highly modified landscape with relatively low human densities (Fig. 4.4), highlights how humans can impact the functioning of entire ecosystems. Here, humans have altered large-scale land cover and habitat conditions via intense forestry practices (Ausilio et al., 2021; Gicquel et al., 2020), changed ungulate diversity and density (Wikenros et al., 2020; Wikenros, Sand, et al., 2015), increased available biomass for scavenger species (Wikenros et al., 2013), and generally altered predator–prey dynamics (Sand et al., 2006a; Wikenros et al., 2009; 2016). This is similar to findings from other systems that suggest human modifications usurp both bottom-up and top-down effects, including those of wolves (Muhly et al., 2013). Yet, time will tell if the ongoing recovery of large carnivores in several parts of their former ranges can restore more natural predator–prey interactions and regulatory processes.

4.7.2 Wolves and Human-Induced Mortality

Worldwide, most large carnivore mortality is caused by humans (e.g., Woodroffe & Ginsberg, 1998), and wolves are no exception (Fuller, 1989; Liberg et al., 2020; Peterson et al., 1984; Smith et al., 2010). It is well understood that human-induced mortality reduces wolf pack size (Sells et al., 2022). For example, Fernández-Gil et al. (2020) found that mean pack size in Spain declined by 22% during winter, likely caused by a combination of natural dispersal and human-induced mortality. However, studies on wolf social dynamics are sparse, and how humans affect those social dynamics via harvest, almost non-existent. This is relevant because most wolf populations are exploited by humans, enduring moderate to high levels of human-caused mortality via both legal and illegal harvest (e.g., Liberg et al., 2020; Peterson et al., 1984; Smith et al., 2010). Here, we examine pack composition patterns in Yellowstone during the 10 years following reintroduction, explore how human-induced mortality might affect wolf sociality and behavior and propose several novel hypotheses about how harvesting wolves may trigger changes in pack dynamics.

4.7.3 Pack Complexity and Population Age Structure

Based on their age structure and composition, we suggest wolf packs can be divided into simple and complex packs. Simple packs are comprised of a breeding pair and that year's offspring, whereas complex packs include the breeding pair, that year's offspring, and other age classes, including derivatives thereof such as >1 breeding pair (Packard, 2003). Both pack composition and age structure are likely heavily affected by human-induced mortality. In their review of wolf population age structure, Fuller et al. (2003) reported that pups formed the single largest age class, suggesting that the age structure of most wolf populations includes a high proportion of pups, and that simple pack structures (i.e., breeding pair and pups) are fairly common across systems. Given that most studies of wolf pack composition have occurred in systems where wolves are harvested, it is poorly understood how both population age structure and pack composition might evolve under more natural circumstances. Recent evidence from Yellowstone, however, suggests that wolf pack composition may be more complex (i.e., breeding pair, pups, and multiple other age classes) and the population may be older in unharvested populations.

Here, we explored wolf pack age structure and composition during the 10 years following wolf reintroduction to Yellowstone in 1995–1996. During this time, wolf hunting was illegal in the areas surrounding the park, and little to no poaching occurred inside the park (Smith et al., 2010). Thus, the first 10 years after reintroduction represent the evolution of pack composition and population age structure following initial territory establishment under little to no pressure from human exploitation. Our results suggest that as packs aged, pack composition became increasingly complex as they accumulated surviving, older individuals who did not disperse. For example, the proportion of subordinate adults in a pack increased over the first 4 years of the packs' life (Fig. 4.8). Furthermore, young of the

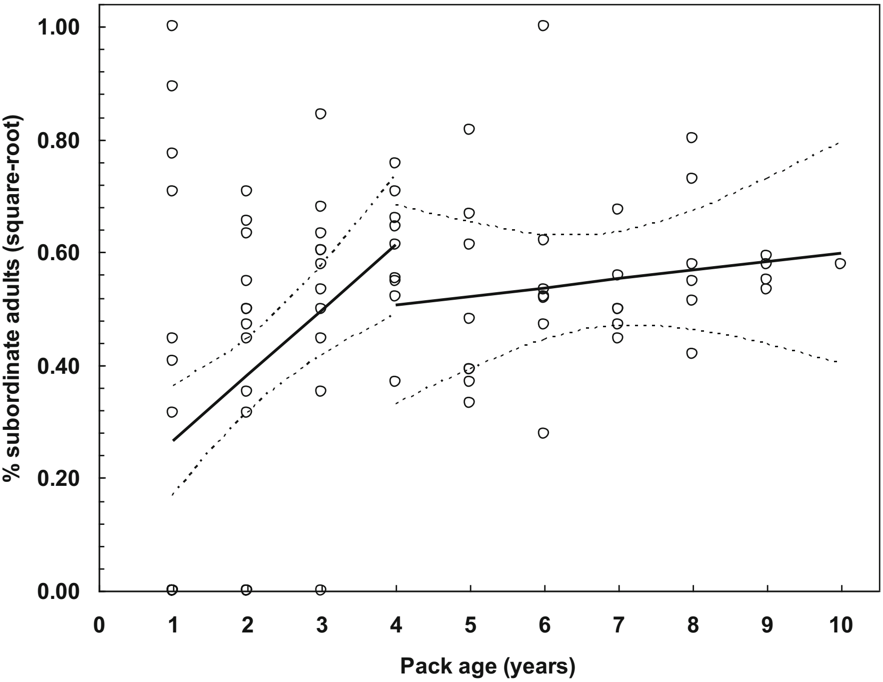

Fig. 4.8 The percent of subordinate adults (on the square root scale) in a pack given the packs age in Yellowstone National Park. Data were collected for the first 10 years after wolves were reintroduced to Yellowstone in 1995–1996

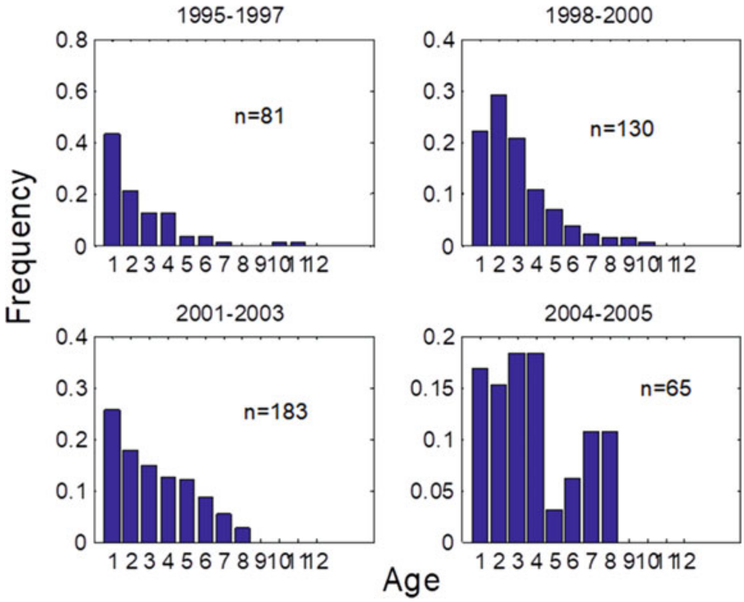

Fig. 4.9 The number of different aged wolves in wolf packs, or wolf pack age structure, over the first 10 years after wolf reintroduction to Yellowstone National Park in 1995–1996. Young of the year formed the largest age class in the years directly following reintroduction (upper-left). In the following years, pack age structure became increasingly even, and after 10 years there was roughly an equal number of 1–4 year olds with a high number of older adults (lower-right)

year formed the largest age class in the years directly following reintroduction, but thereafter pack age structure became increasingly even through time (Fig. 4.9). Ten years after reintroduction, packs were comprised of roughly an equal number of 1–4 year olds, with a high number of older adults (Fig. 4.9), increasing the proportion of complex versus simple packs within the system (Fig. 4.10). This suggests complex pack formation takes time, and that continued human harvest within a wolf population may change population structure and pack dynamics; as a result, packs in exploited wolf populations are likely simpler (Fig. 4.11). Furthermore, the mean percentage of pups in the Yellowstone population decreased through time, starting at 45% between 1997 and 2000 and decreasing to 31% (2001–2009) and 34% (2010–2020).

There are few other wolf populations to compare with the Yellowstone data, as pack composition and population age structure are rarely known (Smith, Cassidy, et al., 2020). Three studies with protected wolf populations can be at least partially compared to Yellowstone in terms of potential pack complexity and overall population age structure: northeast Minnesota, Isle Royale, and Denali, i.e., all from North America. In northeast Minnesota, 57% of the wolves were <3 years old and 82% ≤ 4 (Mech, 2006), though no data were presented on pack composition. Data from Isle Royale show the annual percent of pups in their population averaged ~30% between 1971 and 1995, considerably fewer than in Minnesota, but comparable to

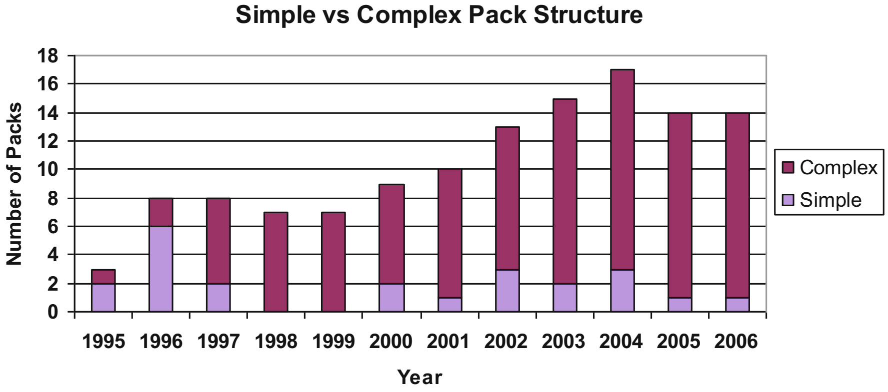

Fig. 4.10 The number and proportion of packs displaying a simple versus complex pack structure during the first 10 years following wolf reintroduction to Yellowstone National Park in 1995–1996. Simple packs are comprised of a breeding pair and that year's offspring, whereas complex packs are a breeding pair and multi-year offspring, or derivatives thereof including >2 breeders and numerous age classes, instead of just pups

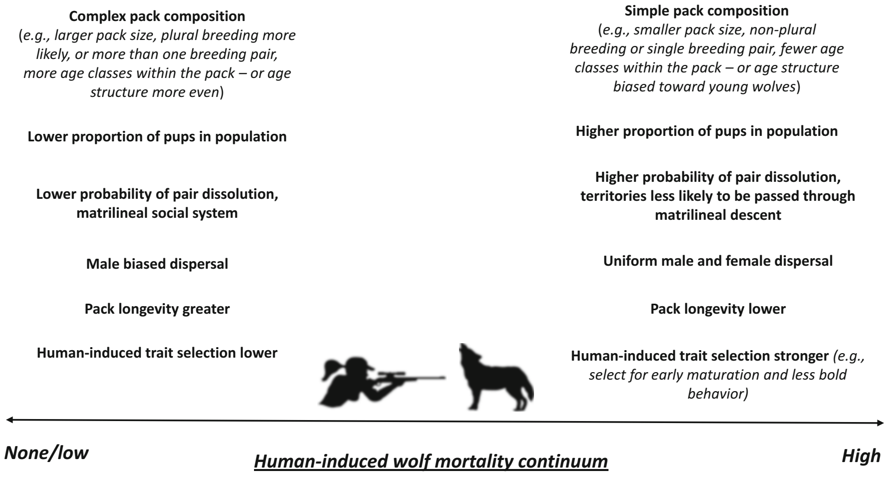

Fig. 4.11 The hypothesized relationship between wolf social dynamics and the level of human-caused wolf mortality (both legal and illegal)

Yellowstone (Peterson et al., 1998). Similarly in Denali, the annual percent of pups in the population during fall averaged 33% (range 7–48%) between 1986 and 1994 (Mech et al., 1998). During that same timeframe in Denali, mean pack size was 8.9 (range 2–29), with individual packs containing a mean 2–17 members per year, and there were four instances of plural breeding (Mech et al., 1998). Most wolves in Denali dispersed between the ages of 2 and 3, suggesting they stayed with their natal pack for at least a year or two (Mech et al., 1998). In Denali, Mech et al. (1998) suggest "a typical pack would consist of two adult breeders, four pups, two yearlings, and one 2-year old" (pg. 39). Altogether, this suggests the protected area of Denali likely also supports more complex packs. Comparing these regions to harvested wolf populations suggests that packs in unharvested populations may have a comparatively older age structure, a concept first introduced decades ago by Fuller and Novakowski (1955). An extreme example of this was observed in the north central subarctic in 1960, where wolves were rebounding from intensive control efforts and pups comprised ~73% of the population (Kelsall, 1968). More recently, Ballard et al. (1997) also found that packs in heavily exploited wolf populations exhibit a younger age structure with a higher proportion of pups.

4.7.4 Sex-Specific Dispersal

It is possible that human exploitation may also affect pack social dynamics. Wolf mortalities can break down pack cohesion and sever genetic lineages, leading to displacement by neighboring packs or new pack formations (Stahler, Smith, et al., 2020). Although such effects occur following natural mortality (e.g., via inter-pack conflicts or natural aging), they may occur at higher rates when mortality happens via harvest (Borg et al., 2015; Brainerd et al., 2008). Dispersal patterns, including sex-specific dispersal, may also be affected (Fig. 4.11). Similar to pack composition, examining heavily manipulated wolf populations might lead to biased conclusions about the natural condition of sex-specific dispersal for wolves. Research suggests that sex-specific dispersal in wolves varies between systems, ranging from generally male-biased (Ballard et al., 1987), with females also dispersing at relatively high rates (Jimenez et al., 2017), to equal dispersal rates between sexes (Peterson et al., 1984). In the protected area of Yellowstone, however, the dispersal system is heavily male-biased, i.e., male wolves are much more likely to disperse than females (Smith, Cassidy, et al., 2020).

In general, sex-specific dispersal is linked to a species' mating system, with female-biased dispersal occurring in patrilineal systems, and male-biased dispersal in matrilineal systems (Greenwood, 1980). Wolves seem to operate within a matrilineal system, where younger females are more likely to stay with the pack to help rear pups, waiting their turn to take over as the main breeder (Smith, Cassidy, et al., 2020). Indeed, breeder turnover is generally fast (2–3 years), which means that the upcoming female is less likely to be paired with her father, but rather with a new, incoming male (Smith, Cassidy, et al., 2020). However, it is possible that heavy human exploitation disrupts this system (Fig. 4.11). For example, if mortality is high across all age and sex classes, and pack dissolution is common (i.e., the matrilineal system is broken), then both males and females may equally benefit from dispersing to seek new mates and territories. Although plausible, further research is needed to understand the consequences of human-induced mortality on sex-specific dispersal in wolves. For the time being, however, we know that human disturbance is one of the most important determinants of wolf dispersal, e.g., in terms of distance traveled, duration, and success of dispersal events (Morales-González et al., 2021; Sanz-Pérez et al., 2018).

4.7.5 Comparing Systems

Wolf social dynamics, including pack complexity and dispersal patterns, are driven by a diverse array of ecological factors. For example, wolf packs may be more complex in systems with either high wolf densities or high prey densities. As previously mentioned, pack size affects the outcome of territorial disputes, and a greater number of larger, older individuals likely facilitate territorial defense (Cassidy et al., 2015; Smith et al., 2015). An abundance of food in a system may also allow for larger, more complex packs, as intraspecific competition for food within the pack, a key element that constrains group size in social species, may be dampened (Peterson & Ciucci, 2003). Thus, there are certainly important drivers of pack complexity, other than human-induced mortality, which must be considered when comparing social dynamics between systems.

As a thought experiment, we can compare Yellowstone with the similarly well-studied Scandinavian system, which has higher rates of human-induced mortality (Fig. 4.12, Box 4.2). Packs in Scandinavia tend to be simple, rather than complex, and there have been no observations of multiple breeding pairs within a pack (Chapron et al., 2016). In Scandinavia, new packs are generally established by lone males and females coming together, while packs in Yellowstone are commonly formed by group dispersal (Stahler, Smith, et al., 2020). Furthermore, pack longevity is generally shorter in Scandinavia, where pair dissolution rates are high (the mean annual probability of pair dissolution is 0.32) and human-induced mortality plays a key role (Milleret et al., 2017). Human-induced mortality of Yellowstone wolves was low between 1995 and 2009, and restricted mostly to vehicle collisions (Smith et al., 2010), but increased since wolf hunting was initiated along the park boundary in 2009 (e.g., in 2012 ~12% of the Yellowstone wolf population was harvested when they forayed outside the park boundary; YNP unpublished data), and has recently ballooned in 2022. Intraspecific aggression is a key driver of wolf mortality in Yellowstone (Cubaynes et al., 2014), while there is only anecdotal evidence of mortality induced by intraspecific strife in Scandinavia (Milleret et al., 2017).

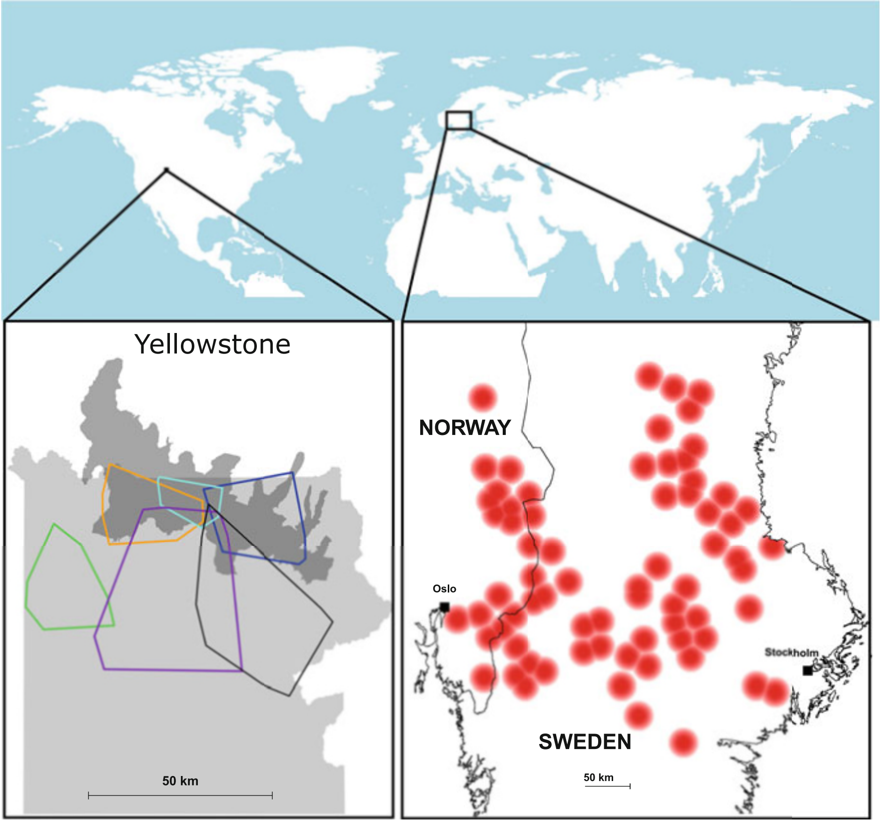

Fig. 4.12 The study systems in Yellowstone National Park, USA and Scandinavia (Sweden and Norway), as referenced in Box 4.2, with pop outs showing an example of wolf pack distribution in each system from 2019 (Smith, Stahler, et al., 2020; Wabakken et al., 2020)

Box 4.2. A Comparison of Human Impacts (A) and Wolf Ecology and Demography (B) in Yellowstone National Park and Scandinavia

Statistics in Yellowstone are calculated park wide, unless noted (NR) for the Northern Range, and within the wolf distribution range in Scandinavia. Wolf density was estimated as the mean density between 1997 and 2020 in Yellowstone and calculated for 2018/2019 in Scandinavia. Note the proportion of pups is based on the number of pups born in Yellowstone and the estimated proportion of pups within the population in Scandinavia.

	Yellowstone National Park	Scandinavia	Citation
(A) Human impacts			
Area type	Protected area (but wolves do range outside the park)	Largely unprotected area (but includes some protected areas)	
Human density	0.40 residents per km^2 (25.6–105 tourists per km^2)	10–132 residents per km^2	www.nps.gov/yell; Wikenros et al. (2020)
Road density	0.06 km/km^2 paved roads 0.03 km/km^2 unpaved roads	0.19 km/km^2 paved roads 0.88 km/km^2 unpaved roads	www.nps.gov/yell; Zimmermann et al. (2014)
Rate of harvest (legal and illegal)	0–12% (0% before 2009; after 2009 mean 2–3% ranging up to 12%)	5–15% (legal harvest) 15–24% ("potential" illegal harvest) (measured independently 2010–2016)	Liberg et al. (2020); Smith, Cassidy, et al. (2020)
(B) Wolf ecology and demography			
Wolf density	13.0 wolves per 1000 km^2 40.4 wolves per 1000 km^2 (NR)	1.6 wolves per 1000 km^2 range 0–28.6 per 1000 km^2	Bischof et al. (2020); Smith, Stahler, et al. (2020)
Mean pack size	Mean = 10.7 (range 2–37)	Mean = 5.6 (range 2–12)	Chapron et al. (2016); Smith, Cassidy, et al. (2020); Svensson et al. (2019)
Main prey type	Primary = elk (*Cervus elaphus*) (secondary = bison (*Bison bison*) and deer (*Odocoileus* spp.))	Primary = moose (*Alces alces*) (secondary = roe deer (*Capreolus capreolus*))	
Hunting success	Elk 24% (bison 4%)	Moose 43% (roe deer 47%)	MacNulty (2002); Wikenros et al. (2009)
Composition of pack	Complex (breeding pair + pups/yearlings/subadults/adults/secondary relatives/unrelated individuals) (plural breeding)	Simple (breeding pair + pups/yearlings; 10–30% of pups stay a second year) (nonplural breeding)	Fig. 4.10, Wikenros et al. (2014)
Intraspecific aggression	High (37% of natural mortality)	Low (anecdotal evidence)	Cubaynes et al. (2014); Milleret et al. (2017)

(continued)

Pack formation	Majority group dispersal and reformation (83%) (only 14% packs formed by single male and female coming together)	Majority single male and single female union (territory establishment by two single wolves or joining a pack with missing breeder)	Milleret et al. (2017); Sanz-Pérez et al. (2018); Stahler, Smith, et al. (2020); Wabakken et al. (2001)
Dispersal	Male-biased (equal between sexes early after reintroduction, then became heavily male-biased) (dispersers older, e.g., > 50% were older 1–3 years old)	Equal dispersal (76% disperse as pups, 24% stayed at least until 2 years old)	Nordli (2018); Smith, Cassidy, et al. (2020)
Population structure (proportion pups)	Pups (45%) (1997–2000) Pups (31%) (2001–2009) Pups (34%) (2010–2020)	Pups (42.4%) (2003–2015)	Yellowstone Wolf Project Annual Reports 1997–2020; Chapron et al. (2016)

However, Scandinavia also has lower wolf densities (Liberg et al., 2020; Smith et al., 2010) and a less diverse prey base than Yellowstone, which complicates comparisons. Yet, wolf density has increased in Scandinavia, and although the mean density within the wolf distribution range is comparatively low, realized local densities vary widely and can be high in some areas (Box 4.2). Although available prey biomass is potentially lower in Scandinavia, food acquisition does not appear to be a limiting factor for wolves there, as evidenced by their relatively high kill rates compared to other wolf populations (Sand et al., 2005). While Yellowstone may have more prey biomass on the landscape, not all prey are equally vulnerable to predation, e.g., bison are relatively invulnerable, although wolves have increasingly started to utilize bison biomass via scavenging (Tallian, Smith, et al., 2017). Pack complexity in Yellowstone has also remained relatively stable since reintroduction, despite a four-fold decrease in the elk population, their primary prey species (MacNulty, Stahler, Wyman, et al., 2020; Smith, Cassidy, et al., 2020). Although direct comparisons between harvested and relatively protected systems that have varied ecological and historical backgrounds are difficult, we suggest that natural-drivers of pack complexity may be overridden by the effects of human-induced mortality, yet another topic that needs further exploration.

While the wide variation in wolf pack size and composition is a function of a variety of ecological factors, for wolves inhabiting anthropogenic landscapes, these dynamics are also likely driven by human pressure. This is important because the composition (i.e., age structure, sex ratio, kinship ties, and mating system) of the pack may have a greater effect on wolf ecology than the mere raw number of individuals. As previously mentioned, large-ungulate hunting success was related to the age of the adult males and not to hunting group size in Scandinavia (Sand et al., 2006b); however, in Yellowstone, group size was clearly a key factor determining the outcome of the hunt (MacNulty et al., 2012, 2014). It is also likely that age and social status of harvested wolves play a key role in pack functionality and dissolution. Research from Alaska, for example, suggests that packs were 1.6 times more likely to persist after breeder loss due to natural compared to anthropogenic causes (Borg et al., 2015). Thus, the human-caused removal of breeders has greater chances of leading to pack dissolution, pack size reduction (via a missed breeding event), and potential territory loss (Brainerd et al., 2008). Furthermore, when prime age males are lethally removed, the most effective hunters are removed from the pack, which has implications for both hunting success and territtorial defense (Cassidy et al., 2017; MacNulty, Smith, Mech, et al., 2009).

As packs are the functional unit of wolf populations (Mech & Peterson, 2003), altering their social structure can affect, among other things, their hunting efficiency and relative effects within an ecosystem. In a study about dingo (*Canis lupus dingo*), Wallach et al. (2009, p. 7) stated that "it is the pack that is the top predator, not the individual dingo. Without the pack, a dingo is functionally equivalent to a large fox." A similar parallel may be drawn for wolves, which rely on pack strength to hunt large prey (MacNulty et al., 2014). Many populations of wolves, as well as other large carnivores, are managed using lethal control and illegal harvest is also very common, which can decrease pack sizes and alter social stability and thus affect the conservation of the species and its ecological function (Fernández-Gil et al., 2016, 2020; Milleret et al., 2017; Ordiz et al., 2013, 2021; Sells et al., 2022; Wallach et al., 2009). Additionally, altered behavior due to consistent human-induced mortality may increase the chances of affiliative behavior and interbreeding with dogs in human-dominated areas where free-ranging dogs largely outnumber wolves (Hindrikson et al., 2017; Salvatori et al., 2020).

4.8 Conclusions

Gray wolves once ranged over most of the Northern Hemisphere (Mech, 1970; Paquet & Carbyn, 2003; Young & Goldman, 1944). In a story that aligns with the fate of many large mammals, including other large social carnivores, wolf range was severely restricted due to human persecution over the past several centuries (Morrison et al., 2007). Although wolves are a highly adaptable species, they were intentionally exterminated in many portions of their original range until the second half of the twentieth century (Boitani, 2003). Since the early 1970s, wolves have been naturally recovering and expanding their range in many European countries, due to a marked departure of people from the countryside to towns and cities, shifting societal values, and widespread conservation efforts (Chapron et al., 2014). Nevertheless, the expansion of wolf populations is still prevented by lethal management and other sources of human-caused mortality in many countries (Ordiz et al., 2015; Quevedo et al., 2018; Ripple et al., 2014; Sunde et al., 2021).

Gray wolves' adaptability and the relaxation of human pressure, such as recent changes in human population densities and levels of tolerance, have facilitated their partial recovery in some human-dominated and human-modified landscapes (Cimatti et al., 2021). In these landscapes, however, wolves are exposed to profound historical and current anthropogenic alterations of their ecological background and are constantly challenged by a variety of direct and indirect human impacts that affect their ecology, conservation, and evolution (Ciucci et al., 2020; Ordiz et al., 2013). Wolves are often considered a resilient species, meaning you can hunt and harvest their population and their numbers will quickly bounce back. For instance, the suggestion that wolves can handle ~30% annual harvest without causing wolf population declines (Fuller, 1989; Fuller et al., 2003) has been widely accepted by managers in landscapes with more intense human footprints; e.g., in some European countries (Quevedo et al., 2018). Yet, we only have an emerging picture of how humans affect wolf sociality, and what this means for the wolves and the systems they live in.

Indeed, wolf numbers may be a resilient demographic parameter, but their pack composition and social dynamics are likely more fragile. This is important because, as we have covered throughout this chapter, changes to pack size and composition can affect everything from a pack's ability to successfully hunt prey, rear pups, and defend their territories, to their overall population dynamics and ecology, and their cascading effects within an ecosystem. Furthermore, anthropogenic effects on wolf behavior, pack composition, and social dynamics have important management implications as well. Hayes et al. (1991), for example, found that ungulate predation rates were higher for pairs that were newly colonizing, as well as for packs that had been severely reduced via harvest. Our growing understanding of animal culture, or information and behavior that is shared with conspecifics via social learning, suggests that culture can influence animal behavior, habitat use, population structure, and evolution (Brakes et al., 2019). Identifying, understanding, and accounting for animal cultures is therefore key to informing effective management and conservation goals (Brakes et al., 2021).

The reality is that there are very few wolf populations worldwide that are not influenced by some sort of human disturbance, whether that is simply wolves living in human landscapes, or wolf populations under regulation via intense harvest. We still know very little about how humans affect wolf social dynamics and culture, partly because it is difficult to study, and partly because there are few untouched ecosystems left with which to compare wolf cultures across gradients of human disturbance. All of this begets two questions: (1) to what extent does the ecology and behavior of wolves in heavily exploited populations depart from those living in more pristine conditions? In other words, can the baseline social dynamics and nominal ecological role of wolves materialize within exploited populations if they are consistently held in the "newly establishing" phase of their lifecycle? Then, (2) is conservation the business of conserving the mere occurrence of wolves (i.e., an image of wilderness) and targeting for certain population sizes, or should we rather aim at preserving the integrity of more subtle, yet fundamental, social, and behavioral traits and use those to assess our conservation outcomes (Brakes et al., 2019, 2021) ?

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Chapter 5
Hunting Success in the Spotted Hyena: Morphological Adaptations and Behavioral Strategies

Jennifer E. Smith and Kay E. Holekamp

Abstract Once considered mere scavengers, it is now widely recognized that hunting is more important than scavenging in the feeding ecology of spotted hyenas (*Crocuta crocuta*). In this chapter, we outline the extraordinary morphological and behavioral adaptations possessed by these bone-cracking hyenas for efficient hunting and foraging within the context of their complex social organization. These social carnivores live in female-dominated societies structured by fission-fusion dynamics in which individuals hunt alone or in small groups to avoid feeding competition but join forces in large-scale cooperation with kin and non-kin groupmates to defend food from African lions (*Panthera leo*) and members of neighboring groups of hyenas. We discuss how social rank and age influence every aspect of their hunting behavior and consider the inevitable trade-offs faced regarding cooperative hunting of ephemeral prey. Finally, we evaluate what is known about the cognitive demands and conservation implications associated with the behavioral flexibility possessed by these efficient hunters.

Keywords Cooperative hunting · Cursorial hunting · Dominance · Fission-fusion dynamics · Feeding competition · Group hunting · Lion · Ontogeny · Prey · Spotted hyena (10 listed, 5–10 requested)

The original version of this chapter was revised: Fig. 5.17 and Fig. 5.18 have been swapped to correspond to their captions. The correction to this chapter is available at https://doi.org/10.1007/978-3-031-29803-5_10

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My decision to study the social lives of spotted hyenas—rather than those of lions—was largely shaped by what started as a typical morning in Kay Holekamp's hyena camp in Kenya. We woke up before the sun for a quick cup of coffee and then drove into the darkness of the Massai Mara Reserve. At 6:28 am, roughly an hour into our morning observations, the African sunrise had faded, and we came upon a lone, immigrant male spotted hyena, Lebowski. He was running along the horizon and testing a herd of wildebeest. By 6:30 am, much to our surprise, he managed to grab onto the hind leg of one adult female wildebeest and bring it down to the ground. Shortly after that, Lebowski started to bite at its stomach and disembowel it. However, this wildebeest was not going down without a fight. By 6:36 am, she emerged on her feet and pushed Lebowski away with her horns before falling down. She attempted to stand up again at 6:39 am. The struggle continued for several minutes. By 6:42 am, Lebowski attempted to feed again. But, at 6:45 am, the wildebeest stood up again and took one final step before taking its final breath. Lebowski fed first on its liver and spleen before moving onto the other organs. This *was a magnificent triumph, given that Lebowski only weighed roughly 100 pounds (48 kg) and his prey weighed roughly three times that. In the distance, another spotted hyena vocalized (whooped), and a lion roared a minute later, but Lebowski continued to quietly eat. By 7:00 am, his stomach was fully distended, and Lebowski had consumed nearly one-third of his own body mass! As I would soon learn, although this hunt was not particularly graceful, finding a male hunting away from members of his group was common. Male hyenas often hunt and eat quietly on their own because females and their offspring are socially dominant to (and can easily usurp food from) immigrant males. Given all of this, I was left to wonder how anyone could ever have mistaken these socially complex and efficient hunters as mere scavengers. – Jennifer Smith*

5.1 Introduction

Once considered mere scavengers in popular culture, Hans Kruuk's (1966, 1972) seminal research surprised many biologists by demonstrating that hunting is more important than scavenging in the feeding ecology of spotted hyenas (*Crocuta crocuta*, Fig. 5.1). Spotted hyenas are efficient hunters that directly kill 43–95% of the food they eat (Holekamp & Dloniak, 2010), typically scavenging one-third or less of their diets from other large carcass-producing hunters (Kruuk, 1972). Since this groundbreaking revelation, dozens of subsequent studies have further confirmed the central role of hunting behavior in the lives of these efficient predators (Bearder, 1977; Cooper, 1990; Hayward, 2006; Henschel, 1986; Henschel & Skinner, 1990; Henschel & Tilson, 1988; Hofer & East, 1993; Holekamp et al., 1997; Mills, 1990; Smith et al., 2008; Smuts, 1979, Tilson et al., 1980).

Unlike the other species in the family Hyaenidae (e.g., striped [*Hyaena hyaena*] or brown [*Parahyaena brunnea*] hyenas), spotted hyenas regularly hunt medium- and large-sized ungulates on their own or with other members of their social group (Cooper, 1990; Hofer & East, 1993; Kruuk, 1972; Mills, 1990; Smith et al., 2008; Tilson & Hamilton, 1984). Spotted hyenas can even capture large ungulates, such as eland (*Taurotragus oryx*) weighing around 500 kg (Mills, 1990). A comprehensive meta-analysis (Hayward, 2006) confirmed several major findings regarding the hunting behavior of spotted hyenas, including that they are efficient hunters capable of killing at least 30 different prey species. Data from 3478 kills reported across 15 studies collected in six countries, capturing the full geographic distribution of spotted hyenas, suggest that spotted hyenas capture virtually every prey species available to them except for adult African elephants (*Loxodonta africana*, Fig. 5.2, Hayward, 2006), although spotted hyenas do prey upon new-born elephant calves in Zimbabwe (Salnicki et al., 2001). Notably, the Hayward (2006) study lacks information on other potential prey species such as hippo (*Hippopotamus amphibious*),

Fig. 5.1 Spotted hyenas are efficient predators able to capture prey exceeding their own body size such as wildebeest and oryx. Individual spotted hyena hunters capture most ungulate prey items when hunting alone or in pairs, but some prey, such as plains zebra, may only be taken down cooperatively (photos by Jennifer Smith, Gus Mills, and Joey Verge)

rhino (*Rhinoceros* spp.), and sable antelope (*Hippotragus niger*) in Kruger (Henschel & Skinner, 1990) and steenbok (*Raphicerus campestris*), duiker (*Sylvicapra grimmia*), springhare (*Peripatopsis capensis*), and Cape hare (*Lepus capensis*) in the Kalahari (Mills, 1990).

At sites for which the following prey species were available, spotted hyenas successfully hunted impala (*Aepyceros melampus*, 11 studies), Thomson's (*Eudorcas thomsonii*) and Grant's gazelles (*Nanger granti*, six studies), Cape bushbuck (*Tragelaphus sylvaticus*, four studies), springbok (*Antidorcas marsupialis*, three studies), and gemsbok (also called oryx, *Oryx gazella*, three studies, Hayward, 2006). They also commonly hunt Greater kudu (*Tragelaphus strepsiceros*), blue wildebeest (also called gnu, *Connochaetes taurinus*), hartebeest (*Alcelaphus buselaphus*), waterbuck (*Kobus ellipsiprymnus*), and Cape buffalo (*Syncerus caffer*, Hayward, 2006).

A single spotted hyena commonly captures prey weighing roughly 100 kg (220 lb.), a mass that far exceeds its own since a typical adult spotted hyena weighs from 45 to 70 kg (90–150 lb., Hayward, 2006). Cooperative hunting permits spotted hyenas to capture even the most difficult prey, such as plains zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), and gemsbok, which may involve 20 or more individuals joining forces to chase prey for up to 4 km and at speeds reaching up

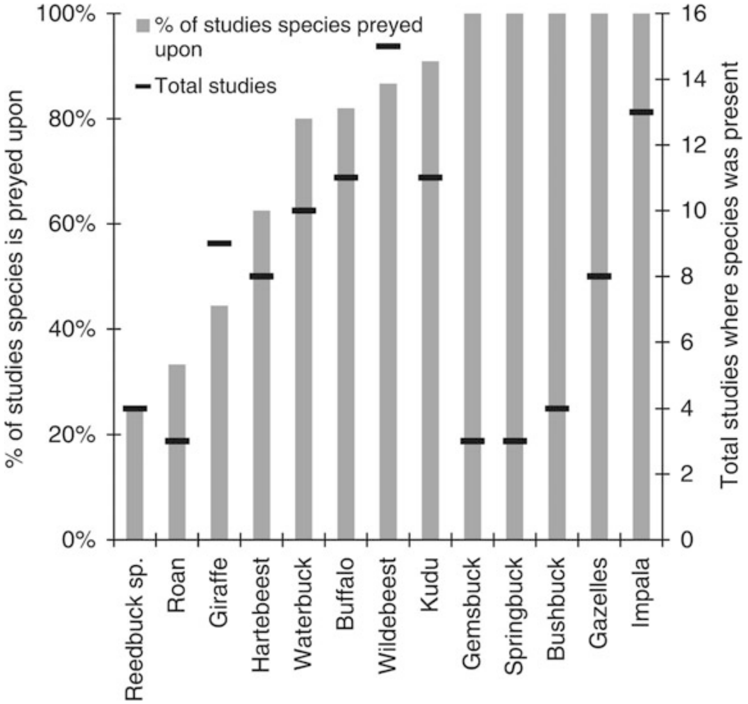

Fig. 5.2 Data from a comprehensive meta-analysis of 15 studies on spotted hyenas observed in six different countries across the full geographic distribution of spotted hyenas demonstrates the common and infrequently killed prey of spotted hyena in relation to prey availability. Reprinted with permission from Hayward (2006) (Figure 1, page 610), Journal of Zoology, 270(4)

to 50–60 km per hour (Kruuk, 1972). As a result, like wolves (*Canis lupus,* see Chap. 4 this book), cheetahs (*Acinonyx jubatus*), and lions (see Chaps. 2 and 3 this book), spotted hyenas are successful in roughly one-third of all hunts (Holekamp et al., 1997), and they regularly capture prey as large as 182 kg (400 lb.) or more (Hayward, 2006).

Spotted hyenas are efficient but socially complex hunters, and in this chapter, we outline the extraordinary morphological and behavioral adaptations possessed by spotted hyenas for efficient hunting within the context of their social organization. We discuss how social rank and age influence every aspect of their hunting behavior and consider the inevitable trade-offs faced regarding cooperative hunting of ephemeral prey that represent short-lived prey patches. Finally, we evaluate what is known about the cognitive demands and conservation implications associated with the behavioral flexibility possessed by these efficient hunters.

5.2 Morphological and Behavioral Adaptations for Efficient Hunting

Spotted hyenas possess myriad morphological and behavioral adaptations, making them more specialized and successful in cursorial hunting than any of the other bone-cracking hyaenids (Mills, 1990; Werdelin & Solounias, 1991). Morphological adaptations of spotted hyenas include their specialized teeth, which permit the capture and consumption of large prey. Rather than relying on stealth for prey capture, as do most felids, spotted hyenas are cursorial hunters that capture prey by running down a selected prey animal and chasing it over long distances (Kruuk, 1972; Mills & Harvey, 2001). Due to their keen eyesight (Calderone et al., 2003), spotted hyenas are capable of successfully capturing prey during the day or at night, and temporal variation in hunting success has not been reported (Kolowski et al., 2007; Kruuk, 1972). A typical hunt involves one or more individuals first rushing at a group of prey animals, standing briefly to observe the prey animals' locomotor behavior, selecting one target individual, and then chasing that individual for 75 m to 4 km before grabbing and disemboweling it (Cooper, 1990; Holekamp et al., 1997; Kruuk, 1972; Mills, 1990; Fig. 5.3). This pursuit hunting is facilitated by the spotted hyena's flexible spine and its specialized limbs/girdles (Andersson & Werdelin, 2003). With hind limbs that are slightly shorter than their forelimbs and tarsal bones that can be greatly overextended (Spoor & Badoux, 1989), spotted hyenas have a distinctive sloping appearance. As a result, these efficient runners exhibit a "rocking-horse gallop" that allows them to cover large distances and lope for hours (Eloff, 1964; Frank, 1986; Hofer & East, 1993; Tilson & Henschel, 1984).

Spotted hyenas use their robust forequarters and thick neck muscles to capture, pull down, drag, and otherwise carry heavy prey. It is the post-cranial skeleton and muscles of spotted hyenas that set them apart as more efficient cursors than any other extant or extinct bone-cracking species of hyena (Werdelin & Solounias, 1991). After being captured, prey can take from 0.5 to 13 min to die (Kruuk, 1972), and feeding competition quickly ensues as additional hyenas recruit to the kill site (Fig. 5.4). When feeding on a freshly killed herbivore, spotted hyenas use their strong canines and incisors to tear into and disembowel prey, often consuming meat from around the loins and anal region of their kill before opening the abdominal cavity to access the soft organs and muscles. After this, individual spotted hyenas often carry off pieces of the carcass, such as a limb or rib cage from an antelope, away from the main kill scene to eat independently elsewhere, away from conspecifics (Fig. 5.5, Kruuk, 1972).

Ungulate carcasses represent ephemeral, defensible, and energy-rich food patches (Engh et al., 2000; Frank, 1986; Smith et al., 2008; Tilson & Hamilton 1984). A single adult spotted hyena is capable of ingesting meat and bone at the rate of 1.3 kg (2.8 lb.) per minute. Moreover, a hungry group of hyenas can devour a large antelope in less than one-half hour, leaving behind only a bloody patch (Kruuk, 1972; Mills, 1990). A single adult spotted hyena can consume 14.5 kg (32 lb.) of meat in a sitting, for example, an adult can consume a gazelle fawn in less than one minute, and a

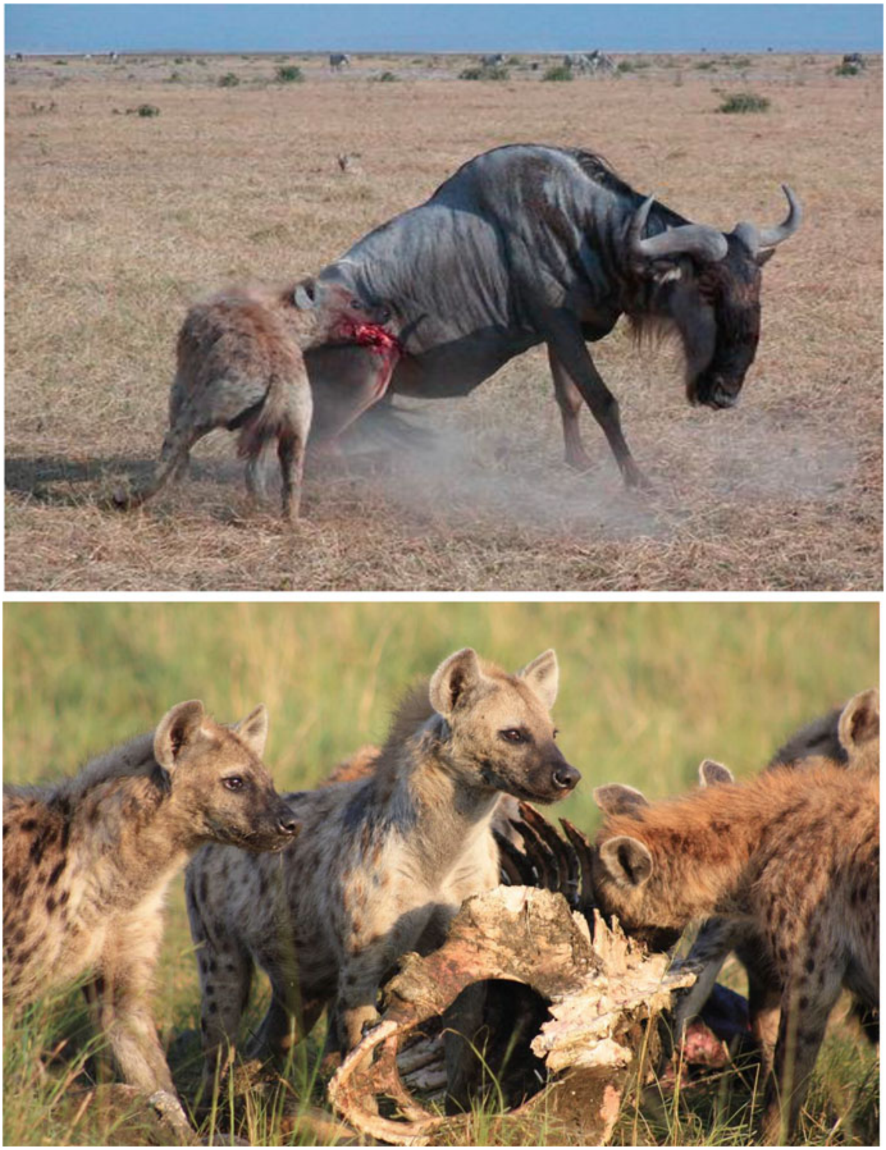

Fig. 5.3 Spotted hyenas are efficient hunters that directly kill 60–95% of the prey they consume and regularly capture prey nearly three times their own size, such as the wildebeest (above) and a hippo (below). Their powerful jaws permit these bone-cracking hyenas to devour the entire prey item to a pile of bones in a matter of minutes (photos by Heather E. Watts and Kate Yoshida)

group of 35 hyenas can devour an adult zebra (up to 450 kg or 1000 lb.) in as few as 36 min (Kruuk, 1972). As a result, individual spotted hyenas experience competition when feeding on fresh ungulate carcasses, and individuals often gain a competitive

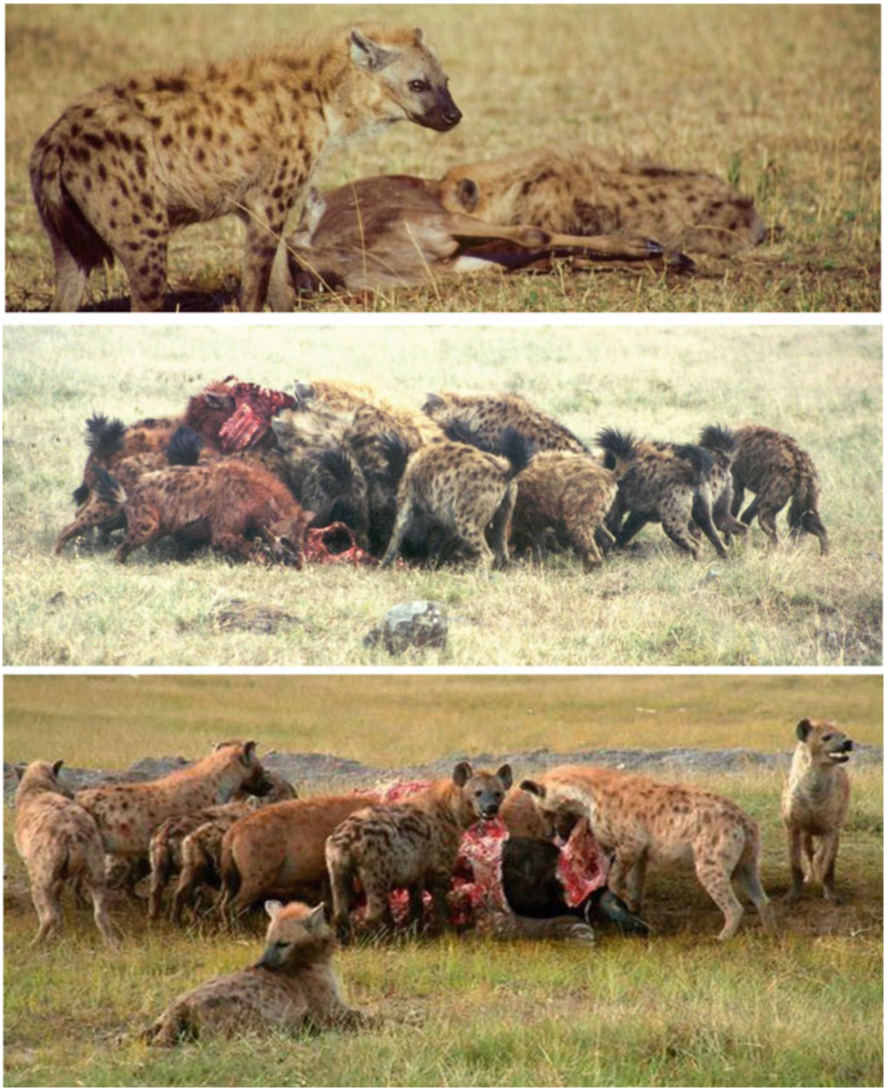

Fig. 5.4 Scramble feeding competition is extremely intense among spotted hyenas. These animals feed on rich, but ephemeral, fresh ungulate carcasses in subgroups containing up to 56 competitors. A hyena's relative rank position in the social dominance hierarchy of the clan determines its priority of access to food at kills. Low-ranking hyenas often must wait on the sidelines and feed only after high-ranking hyenas have had their fill (photos by Joseph Kolowski, Kay E. Holekamp, and Anne L. Engh)

advantage over conspecifics by feeding quickly (Kruuk, 1972). Moreover, dominance relationships determine an individual's priority of access to food (Engh et al., 2000; Frank, 1986; Smith et al., 2008; Tilson & Hamilton 1984).

Fig. 5.5 Spotted hyenas will often carry off parts of the main kill to avoid scramble competition to forage on their own. This hyena in the top photo is walking off with the leg of a kudu, presumably to avoid feeding competition with competitors at the main kill scene (photo by Bernard Dupont). In the bottom photo, one hyena is running away with a topi skull and spine while being chased by a second hyena (photo by Eli M. Swanson)

5.3 Female-Dominated Societies Structured by Fission-Fusion Dynamics

Spotted hyenas are social carnivores that live in permanent complex and female-dominated societies called clans that contain as few as six (Tilson & Henschel, 1984), and more than 120, individuals (Green et al., 2018). Adult females and their offspring are socially dominant to all adult immigrant males (Frank, 1986; Kruuk, 1972). Immigrant males queue for social status within groups and use affiliative behavior to court females (East et al., 2003; East & Hofer, 2001; Szykman et al., 2007). As is the case for many group-living animals (Aureli et al., 2008), spotted hyena societies are characterized by fission-fusion dynamics (Holekamp et al., 2000; Smith et al., 2008). Even though 120 or more individuals may concurrently belong to a single clan of spotted hyenas, all clan members are rarely, if ever, found together in a single location. Instead, individual animals make active decisions to leave (fission) or join (fusion) group-mates belonging to the larger social unit on an hour-to-hour basis (Smith et al., 2008). To avoid costly feeding competition, most social carnivores (Creel & Macdonald, 1995; Smith et al., 2012), including African lions (*Panthera leo leo*) (Packer et al., 1990), live in groups structured by fission-fusion dynamics. Individual spotted hyenas regularly separate from group-mates (fission) to forage on their own when food is scarce and come together (fusion) again when food is abundant or cooperative defense against intruders is beneficial (Smith et al., 2008). Whereas the ability to capture a larger array of prey animals more successfully appears to be a by-product of group-living, the benefits of cooperative defense of shared resources from lions and neighboring conspecifics rather than those associated with group hunting appear to have favored group-living (Smith et al., 2008). The constraints imposed by limited food resources explain the tendency for spotted hyenas to spend much of their time alone, even for individuals residing in large clans and areas of high prey abundance (Smith et al., 2008). These patterns vary with ontogeny, social rank, and reproductive state. Adults spend roughly 20–40% of their time alone (Smith et al., 2008).

The structure, size, and complexity of spotted hyena clans are more similar to those of cercopithecine monkeys than those of other social carnivores, which typically reside in small groups of closely related individuals, at least among members of one sex (Holekamp et al., 2015). Large clans may contain several different matrilineal kin groups and several immigrant males born elsewhere. Mean relatedness is very low between members of different matrilines, due mainly to rapid and constant gene flow via male dispersal among clans (Holekamp et al., 2012; Van Horn et al., 2004). As in many cercopithecine monkeys (e.g., Chapais, 1992; Cheney, 1977; Horrocks & Hunte, 1983; Walters, 1980), coalition formation plays an important role in the acquisition and maintenance of a stable social relationship (Fig. 5.6, Engh et al., 2000; Holekamp & Smale, 1993; Smale et al., 1993, Smith et al., 2010, Strauss et al., 2020; Strauss & Holekamp, 2019; Zabel et al., 1992). Early in ontogeny, each hyena comes to understand its own position in its clan's dominance hierarchy (Holekamp & Smale, 1993; Smale et al., 1993). This

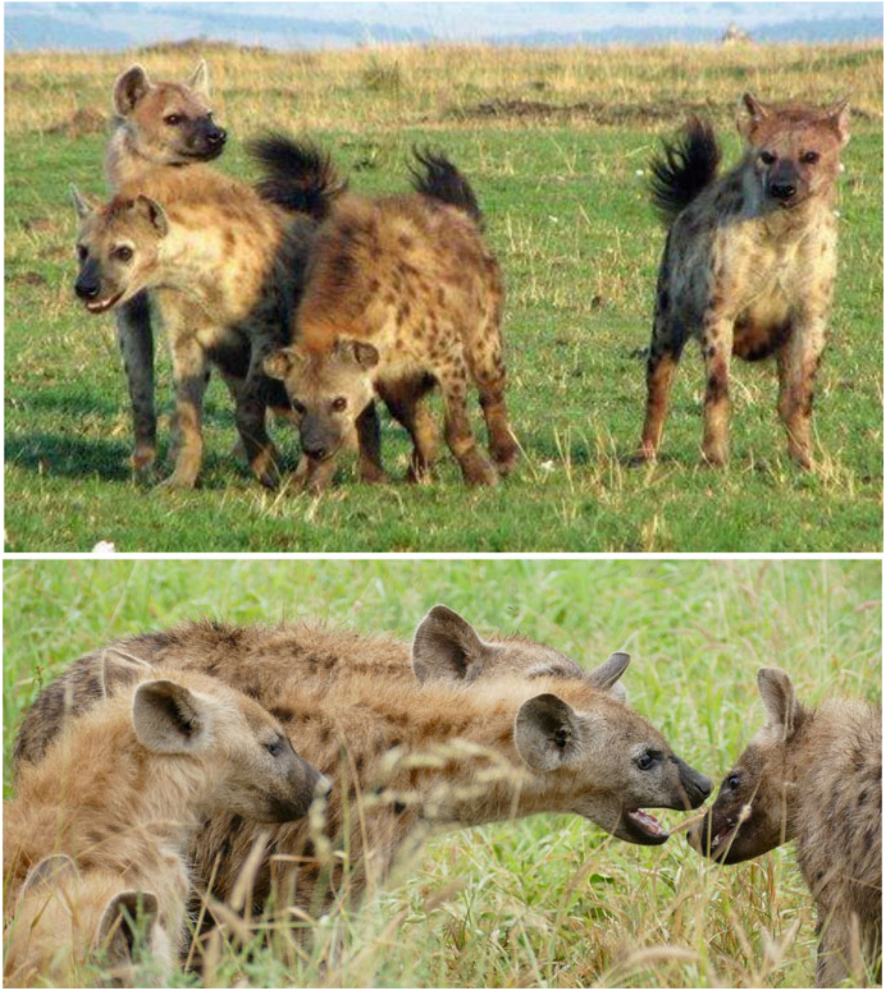

Fig. 5.6 Spotted hyenas inherit their social rank directly below that of their mother based on a period of associative learning over which mothers intervene on behalf of their offspring. An individual's social rank within the female-dominated societies of spotted hyenas determines priority of access to food at kills (photos by Kate Yoshida and Bernard Dupont)

process requires a type of associative learning called "maternal rank inheritance" in which the mediating mechanisms are identical to those observed in cercopithecine primates (Engh et al., 2000; Holekamp & Smale, 1991). As a result, dominance relationships are extremely stable across time and contexts. Because social rank determines a hyena's priority of access to energetically rich but ephemeral kills, dominance rank is particularly important when multiple individuals arrive to feed together on a fresh carcass (Frank, 1986; Smith et al., 2011).

5.4 Effects of Social Rank and Age on Hunting and Feeding Success

Because reproductive success among female spotted hyenas is determined by food consumption (Holekamp et al., 1996), and because social rank determines priority of access to food, social status profoundly affects the reproductive success of spotted hyenas (Frank et al., 1995; Hofer & East, 2003; Holekamp et al., 1996), such that high-ranking offspring grow faster, survive better, and reproduce earlier than their low-ranking counterparts (Frank et al., 1995; Hofer & East, 2003; Holekamp et al., 1996; Watts et al., 2009). Prenatal exposure to maternal hormones evidently differentially prepares offspring for competition at kills (Dloniak et al., 2006; Holekamp et al., 2013; McCormick et al., 2021), high-ranking mothers expose their offspring to higher levels of circulating androgens in utero than do low-ranking mothers.

Beyond the effects of social rank, cubs of both sexes born to mothers with high concentrations of androgens exhibit significantly higher rates of aggression across the lifespan than do individuals born to mothers with low concentrations (Dloniak et al., 2006; Holekamp et al., 2013; McCormick & Holekamp, 2022). Androgen exposure apparently enhances maternal aggression, without which youngsters would rarely be able to feed at kills because young hyenas are unable to tear off and consume pieces of a carcass nearly as quickly as can adults (McCormick et al., 2021). Skull development is not complete until 35 months of age, which is nearly 2 years after weaning, and more than 1 year after reproductive maturity, which occurs at roughly 24 months old (Fig. 5.7, Tanner et al., 2008). Thus, aggressive displacement of clan-mates from kills by their mothers allows young to feed at carcasses, juveniles are otherwise severely handicapped during competitive feeding by the slow and protracted development of their skulls (Watts et al., 2009).

In addition to being severely handicapped while competing with adults to quickly consume ungulate prey once captured, young hyenas are also poor at capturing prey in the first place (Fig. 5.8). Juveniles are relatively slow to arrive at fresh kills (East & Hofer, 1991; Holekamp et al., 1997). Hunting behavior of juvenile hyenas differs from that of adults in multiple respects, each of which is detrimental to their overall feeding success compared to adults (Fig. 5.9). As occurs in most large carnivores as part of the learning process, juvenile spotted hyenas stalk more non-mammalian prey and smaller mammals than do adult spotted hyenas (Holekamp et al., 1997; Mills, 1990).

In some cases, juvenile spotted hyenas hunt passerine birds and invertebrates in their first few months of life, but in general, juveniles are unable to successfully capture even small mammalian prey until roughly 9 months old or later (Holekamp et al., 1997). Juveniles more frequently require assistance in securing prey than do older animals and sometimes employ inappropriate hunting tactics, such as attempting to capture a zebra on their own (Holekamp et al., 1997). When juveniles hunt ungulate prey, they often do so by joining larger hunting groups than adults, and they are less successful at hunting than are adult hyenas (Holekamp et al., 1997). Most juveniles are unable to successfully capture an antelope on their own until

Fig. 5.7 Juvenile spotted hyenas are handicapped because they lack the well-developed feeding apparatus of adult competitors. Unlike juveniles, adult spotted hyenas can easily crack large bones such as this giraffe femur shown here. An ontogenetic series of spotted hyena skulls illustrating changes in size and shape throughout development in frontal view (from left to right) at 3 months, 11 months, 22 months, and 11 years of age. Note that skull development is still far from complete at 22 months. In fact, skull development is not complete in this species until at least a year after puberty, which occurs in both sexes at roughly 24 months of age (photos by Anne L. Engh, Bernard Dupont, and Jeremy Herliczek)

reaching 1.4 years of age, and young hyenas do not achieve adult competency levels at hunting until they are 5–6 years old, long after sexual maturity (Holekamp et al., 1997). Thus, juveniles and young adult hyenas are generally ineffective predators that only reach adult competency levels after years of practice, a behavioral pattern that appears to distinguish spotted hyenas from other large carnivores.

As one of the three species of bone-cracking hyenas, adult spotted hyenas (but not juveniles) can eat and digest nearly all parts of their prey (Wilson & Russell, 2009). This aspect of the spotted hyena’s life results in the production of feces that, when dried by the sun on the African savannah, are notably bright white with a powdered bone matrix containing high levels of calcium, this also occurs for feces of striped and brown hyenas (Kruuk, 1972; Mills, 1990). Only adult spotted hyenas can generate enormous bite forces (Tanner et al., 2008), including those large enough

Fig. 5.8 Juvenile spotted hyenas are physically smaller than adults and lack the skills required to efficiently capture ungulate prey on their own, only reaching full competency at 5–6 years of age, long after reaching reproductive maturity at 24–36 months (photos by Bernard Dupont)

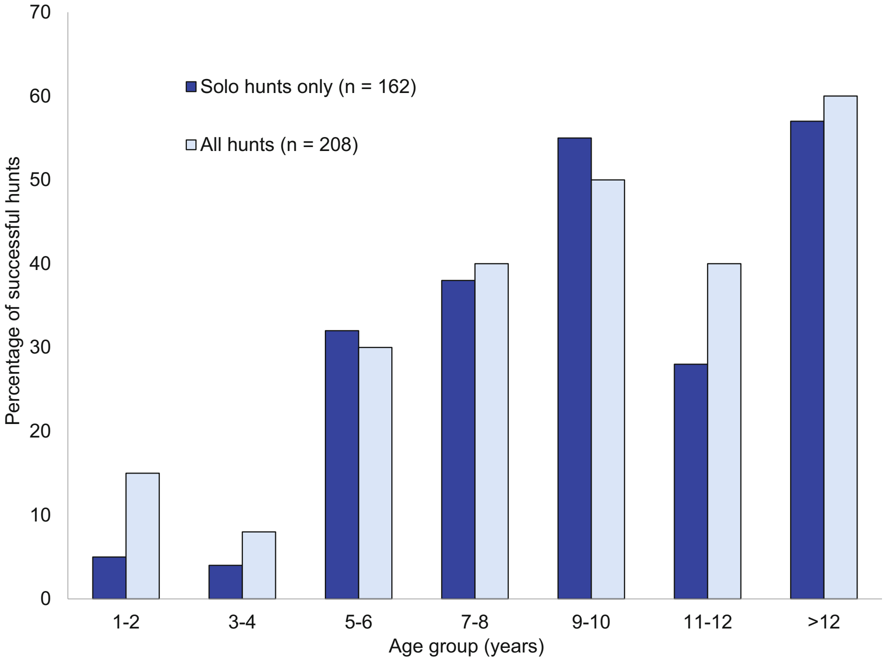

Fig. 5.9 Effects of age on the percentage of successful hunts by spotted hyenas in the Maasai Mara Reserve in Kenya. Redrawn with permission from Holekamp et al. (1997) (Figure 6, p. 12), Journal of Zoology, 242

to break open the leg bone of a giraffe and other large bones to access the nutritious marrow hidden inside (Fig. 5.7, Kruuk, 1972).

The large body size of adult females appears to have an evolutionary advantage, the largest adult female hyenas enjoy the highest lifetime reproductive success (Swanson et al., 2011). Although low-ranking females who survive to adulthood are generally larger than their high-ranking counterparts, and although their larger size may allow them to intimidate males better, body size is not a good predictor at all of rank, and even small subadult females can dominate males (Holekamp & Smale, 1993). Instead, we hypothesize that the larger body size of the low-ranking females may help them by allowing them to bring down animals like wildebeest and topis (*Damaliscus lunatus jimela*) on their own more efficiently than if they were smaller (Holekamp et al., 1997). That is, if a large body size appears to be especially helpful to low-ranking females, then a large body size may enhance the ability of large females to kill, steal, or process food more effectively than smaller females. Further data are required to understand the extent to which selection on large body size in female spotted hyenas is more strongly linked to running speed and hunting ability (e.g., long legs for cursorial hunting) or increased feeding performance at kills. The combined evolutionary history of bone-cracking (an attribute unique to Hyaenids) and its associated morphology, hunting of live prey, and intensive feeding competition in groups, is unique among mammalian carnivores. These combined traits likely led to the evolution of female aggressiveness, females that are slightly stronger and larger than males, and female dominance in spotted hyenas.

5.5 Social Coordination and Cognitive Demands of Hunting

Because group hunting permits individuals to capture prey animals many times larger than can be captured by a lone hunter, researchers have speculated that group hunting in gregarious carnivores from wolves and lions to spotted hyenas likely requires intelligent coordination and division of labor to facilitate coordinated attacks (e.g., Guggisberg, 1962; Peters & Mech, 1975). Comparative studies suggest that the co-evolution of large brains (relative to body size) is an important correlate of cooperation among mammalian carnivores (Creel & Creel, 1991; Finarelli & Flynn, 2009; Smith et al., 2012). Others have suggested that understanding the evolution and mechanisms of cooperation among mammalian carnivores can even provide useful insights into understanding early hominids (Hill, 1982; Kaplan & Hill, 1985; Schaller & Lowther, 1969; Smith et al., 2012).

Spotted hyenas possess the ability to solve the same problem in multiple ways and regularly use a single behavior to solve multiple problems, traits that are often characteristic of intelligent mammals living in complex societies, including monkeys and apes (Holekamp et al., 2007). Thus, it is possible that spotted hyenas could also engage in cognitively demanding problem-solving when attempting to engage in cooperative hunting. However, all current evidence available from spotted hyenas raises the provocative notion that not all coordinated group hunting in large carnivores requires primate-like mental processes or even role specialization (Holekamp et al., 2007). Instead, the most parsimonious explanation is that social facilitation and simple rules of thumb, such as “Take your own best line of approach to the target prey animal, unless another hunter already occupies that position” may explain patterns of cooperative hunting in spotted hyenas (Holekamp et al., 2000).

The lack of evidence for complex mental algorithms for cooperative hunting by spotted hyenas is of particular interest since multiple lines of evidence indicate that the social complexity and social intelligence of spotted hyenas exceeds that of other mammalian carnivores (Figs. 5.10 and 5.11). For example, spotted hyenas regularly form coalitions (Engh et al., 2000; Smith et al., 2010), reconcile after fights (Smith et al., 2011; Wahaj et al., 2001), discriminate among social partners (Smith et al., 2007; Wahaj et al., 2004), innovate to solve problems (Benson-Amram & Holekamp, 2012), and follow leaders to coordinate collective behavior (Smith et al., 2015, 2016). Thus, spotted hyenas make adaptive social decisions, and when asked to solve a foraging problem on their own, spotted hyenas innovate by inventing novel solutions using a diversity of exploratory behaviors (Benson-Amram & Holekamp, 2012; Drea & Carter, 2009). For example, in captivity, pairs quickly learned to tug two ropes in unison to earn a food reward without training and experienced hyenas helped inexperienced partners solve this cooperation task (Drea

Fig. 5.10 Spotted hyenas live in socially complex groups in which they coordinate multiple forms of collective action outside of the hunting domain, such as forming coalitions directed toward intruders and groups mate (photos by Kate Yoshida and David Greene)

& Carter, 2009). In their natural habitat, free-living hyenas with the greatest diversity of exploratory behaviors, a measure similar to creativity in humans, are most likely to solve a puzzle box for a food reward (Benson-Amram & Holekamp, 2012).

Foraging by spotted hyenas is more complex than in other social terrestrial carnivores because hyena hunting and feeding involve interactions among group members of low mean relatedness (Van Horn et al., 2004). For example, hyenas hunt

Fig. 5.11 Spotted hyenas offer new insights into animal minds based on their interactions with an experimental box containing a food reward during a test trial in the natural habitat in Kenya (photo by Sarah Benson-Amram)

cooperatively with group-mates that include kin and non-kin (Holekamp et al., 1997), and similar to mammal hunting killer whales (*Orcinus orca*, Reisinger et al., 2017), preferentially tolerate some non-kin over others in feeding contexts (Smith et al., 2007), suggesting a degree of meat sharing (feeding tolerance) among unrelated spotted hyenas. This is in contrast to patterns for other carnivores, such as lions and African wild dogs (*Lycaon pictus*, Creel & Creel, 1995; Packer et al., 2001), that only hunt cooperatively and share meat within family units (reviewed by Clutton-Brock, 2009). Interestingly, male coalitions of cheetahs (*Acinonyx jubatus*) also sometimes share food with non-relatives (Mills & Mills, 2017). Field experiments aimed at revealing the cognitive processes involved in joining kin and non-kin in group hunting should further elucidate the rules governing this form of cooperation.

Given their social complexity and their ability to innovate to accomplish foraging tasks, one might also expect spotted hyenas to engage in socially complex foraging strategies when hunting. In several species of socially complex mammals, there is evidence that members of different populations hunt using different tactics. For example, only some populations of Indo-Pacific bottlenose dolphins (*Tursiops sp.*) engage in sponging behaviors, the carrying of sea sponges to protect their rostrums from sharp rocks when hunting (Krützen et al., 2005) and cooperative tendencies, as well as prey selection, varies among chimpanzee (*Pan troglodytes*) populations (Newton-Fisher, 2007). Although we currently lack evidence of among clan differences in social hunting strategies, there are clear differences in ways hyenas in different regions track migratory prey.

In the Serengeti of Tanzania spotted hyenas commute to capture migratory prey for 46–62% of the year, with a mean commuting distance of 40 km and each trip spanning from 3 to 10 days (Hofer & East, 1993) whereas those of the Maasai Mara of Kenya usually only hunt within their home territories (Holekamp et al., 1997). Future work should investigate potential interpopulation differences in social hunting strategies and prey selection across multiple clans, both of which are likely driven by local ecology.

Although spotted hyenas may use one or more communicative behaviors to coordinate grouping behavior prior to setting off to hunt, we currently lack definitive evidence of advanced planning of hunting behavior per se in spotted hyenas. However, Kruuk (1972) speculated that individual spotted hyenas may use long-distance calls to recruit additional hunting partners prior to starting a hunt and there is some evidence that hyena hunters produce rallying vocalizations, called "whoops," to gather scattered group members where their assistance is needed to acquire or defend resources (East & Hofer, 1991; Gersick et al., 2015). We also know that spotted hyena greetings, which occur when two hyenas stand parallel to one another, lift their legs, and each sniffs the other's anogenital region (East et al., 1993; Kruuk, 1972), serve multiple social functions. Greetings promote social cohesion, reduce conflicts at reunions, and promote coalition formation (Smith et al., 2011, 2015; Wahaj et al., 2001). Although the role of greetings in promoting cooperative hunting remains to be studied for spotted hyenas, African wild dogs (Creel, 1997; Creel & Creel, 2002) and gray wolves in North America (Mech, 1970) regularly engage in greetings and other social "rallies" prior to setting off on a group hunt. Thus, the role of whoops and greetings in rallying hunting parties also warrants further study in the spotted hyena.

Role specialization during hunting has been documented for a few animals such as dolphins (Gazda et al., 2005), African lions (Heinsohn & Packer, 1995; Stander, 1992), and Taï chimpanzees, *Pan troglodytes verus* (Boesch, 2002). In these species, particular individuals within the social group repeatedly assume the same specific role when hunting. However, there is little evidence for role specialization as a cooperative hunting strategy among spotted hyenas. Instead, spotted hyenas appear to follow simple rules of thumb such as "Move wherever you must during a chase to keep the selected prey animal between you and another hunter" (Holekamp et al., 2000). However, some categories of individuals (rather than specific individual animals) are significantly more likely to initiate or participate in hunting than others. Low-ranking females hunt at significantly higher rates and in smaller hunting parties than do high-ranking individuals (Holekamp et al., 1997, Fig. 5.12). This finding is particularly interesting given that in many other circumstances adult females, particularly high-ranking ones, most often assume leadership roles to promote collective behaviors (Smith et al., 2020; Smith & van Vugt, 2020). For example, high-ranking adult females are most likely to initiate group travel (Holekamp et al., 2000; Smith et al., 2015), coalition formation (Engh et al., 2000; Smith et al., 2010), and between-group conflicts ("clan wars," Boydston et al., 2001).

Because adult male hyenas are physically smaller and weaker than their adult female or large juvenile followers, why do they initiate hunts most often (Holekamp

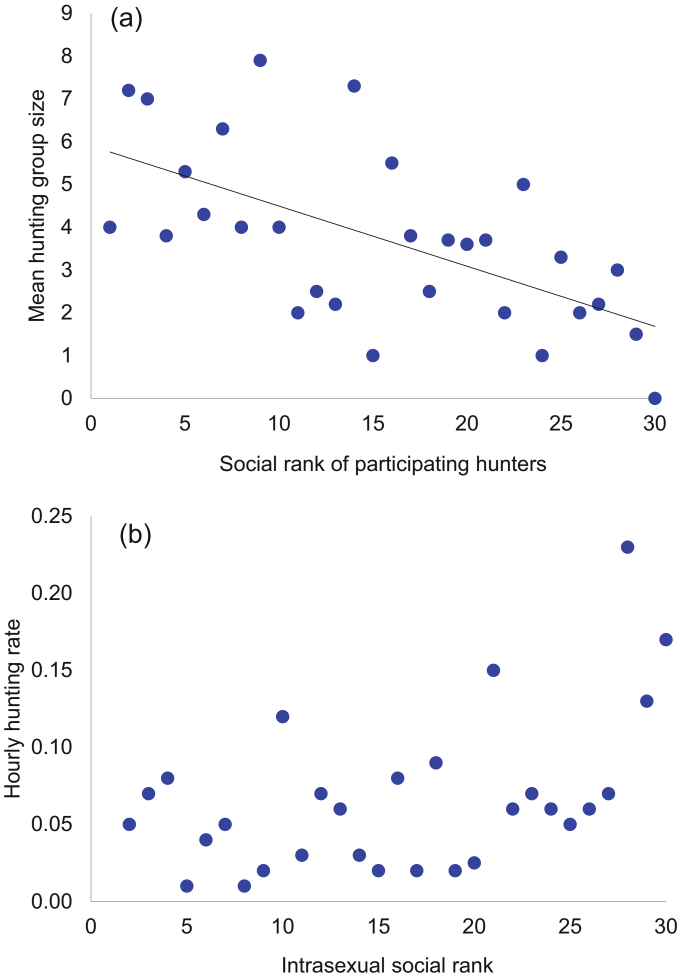

Fig. 5.12 Effects of adult female social rank on (**a**) mean hunting group size and (**b**) hourly rates in spotted hyenas. Redrawn with permission from Holekamp et al. (1997) (Figures 3 and 5, pp. 8 and 10), Journal of Zoology, 242

et al., 1997)? This is likely because immigrant males in each clan have the lowest priority of access to food (Frank, 1986; Kruuk, 1972; Tilson & Hamilton, 1984). Low-ranking individuals must therefore initiate hunts more often than high-ranking individuals because they are most likely to be displaced from carcasses by socially-dominant animals once kills are acquired through displacements of low-ranking males by high-ranking ones. Thus, "cooperative aiding" in hunts by dominant followers may be more akin to free-riding than social support per se, and high-ranking individuals often also benefit from cooperative defense of kills from lions, which are their main interspecific competitors.

A review of 13 studies documents that spotted hyenas lose many kills to lions (70%, versus only 35% lost by lions to hyenas, Périquet et al., 2015). Because even the largest spotted hyena is much smaller than a lion, multiple spotted hyenas must join forces to defend kills from kleptoparasitism by lions (Fig. 5.13). It is in this context that cooperative strategies appear most complex, group defense involves many more hyenas cooperating when spotted hyenas join forces against lions or during clan wars than is typical for either hunting itself or most other forms of cooperative behavior (Smith et al., 2008, Fig. 5.14).

5.6 Cooperative Hunting Improves Hunting Success

Cooperative hunting generally improves hunting success in spotted hyenas, and members may only capture certain prey species (e.g., adult zebra, buffalo, giraffe) when hunting cooperatively with group-mates (Holekamp et al., 1997). Hunting group size is defined based on the number of hyenas participating at the end of a chase. That is, a solo hunt was one conducted from start to finish by a single hyena whereas a group hunt ended with 2 or more participating hyenas (Holekamp et al., 1997). Overall, two or more adults are about 25–35% more successful in capturing targeted ungulate prey than are solo hunters (Cooper, 1990; Gasaway et al., 1991; Holekamp et al., 1997; Kruuk, 1972; Mills, 1990), but quantitative measures of this advantage vary across study areas and with the prey species hyenas are targeting.

In the Serengeti of Tanzania, cooperative hunting increased capture success by 33% and 34%, respectively, when targeting gazelle and wildebeest (Kruuk, 1972). For example, lone hunters only captured wildebeest calves in 15% of attempts but captures increased to 23% for pairs and to 31% for hunting parties of three or more (Kruuk, 1972). In the Kalahari Desert, the increased benefit of cooperative hunting was reported as 31% for gemsbok, 39% for wildebeest, and 50% for young eland (Mills, 1990). In the Maasai Mara of Kenya, Holekamp et al. (1997) demonstrated the importance of cooperation for hunting success by demonstrating that the probability of an individual hyena successfully capturing a prey animal increases by approximately 20% with the presence of a second hunter, but that the addition of subsequent hunters does not significantly increase hunting success. These data were further supported by Smith et al. (2008) who demonstrated the extraordinary costs of ensuing feeding competition incurred by pairs of hunters compared to solo hunters. Taken together, these findings suggest that while spotted hyenas are more likely to capture prey when hunting cooperatively rather than on their own, there are diminishing returns for increasing hunting party size beyond that necessary for the effective capture of a particular prey species. We discuss these trade-offs in more detail in the next section.

Fig. 5.13 Spotted hyenas routinely engage in complex forms of cooperation when joining forces with clan members to direct coalitionary aggression toward lions (which are three to five times larger than a single hyena). Multiple spotted hyenas are therefore required to cooperatively defend kills produced by spotted hyenas hunting from kleptoparasitism by lions (photos by Stephanie Dloniak and David Greene)

5.7 Feeding Competition Limits Social Cohesion

Despite the obvious benefits of enhanced prey capture from group hunting, roughly three-quarters of hunts are made by lone hyenas and this has puzzled many researchers (Cooper, 1990; Holekamp et al., 1997; Kruuk, 1972). In the Maasai Mara of Kenya, most species of prey were pursued by lone hunters, and the mean hunting group size for these spotted hyenas is only 1.7 hyenas (Smith et al., 2008, Fig. 5.14), varying with the size of the prey hunted with mean ± S.E. hunting group sizes for 1.2 ± 0.1 for topi, 1.7 ± 0.3 for impala, 2.1 ± 0.1 for Thompson's gazelles, 2.9 ± 0.3 for wildebeest, and 9.1 ± 0.5 for zebra (Holekamp et al., 1997). Detailed

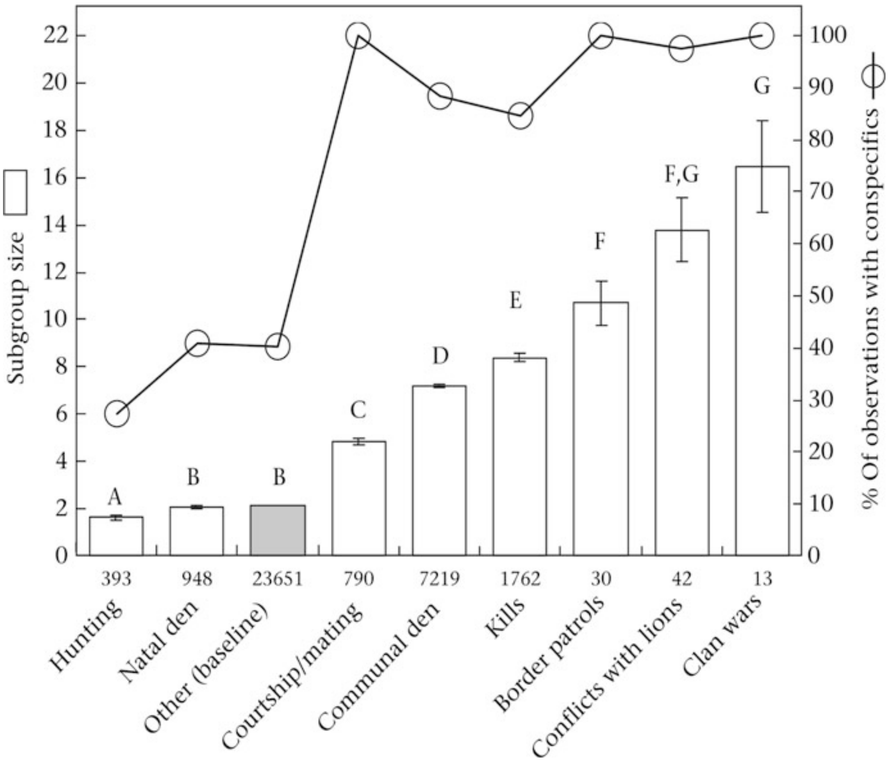

Fig. 5.14 Mean ± SE subgroup size and proportion of observations in which spotted hyenas were found in subgroups containing more than one individual as functions of the context in which groups formed. Sample sizes, shown below each bar, represent numbers of observation sessions assigned to each context. Different letters indicate statistically significant differences between contexts after correcting for multiple testing. The shaded bar represents the baseline value of subgroup size occurring in "other" sessions, against which other groups were compared. Reprinted with permission from Smith et al. (2008) (Figure 4, p. 627), Animal Behaviour, 76(3)

Fig. 5.15 Feeding subgroup size during the first 15 min after solo hunters or pairs of hunters killed ungulates of similar size ($N = 9$ matched pairs of hunts). Feeding competition is more intense when spotted hyenas hunt cooperatively than when they hunt alone. Reprinted with permission from Smith et al. (2008) (Figure 7, P. 630) from Animal Behaviour, 76(3)

observations of grouping patterns before and after hunting offer definitive insights into why cooperative hunting is so rare.

One long-term study in the Maasai Mara compared the numbers of new arrivals and total competitors present 5, 10, and 15 min after either solo hunters or pairs of hunters successfully captured wildebeest or topi (Smith et al., 2008, Fig. 5.15). They found that the total numbers of competitors present at kills only increased significantly over these 15 min when multiple hyenas cooperatively captured prey. In the first five minutes, an average of two more competitors arrived at kills made by pairs than at kills made by solo hunters. Furthermore, ten minutes after prey capture, more than six competitors were present at kills made by two hunters, whereas lone hunters almost always continued to feed alone and very few new conspecifics arrived at any of the kills sampled more than 10 min after prey capture. These investigators also found that, although the most common hunting group size is one hyena, the average feeding group size was eight, and feeding groups contained as many as 56 hyenas all competing to feed on the same kills (Fig. 5.14). These data suggest that, by hunting alone, an individual may feed for up to 15 min without competitors, consuming up to 20 kg of flesh, a mass that greatly exceeds its daily energy requirement. Thus, solo hunting generally increases an individual's net energy gain (Fig. 5.16). The costs of competition are particularly high for low-ranking individuals because although the amount of food, on average, that any individual consumes declines as foraging group sizes increase, dominance rank determines priority of access to food during these competitive feeding situations. Moreover, once the food is obtained directly from hunting, or in fewer cases scavenged from the landscape, the number of spotted hyenas that gather to feed at a carcass roughly match the relative mass of the carcass (Fig. 5.17, Smith et al., 2008).

Prey abundance influences prey selection, the tendency for hyenas to spend time with conspecifics (rather than alone), the density of spotted hyenas in an area, and the average sizes of spotted hyena clans, hunting parties, and foraging groups

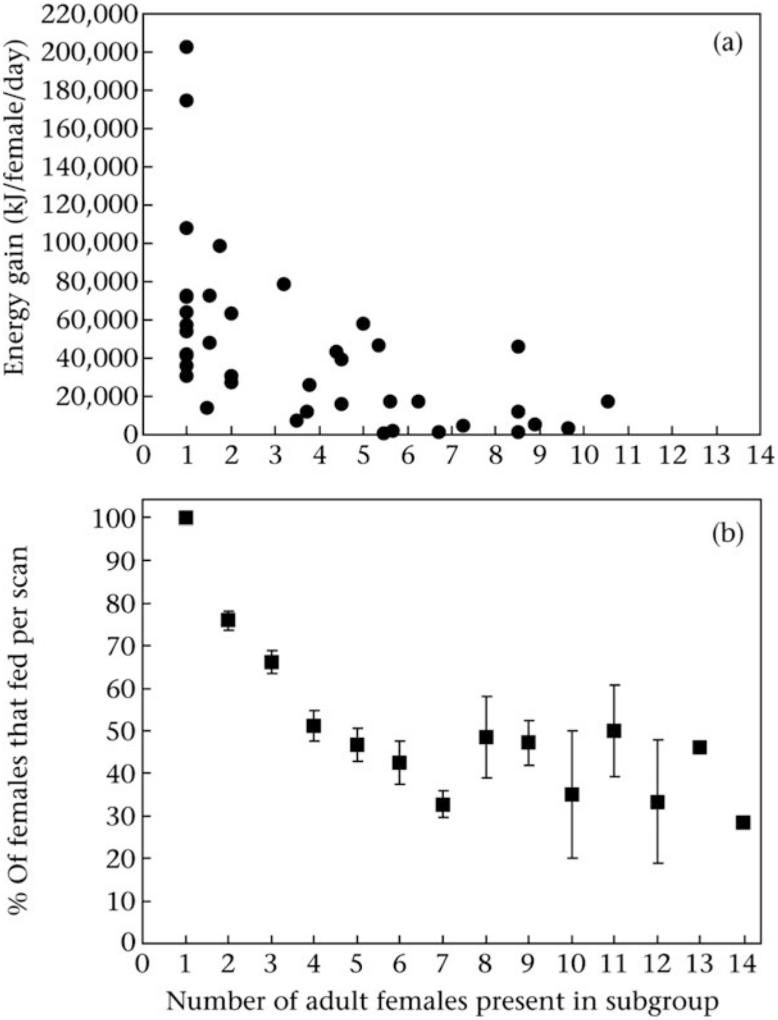

Fig. 5.16 (**a**) Per capita daily energy gain as a function of the number of adult females present at fresh ungulate kills ($N = 41$) and (**b**) mean ± SE percentage of adult females observed feeding per scan as a function of the number of adult females present within each subgroup at kills ($N = 426$ sessions). Reprinted with permission from Smith et al. (2008) (Figure 8, page 630), Animal Behaviour, 76(3)

(Figs. 5.14, 5.17, and 5.18). Spotted hyenas also generally allocate hunting efforts to prey species that are most locally abundant (Cooper, 1990, Holekamp et al., 1997, Kruuk, 1972). Moreover, during times of the year when resident ungulates are joined by migratory wildebeest and zebra, hunting success for spotted hyenas also generally increases (Holekamp et al., 1997). Although adult buffalo are particularly difficult

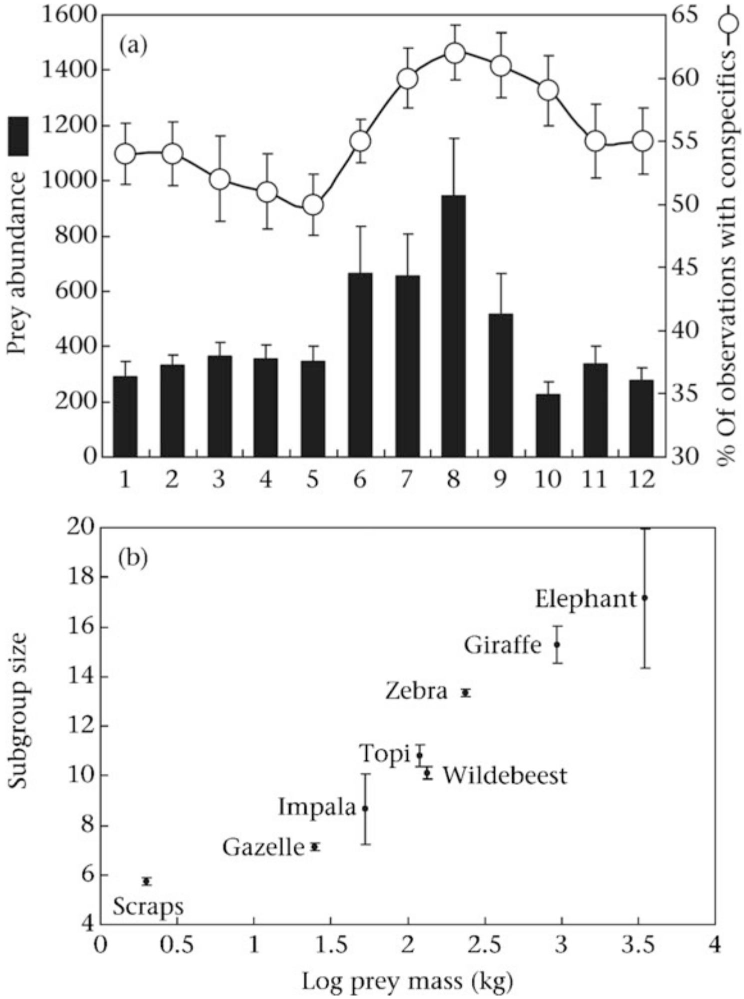

Fig. 5.17 Monthly mean ± SE (**a**) numbers of prey animals counted each month during biweekly ungulate censuses and percentage of observation sessions in which spotted hyenas were found in subgroups containing more than one individual and (**b**) subgroup sizes as a function of prey mass from observations at sessions with scraps ($N = 1315$) or fresh kills of Thomson's gazelle ($N = 382$), impala ($N = 53$), wildebeest ($N = 706$), topi ($N = 108$), zebra ($N = 193$), giraffe ($N = 29$), and elephant ($N = 13$). Reprinted with permission from Smith et al. (2008), Figure 6 (page 629), Animal Behaviour, 76(3)

for spotted hyenas to capture even when hunting in groups, spotted hyenas allocate more hunts toward capturing buffalo prey when buffalo are relatively abundant in the area (Höner et al., 2002). Spotted hyenas hunt some of the most energetically valuable of the ungulates (e.g., buffalo, giraffe, and plains zebra) at lower rates than they hunt most smaller ungulates (Hayward, 2006). This is likely because medium-

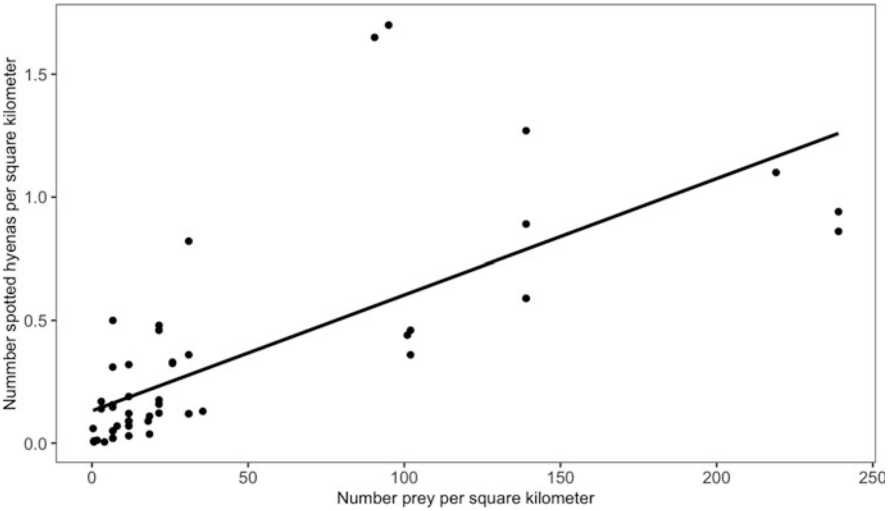

Fig. 5.18 The positive relationship between the densities of prey and spotted hyenas per square kilometers from a total of 51 published from 29 unique sites across sub-Saharan Africa ($R^2 = 0.53$, $F_{1,50} = 55.6$, $P < 0.00001$, regression line: $y = 0.005x + 0.131$). Data drawn from published studies listed by Holekamp and Dloniak (2010) in their Table 3 and new information from Bauer (2007), Bauer et al. (2015), Bohm (2012), Cozzi et al. (2013), Creel and Creel (2002), Crosmary et al. (2018), Davis (1964), Gasaway et al. (1991), Graf et al. (2009), Henschel et al. (2014), Kirsten et al. (2017), Loveridge et al. (2016), Mills (2006), M'soka et al. (2016), Purchase (2004), Smuts (1976), Tilson and Hamilton (1984), Trinkel (2003)

sized gazelles and wildebeest are easily captured by lone hunters, but some prey, such as zebras, are only effectively captured by large groups (e.g., 9–11 spotted hyenas, Holekamp et al., 1997; Kruuk, 1972; Mills, 1990). Hunting group size consistently increases with size of the selected prey (Cooper, 1990; Kruuk, 1972). Future studies are needed to understand the precise effects of prey size and hunting group size on hunting efficiency (per capita consumption).

5.8 Conservation Implications of Behavioral Flexibility While Foraging

Despite their striking abilities to capture large prey under challenging circumstances, most terrestrial species in the mammalian order Carnivora have experienced substantial population declines and range contractions over the past two centuries (Ripple et al., 2014). With human populations rapidly changing landscapes across the globe, many carnivores with their large home ranges, high energetic demands, and conflicts with humans are vulnerable to habitat fragmentation, overhunting, and poisoning (Woodroffe & Ginsberg, 1998). Compared to other species of large mammalian carnivores, however, spotted hyenas are coping with anthropogenic threats relatively well. They are ecologically and numerically dominant to other carnivores in sub-Saharan Africa (Holekamp & Dloniak, 2010). This is partly due to the extraordinary behavioral, physiological, and morphological flexibility of spotted hyenas. They occupy a diverse range of habitats across Africa, including savanna, desert, swamps, woodland, and montane forest up to 4000 m of elevation and, like most carnivores, rarely require direct access to water (Holekamp & Dloniak, 2010). They even co-exist in areas with high human densities, such as in urban centers in northern Ethiopia (Abay et al., 2011; Yirga et al., 2013, 2017).

The apparent success of this species is in part attributed to their combined powerful bone-cracking morphology, their ability to chase down and kill antelope, and their behavioral flexibility, which permits them to forage on foods ranging from termites to elephants and to hunt the broad range of ungulate prey discussed earlier in this chapter, depending upon the relative abundance and species of prey locally available. Thus, unlike lions, adult spotted hyenas are efficient extractive foragers endowed with bone-cracking jaws capable of meeting their energetic demands through scavenging. Because lions and spotted hyenas actively compete for access to the same prey items (Hayward, 2006), the human killing of lions can even act to indirectly benefit spotted hyenas in highly disturbed areas (Green et al., 2018; M'soka et al., 2016). For example, anthropogenic disturbances acting to decrease lion numbers are associated with an increase in juvenile survival by spotted hyenas in Masai Mara National Reserve, Kenya (Green et al., 2018). Nevertheless, despite its large overlap in its foraging niche with lions, the spotted hyena's flexible foraging habits likely permit its success across its geographic range (Hayward, 2006; Yirga et al., 2012). Moreover, the immune systems of spotted hyenas appear to cope far better with bacteria and diseases acquired while foraging than those of sympatric carnivores without an evolutionary history of foraging on carrion (Flies et al., 2016).

Further insights about how anthropogenic activity shapes varied aspects of a spotted hyena's behavioral repertoire relevant to hunting decisions can be gleaned from comparing the behavioral responses of individuals adjacent to human settlements and those at a relatively undisturbed part of the same national park. For example, spotted hyenas born in disturbed areas are more likely to interact with novel objects and are more exploratory than juveniles residing at less disturbed sites (Greenberg & Holekamp, 2017; Turner et al., 2020). In contrast to the results of studies on birds and small mammals, juveniles living in disturbed areas are more—not less—risk averse than those born in less disturbed ones (Greenberg & Holekamp, 2017; Turner et al., 2020). Moreover, although highly social hyenas live the longest, there is stabilizing selection on boldness suggesting trade-offs between the costs and benefits associated with risk-taking in the presence of lions (Yoshida et al., 2016). Bold or shy females had shorter lifespans than those in the middle of the shy-bold continuum (Yoshida et al., 2016).

Despite this, the extraordinary plasticity of spotted hyenas appears to permit them to modify their diets more easily than is possible for other sympatric carnivore species (Holekamp et al., 2012). Their flexible dietary niche has some consequences for their social structure. First, individuals spend significantly more time away from conspecifics when ungulate prey are relatively scarce (e.g., fewer ungulates, Smith et al., 2008) and social networks are generally sparser during these periods of time (Holekamp et al., 2012). However, spotted hyenas still preferentially associate with kin over non-kin during times of prey scarcity (Holekamp et al., 2012) and are significantly more likely to engage in elaborate greetings with kin at reunions during times of prey scarcity to reinforce social bonds (Smith et al., 2011).

Despite being a conservation success story compared to other large carnivorous mammals, and despite retaining the status of the most abundant carnivore in Africa today, populations of spotted hyenas are declining outside of protected areas. Humans represent a major mortality source (Watts & Holekamp, 2009), and humans often directly kill hyenas in response to (or in fear of) livestock depredation (Kissui, 2008; Kolowski & Holekamp, 2006). Unfortunately, domesticated livestock are easy prey for spotted hyenas living in human-altered landscapes (Fig. 5.19, Hoffmann & Montgomery, 2022; Kolowski & Holekamp, 2006; Mukeka et al., 2019). Intentional poisoning by humans can influence social and demographic patterns of spotted hyenas (Holekamp et al., 1993), and patterns of human activity can also influence their hunting behavior, thereby restricting access to prey (Mills & Harris, 2020). Thus, spotted hyenas are being negatively affected by humans. For example, anthropogenic disturbance by pastoralist activity is also a stressor in their lives (Van Meter et al., 2009), influencing activity patterns (Kolowski et al., 2007). Although not yet empirically studied, we suspect that the disruption of social units by humans negatively influences the fitness of individuals and reduces group efficiency. This has important consequences for the loss of African grasslands which are of great ecological, cultural, and economic importance.

Because spotted hyenas are relatively easy to monitor over long periods and more ecologically resilient to human perturbations than are other large African carnivores, long-term studies on spotted hyenas offer a useful indicator of how and the extent to which large carnivores can cope with and respond to human-induced rapid environmental change (Smith et al., 2017; Green et al., 2019). Many questions remain regarding the potential for anthropogenic factors to affect the hunting and feeding habits of these top predators, including effects on their patterns of cooperation and competition, ranging from social cohesion to group-level phenomena such as group defense, in this socially complex and highly intelligent mammalian carnivore.

Fig. 5.19 Like many large carnivores, spotted hyenas are in conflict with humans over resources, and they sometimes kill livestock such as the sheep (above) and cow (below) as shown here. Spotted hyenas are commonly killed in response to livestock depredation, even within protected areas (photos by Wilson Kilong and Joseph M. Kolowski)

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Chapter 6
Hunting Behavior and Social Ecology of African Wild Dogs

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Abstract African wild dogs (*Lycaon pictus*) are cooperatively breeding highly social hyper-carnivores. The basic social unit is the pack, which in its simplest form revolves around an unrelated dominant pair and their offspring. Group

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cohesion is central to pack social dynamics, with litters reared collectively, decisions to move made semi-democratically, and hunting occurring collectively—if not collaboratively—over home ranges of several hundred square kilometers. These large ranges coupled with strong Allee effects make this species extinction prone, and urgent conservation actions require a detailed fundamental understanding of the complex inter-pack and inter-individual dynamics that make up the social fabric of this iconic species. In this chapter, we provide an overview of African wild dog social adaptations, particularly about hunting. We present a conceptual framework illustrating the common phases and transitions of a typical hunt, populating descriptions of these phases with examples from different regions and environments within the extant range. Finally, we consider the direct and indirect challenges faced by African wild dogs as they navigate the Anthropocene, including climate impacts and the need to consider complex social dynamics within population management approaches.

Keywords *Lycaon pictus* · Hunting · Sociality · Kleptoparasitism · Feeding · Prey · Hunting success · Competition · Cooperation

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Artistic rendering by Britney Danials. Original photo credit: Bobby-Jo Vial

Where giants grey meandering browse, golden moths from winter boughs
Painted piles digest the day; as shadows lengthen, fade away
Elder hunters—dust their wake—running hard to claim their stake
As scrambling stragglers reach the site, incumbents leave without a fight
Youngsters eat unjust deserts, while others orbit keen, alert
When all but skin and bones are gone, the bloodied barrels leave as one
Remotest woodland's cool embrace, provides a temporary resting place
Black satellites survey the night, as hunger builds to dawn's new light
– N.R. Jordan

6.1 Introduction

This chapter focuses on social strategies and adaptations in African wild dogs, particularly those related to the acquisition and defense of food. African wild dogs are highly social by nature (Kat et al., 1996). A single female most often monopolizes breeding in the pack (Frame et al., 1979, but see Marneweck, Druce, et al., 2019; Spiering et al., 2009), and many aspects of individual survival and fitness in this obligate cooperative breeder are related to pack size, environmental factors, and social behavior (Buettner et al., 2007; Marneweck, Druce, et al., 2019; McNutt and Silk, 2008; Rabaiotti et al., 2021). After briefly considering inter-pack dynamics, we center this chapter on reviewing and summarizing within-pack social dynamics, focusing on strategies for the acquisition, retention, and consumption of food. We also consider the potential impact of heterospecific competition, and particularly kleptoparasitism, in shaping the social structure of African wild dogs.

In compiling this chapter, we have drawn on expertise and available information from across the extant range of the species, noting that varying data and insights are available from each region. Acknowledging and exploring the variation in social behavior under a range of ecological conditions within the extant range is necessary to draw as full an account as possible. Nevertheless, we have attempted to frame the core of this chapter around key phases and transitions that characterize the core features of African wild dog social life and hunting behavior. This provides a useful framework to explore variation in hunting and hunting-related behavior under various social and environmental conditions while emphasizing the core components of an African wild dog's social life.

6.2 The Most Social Canid?

While the basic social system of canids is rooted in monogamy and about 85% of canids are solitary (Kleiman, 1977), some are flexible in their social structure, adopting a plastic approach to group size and sociality according to their environment (Macdonald, 1979). Black-backed jackals (*Lupulella mesomelas*), for example, can live in pairs or packs, depending on the resources available (Jenner et al., 2011), retaining helpers where resources are sparse and home ranges are larger as a consequence. Elsewhere, canids rely on group-living, with offspring survival often increasing with group size (Marneweck, Druce, et al., 2019). Social behavior is so fundamental to African wild dogs that they have been described as the most social canid (Kat et al., 1996).

The pack is the core social unit for African wild dogs. At its most basic level, a pack can comprise an opposite-sex pair of unrelated adult individuals, and packs theoretically extend to any group size beyond—but always including—that core unit. Despite extremely rare occasions where pairs successfully raise offspring (Woodroffe et al., 2009), African wild dogs are considered obligate cooperative breeders, with larger packs generally producing larger litters (Malcolm & Marten 1982; Marneweck, Druce, et al., 2019; McNutt & Silk, 2008; Woodroffe, O'Neill, et al., 2020), with higher pup survival overall (Creel et al., 2004; Gusset & Macdonald, 2010; Marneweck, Druce, et al., 2019; Rasmussen et al., 2008; Woodroffe et al., 2017). In general, older females in large packs raise a high proportion of pups (Marneweck, Druce, et al., 2019; McNutt & Silk, 2008). As a species, and in relation to their body size in particular (Geffen et al., 1996), female African wild dogs produce very large litters, sometimes numbering up to 22 pups (McNutt & Silk, 2008).

Pack size is crucial to many aspects of African wild dog society beyond pup-rearing. Increasing pack size increases the per capita gains from hunting (Creel & Creel, 1995), and increases survival more generally (Buettner et al., 2007; McNutt & Silk, 2008), strongly suggesting that both survival and reproduction might be compromised if pack size were too small (Courchamp et al., 2000). However, there is also an upper limit to pack size in different contexts, for example, the per capita benefits of hunting peak at a certain pack size before declining (Creel & Creel, 1995), at least partially explaining why mean contemporary pack size seems to center around 5–15 adults and yearlings across their extant range (Table 6.1), with packs of 50 or so only very rarely reported (Frame et al., 1979). Indeed, though such larger packs may occur for short periods, they are likely to be unsustainable in the long term. Data from Selous (Tanzania) suggest an optimal pack size of approximately 12–14 individuals (Creel & Creel, 1995), which suggests that earlier popular accounts of "super-packs" of several hundred dogs (Kingdon, 1988 in Lovett, 2016) are almost certainly apocryphal tales. It is also worth noting that pack size is related to the age of the pack, with older packs tending to be larger due to accummulated recruitment from a larger number of previous litters. Furthermore, where breeding and dispersal occur seasonally (Woodroffe, O'Neill, et al., 2020), group size may also fluctuate throughout the year. Nevertheless, the pack unit is crucial to African wild dogs, and social behaviors, conventions, and the costs and benefits of these enhance our understanding of this globally endangered species.

While the factors underpinning optimal pack size are well understood and broadly consistent with other species, inverse relationships between prey densities and African wild dog population densities are less intuitive. Carnivores generally live at higher densities in areas with abundant food resources (e.g., Ethiopian wolves, *Canis simensis* (Marino, 2003); dingoes, *Canis lupus dingo* (Newsome et al., 2013)). By contrast, African wild dog densities are often inversely related to the density of their main prey (Mills & Gorman, 1997), and the resource dispersion hypothesis of larger group size in resource-rich patches (Macdonald, 1983) does not seem to apply to this species (Marneweck, Becker, et al., 2019; Marneweck, Marneweck, et al., 2019). It has been suggested that other factors—e.g., heterospecific competitors, and primarily lions (*Panthera leo*)—can have a significant impact on wild dog survival (Mills & Gorman, 1997) and the risk of encountering apex predators can shape behavioral responses and spatial and temporal activity patterns. For example, lions affect activity patterns of wild dogs (Cozzi et al., 2012), drive den site selection into craggy (van der Meer et al., 2013) or marginal habitat, and increase the associated commuting costs between these dens and prey-rich hunting grounds (Alting et al., 2021). Landscape features, however, can also impact inter-specific dynamics, with highly heterogeneous landscapes facilitating the coexistence of African wild dogs and their competitors (Davies et al., 2021), even in areas with high prey abundance (Marneweck, 2020). Optimal pack size and densities are clearly shaped by several extrinsic as well as intrinsic factors.

Table 6.1 African wild dog pack sizes across the extant range

Region	Country	Reserve/area	Area type[a]	Fenced?[b]	Pack size[d]				Reference
					Mean ± Error	Min-Max	N packs	Demographics counted[c]	
Southern Africa (free-ranging)	Botswana	Moremi GR	Protected	N	10.4	2–30	8	AY	Creel et al. (2004)
	Botswana	Moremi GR	Protected	N	8.8 ± 3.6^{SD}		5	A	Walker et al. (2017)
	South Africa	Kruger NP	Protected	P	11.1 ± 2^{SE}	2–30	13	AY	Marneweck, Marneweck, et al. (2019)
	South Africa	Kruger NP	Protected	P	10.4	2–36			Creel et al. (2004)
	Zimbabwe	Savé Valley Conservancy	Protected	Y (but leaky)	9.5	2–28		AY	Rabaiotti et al. (2021)
	Zimbabwe	Hwange NP	Protected	N	4.92 ± 2.7^{SD}		8	A	Tafadzwa (2013)
	Zimbabwe	Mana Pools NP	Protected	N	12.38 ± 5.5^{SD}		7	A	Tafadzwa (2013)
	Zambia	Lower Zambezi	Protected	?	7.2 ± 3.7^{SD}	3–12	12	A	Leigh (2005)
Southern Africa (managed metapopulation)	South Africa	Multiple	Protected	Y	11.0 ± 0.76^{SD}		5–20	AY	Davies-Mostert et al. (2015)
	South Africa	Hluhluwe-iMfolozi Park	Protected	Y	10.9	3–24	39	AY	Marneweck (2020)
East Africa	Tanzania	Selous GR	Protected	N	8.9	2–24		A	Creel et al. (2004)
	Tanzania	Selous GR	Protected	N	7.7 ± 0.23^{SE}	3–20		A	Creel and Creel (1995)
	Tanzania	Loliondo Game Controlled Area		N	16.5 ± 7.5^{SD}	4–25	8	AYP	Masenga (2011)

			Multiple land use / partially protected						
	Kenya	Samburu-Laikipia	Not protected	N	10.1 ± 4.9^{SE}	2–24		AY	Woodroffe, O'Neill, et al. (2020)
Central Africa[e]	Cameroon	N/A—across N Cameroon	Mixed	N	4.7	1–15	3		Breuer (2005)

SE, standard error; SD, standard deviation

[a] Protected, livestock-dominated, multi-use, other

[b] Y, fenced; N, unfenced; P, partially fenced

[c] A, adults only; AY, adults (>24 months) and yearlings (12–24 months); AYP, adults, yearlings and pups (<12 months)

[d] There is currently no convention for when pack size is recorded, and so some variation here may reflect seasonal fluctuations in pack size rather than differences between populations. For consistency between study populations, future studies should consider a pack-size census around whelping

[e] Only scarce and patchy records exist for this region

Many factors, including naturally low densities and related wide-ranging behavior, affect the persistence of African wild dogs in landscapes, and the species has been listed as endangered since 1990 (Ginsberg & Macdonald, 1990). While remnant subpopulations persist or have been reintroduced to several states (Bouley et al., 2021; Davies-Mostert et al., 2015; Gusset et al., 2008), the three largest contemporary free-ranging subpopulations are found in, or are contiguous with, the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA) in southern Africa, in East Africa (particularly in southern Tanzania), and the Greater Limpopo Transfrontier area (Kruger/Mozambique) again in southern Africa (Woodroffe & Sillero-Zubiri, 2020). The contribution of other subpopulations to the global population may be limited, and certainly their contribution to our understanding of African wild dog social ecology has been limited to date. Much of what we know of the species in terms of detailed social dynamics comes from the three core contemporary subpopulations (e.g., see Creel et al., 2004), but we have made a conscious effort here to try to incorporate insights from as broad a sample of their extant range as possible, including recently reintroduced packs and the metapopulation managed across a number of South African reserves in particular.

6.3 Hunting Success

African wild dogs are commonly referred to as the most successful hunters. It is however incredibly challenging to compare hunting success across species, due to inter-specific variation in hunting strategies. By contrast, variation in hunting success within a given species under different social and ecological conditions can provide insights into important determinants of hunting ecology and social behavior more broadly.

Determining hunting success clearly depends on how attempts are measured, but defining discrete hunts is challenging, and perhaps particularly so for a social cursorial hunter. This is because opportunistic encounters with—and capture of—prey can occur even when the packs are not overtly hunting. Nevertheless, an African wild dog hunt has been defined as a high-speed pursuit of prey >50m which either ended in a kill or with prey escape (including intense testing of prey at bay) (Creel & Creel, 1995). This is pragmatic as it allows the inter-kill effort (e.g., distance traveled) to be measured, and therefore, the costs of making a kill can be incorporated into calculations of the net per capita benefits of hunting in different social scenarios (Creel, 1997, 2001; Creel & Creel, 1995, 2002). The majority of work has been conducted on success as a factor of pack size, with limited insights into the specific social composition of packs.

Before Creel's pioneering work in this area, most studies simply considered hunting success as the proportion of hunts resulting in one or more prey captured. Using this approach—essentially ignoring the number of prey killed in discrete hunts, ignoring any differences in captured prey size, and simplifying the effort required to catch them to a count of hunts regardless of hunt length—small and large packs had almost identical hunting success (35% and 34%, respectively (Creel, 2001); see Supplementary Table 6.1 for data on hunting success in various situations across key parts of their extant range). When the gross benefits of pack hunting are considered, prey size increases with pack size in the Selous (Tanzania) population, which has been most intensively studied in this regard, largely because small packs (<10 dogs) tend toward killing impala (*Aepyceros melampus*), while larger packs focus on blue wildebeest (*Connochaetes taurinus*) (Creel, 2001). Hunting in larger packs also increased gross benefits due to larger packs also being more likely to make multiple kills in any given hunt. Such multiple kills per hunt are not uncommon either, with 22% of prey killed along with others in the same hunt (Creel, 2001). Increased pack size also reduces the gross hunting costs, with larger packs tending to pursue prey over shorter distances (Creel, 2001; Creel & Creel, 1995, 2002). As Creel eloquently argues, it is not the gross costs and benefits but the net benefit per capita that ultimately matters when looking at the drivers of cooperative hunting, and to understand this both he (Creel, 1997, 2001) and others (Gorman et al., 1998) first estimated the gross costs and gains of hunting. While each converted inter-hunt travel costs into units of energy in different ways, the two methods produced very comparable results estimating 3.04 MJ and 3.14 MJ per hour of travel, respectively (Creel, 1997; Gorman et al., 1998). Both studies also used prey size and estimated the total food consumed by the pack (Creel, 1997), allowing Creel to estimate the net gain per capita in different pack sizes.

Overall, data suggest that hunting favors living in as large a pack as possible both from a per capita energetic perspective and through the benefit of better defence of kills against kleptoparasites in some areas (Fanshawe & Fitzgibbon, 1993). There are of course many other factors that combine to constrain pack size and set an overall optimum pack size below what would be optimal if hunting were the sole driver. Constraints to African wild dog pack size are likely to include high reproductive skew (dominants near-monopolizing breeding), which incentivizes subordinates to disperse rather than join a burgeoning queue for a potential future breeding position in their natal pack. In summary, ecological interactions, including the acquisition and defence of food, favor large packs, but pack size is constrained by intra-pack reproductive competition (Creel, 2001) among other factors.

While the benefits of increasing hunting pack size (to a point) is now well understood, there is much left to discover on how variation in African wild dog pack composition beyond pack size affects hunting strategies and success. Neither hunting effort nor hunting success was related to adult sex ratio (Creel & Creel, 1995), and other social factors within the pack have not yet been considered in African wild dogs and likely represent a fruitful avenue of future research.

As noted above, while the merits of quantifying a species' hunting success are fraught with difficulty, especially for the questionable purpose of comparing with other species, a simple metanalysis of the hunting success of the species (kills/pack hunt) as presented in Table 6.2 should lay rest to popular claims that African wild dogs have over 80% hunting success. Including all published studies where the number of hunts and number of kills had been recorded, African wild dogs were successful approximately once in every three attempts.

Table 6.2 Summary of percentage hunting success (kills/hunt) of African wild dogs by prey species

Prey species	Prey age category	% success	Kills	Hunts
Thomson's gazelle	Unspecified age	32.6	44	135
	Juveniles (<2 months), incl. fawns	93.9	46	49
	Others (>2 months)	56	47	84
	Adolescents/half grown	69.2	18	26
	Adults (incl. >2 months)	34.3	99	289
	All individuals	**43.6**	**254**	**583**
Blue wildebeest	Unspecified age	52.3	34	65
	Juveniles (<6 months)	74	74	100
	Adults and others (>6 months)	54.8	23	42
	All individuals	**63.3**	**131**	**207**
Zebra	Unspecified age	44.3	27	61
	All individuals	**44.3**	**27**	**61**
Impala	Unspecified age	41.4	24	58
	All individuals	**41.4**	**24**	**58**
Grant's gazelle	Unspecified age	23	5	23
	Juveniles (<6 months)	100	7	7
	All individuals	**40**	**12**	**30**
Nyala	Unspecified age	71.4	20	28
	All individuals	**71.4**	**20**	**28**
Brown hare	Unspecified age	29.2	7	24
	All individuals	**29.2**	**7**	**24**
Warthog	Unspecified age	27.8	5	18
	All individuals	**27.8**	**5**	**18**
Topi	Unspecified age	0	0	6
	All individuals	**0**	**0**	**6**
Cape buffalo	Juvenile	0	0	3
	All individuals	**0**	**0**	**3**
Kudu	Juvenile	0	0	2
	All individuals	**0**	**0**	**2**
Springhare	Unspecified age	100	2	2
	All individuals	**100**	**2**	**2**
Red duiker	Unspecified age	100	1	1
	All individuals	**100**	**1**	**1**
Unspecified prey (direct obs.)	Unspecified age	34.2	525	1536
	All individuals	**34.2**	**525**	**1536**
Unspecified prey (remote data)	Unspecified age	21	116	564
	All individuals	**21**	**116**	**564**
All species	All data	30.3	2001	6603
All species	**Direct observations only**	**31.2**	**1885**	**6039**

Data compiled from Supplementary Table 6.1, and all studies cited therein

6.4 Social Dynamics Between Packs

6.4.1 *Acquiring and Defending a Territory*

African wild dogs are "spatially demanding," territorial large carnivores (Tshimologo, 2014), specialized for a hyper-carnivorous diet (Hayward et al., 2006). While the acquisition of food is an important aspect driving large home-range size in this species, and in carnivores in general (Gittleman & Harvey, 1982), ranges that extend over significantly larger areas than would be required for food alone are common in this species (Table 6.3 (Pomilia et al., 2015)). This further indicates that other factors contribute to determining optimal range sizes in different locations, and likely include inter-specific competition as described above.

Due to their inherent low density and wide-ranging nature, some historical accounts questioned whether African wild dogs were territorial at all, assuming that infrequent sightings were suggestive of a nomadic lifestyle. African wild dogs are in fact not nomadic, but they do inhabit large annual home ranges which overlap with those of neighboring packs. The highest level of home-range overlap between packs is recorded in Kruger National Park (South Africa; 30–38% of the outer 95%; (Marneweck, Becker, et al., 2019; Marneweck, Marneweck, et al., 2019; Mills & Gorman, 1997; Reich, 1981)). Packs in other regions showed varying degrees of overlap (Selous Game Reserve, Tanzania average 22% (Creel & Creel, 2002), Moremi Game Reserve, Botswana 7–22% (Jackson et al., 2017; Parker, 2010), 13% in Hluhluwe-iMfolozi Park, South Africa (Marneweck, 2020), 37% in Lower Zambezi National Park, Zambia (Leigh, 2005)). Such home-range overlap and infrequent sightings do not of course suggest an absence of territoriality. Indeed, African wild dogs engage in a number of territorial-linked behaviors including scent-marking (Jordan et al., 2013, 2014, 2016), and infrequent interactions between neighboring, overlapping packs (Jordan et al., 2017) are suggested to be due to temporal avoidance (Creel & Creel, 2002). Moreover, overlap of the core 50% of the home range is minimal, and packs may scent-mark more in the center of their range compared to the outer regions (Parker, 2010), suggesting that packs may actively defend the core region of their range against neighbors and intruders—a central tenet of territoriality.

In contrast to other canids (e.g., gray wolf, *Canis lupus* (Harrington & Mech, 1978) and dingoes (Déaux et al., 2016)), African wild dogs do not use long-distance territorial vocalizations such as howls. Instead, their vocalizations tend to be short-ranging and are therefore more likely to have a role in communication within packs rather than between them (Robbins, 2000; Webster, 2009). The "hoo-call" is a possible exception; individuals use this more long-distance call when they are separated from the pack, and its structure is individually specific (Hartwig, 2005), potentially allowing dogs to respond differently to different individuals. Hoo-calling is also an important indicator of social cohesion, where decreased hoo-calling during artificial pack formation for reintroductions is a predictor of the ultimate success of social integration between two opposite-sex groups (Potgieter et al., 2015). In one

Table 6.3 Annual home-range estimates for African wild dogs, *Lycaon pictus*, across their range and expanded from Pomilia et al. (2015)

Region	Country	Reserve/area	MCP (KM^2)			95% KDE (KM^2)			TAP (KM^2)			LoCoH (KM^2)			Reference
			Mean ± error	Range	*n*	Mean ± error	Range	*n*	Mean ± Error	Range	*n*	Mean ± error	Range	*n*	
Southern Africa (free-ranging)	Botswana	Moremi GR	1043	412–1608	7	739	367–999	7	748	340–975	7	748	340–975	7	Pomilia et al. (2015)
	Botswana	Moremi GR	617	375–1050	9	513	176–762	7							Fuller et al. (1992)
	Zambia	Lower Zambezi NP	273	74–459	7										Leigh (2005)
	Zimbabwe	Hwange NP	423	260–633	4										Fuller et al. (1992)
	Zimbabwe	Savé Valley Conservancy	499 ± 158^{SE}	352–844	10										Pole (2000)
	South Africa	Kruger NP	537 ± 75^{SE}	150–1110	8										Mills and Gorman (1997)
	South Africa	Kruger NP										559 ± 67^{SE}	192–942	13	Marneweck, Marneweck, et al. (2019)
East Africa (free-ranging)	Tanzania	Serengeti NP	665	620–710	2										Schaller, (2009) in Fuller et al. (1992)
	Kenya	Samburu-Laikipia	278	60–718	29	423	212–833	29							Woodroffe (2011b)
	Kenya	Masai-Mara GR	660		1										Fuller et al. (1992)
	Tanzania	Selous GR				379 ± 74^{SE}	206–851	8							Creel and Creel (2002)
Southern Africa (metapopulation)	South Africa	Hluhluwe-iMfolozi Park[a]	175	15–621	88	281	99–648	88							D. Marneweck, unpublished data

KDE, kernel density estimation; MCP, minimum convex polygon (100% MCP); TAP, traversed area polygon; LoCoH, local convex hull

[a] Only includes packs with at least 14 fixes per season, following Woodroffe (2011b); SE, standard error; SD, standard deviation

instance, while unrelated opposite-sex groups were being integrated for pack formation, a further unrelated female arrived outside of the enclosure and its hoo-calling was met with hoo-calls from both sexes inside the enclosure (Marneweck, Marchal, et al., 2019). Upon release of the newly formed pack, this female joined and remained with them.

Direct inter-pack encounters have been documented within subpopulations in this species. Remotely detected encounters through simultaneous high-resolution GPS collars in contiguous packs in Moremi (Botswana) suggested that African wild dog packs meet each neighboring pack approximately twice annually, and meet a pack (i.e., any pack) on average every 47 days (Jordan et al., 2017). Similarly, packs in Selous (Tanzania) (Creel & Creel, 2002) and Laikipia-Samburu (Kenya) made contact with another pack approximately every 40 days (Woodroffe & Donnelly, 2011). Despite most studies of African wild dog inter-pack encounters relying on VHF-tracking and direct observation (Creel & Creel, 2002; Mills & Gorman, 1997), or limited temporal activities of GPS collars (Woodroffe & Donnelly, 2011)—all of which are likely to result in underestimates of encounter rates—rates recorded in these studies closely matched those from continuous high-resolution GPS, suggesting that inter-pack encounter rates are remarkably similar across these populations.

While inter-pack encounter rates are similar in several subpopulations, the impact of pack size and social composition in determining the encounter outcomes appears to vary. Regarding pack size first, in Selous (Tanzania), 11 of 13 encounters involved the larger pack chasing or attacking the smaller pack (Creel & Creel, 2002), and a similar effect of pack size was found in Moremi (Botswana) (Jordan et al., 2017). When the demographic composition of these interacting packs was assessed to determine whether the specifics of pack composition might affect inter-pack encounter outcomes, no relationship was found. Given that similar studies in gray wolves demonstrated that inter-pack encounter outcome was related to the relative social composition of interacting packs (Cassidy et al., 2015), the lack of this effect in African wild dogs may perhaps be due to small sample size.

Descriptions of individuals preferentially attacking same-sex individuals from opposing packs (Creel & Creel, 2002) suggest that pack compositions are likely to affect the social—and particularly aggressive—interactions between packs during these events. In Hluhluwe-iMfolozi (South Africa), two male wild dogs were confirmed to have been killed by unrelated same-sex conspecifics during pack take-over events (Marneweck, 2020). In this latter example, in each case the victim was the last remaining adult male and was killed by an incoming multi-male cohort. In contrast to these studies, however, outcomes in Moremi (Botswana) were surprisingly unaffected by the inter-pack ratio of same-sex individuals involved, or the potential reward of interacting (the sex ratio in the opposing pack) that encounters presented (Jordan et al., 2017). Overall, injuries were rare (<15% of encounters) in Moremi (Botswana) compared to those elsewhere, including 38% in Selous (Tanzania) (5/13 encounters) where there were also two fatalities. While no mention is made of inter-pack relatedness in this context in the Selous (Tanzania) population (Creel & Creel, 2002), both documented events resulting in injury in Moremi

(Botswana) involved unrelated packs, though rates of injury in unrelated versus related dyads were not significantly different, possibly due to the small sample size (Jordan et al., 2017).

Avoidance of dangerous inter-pack interactions may be achieved by ritualized communication. In common with other canids (MacDonald, 1980), scent-marking is likely to be multi-functional and include advertisement and defense of territories. Although detailed patterns are known within packs (Jordan et al., 2013, 2014, Parker, 2010), inter-pack patterns have been less widely studied and are therefore not well understood (Jordan et al., 2016). Anecdotally, Creel and Creel (2002) describe large packs following the scents of smaller packs—a pattern that has also been anecdotally documented in Moremi (Botswana) (see supplementary material in Jordan et al., 2017). In contrast, small packs in Selous (Tanzania) were described as fleeing in response to the scents of larger, neighboring packs (Creel & Creel, 2002), and scents from another pack were used to direct a pack back into a protected area around Tuli Game Reserve (Botswana) (Jackson et al., 2012). Whether pack size, and by inference potential threat level, is determined from information in clusters of scent marks that are encountered in the environment, or by drawing on direct knowledge of past encounters of these packs (sensu the scent-matching hypothesis (Gosling, 1982)), is not known. The recent discovery of African wild dogs repeatedly visiting marking sites that they share with their neighbors suggests that olfactory communication between packs may be more common and important than previously thought (Claase et al., 2022; Apps et al., 2022). Although scent marks are clearly important for African wild dog long-term communication (Jackson et al., 2012; Jordan et al., 2013, 2014, 2016; Parker, 2010), there remains much to learn about inter-pack communication and social dynamics in particular.

Although few direct encounters indicate that packs can avoid others, dispersing individuals are good at finding opposite-sex groups with which to form new packs. Females were once thought to be the dispersing sex in this species (Frame & Frame, 1976), but subsequent work (e.g., Behr et al., 2020; Cozzi et al., 2020; Davies-Mostert et al., 2012, Girman et al., 1997; Masenga et al., 2016; McNutt, 1996b; Woodroffe, Rabaiotti, et al., 2020) has shown that both sexes disperse, albeit at slightly different times throughout the year, depending on the location. For seasonally breeding packs, males tend to disperse later than females (Behr et al., 2020; Cozzi et al., 2020; McNutt, 1996b). Dispersal forays can occur over long distances, and there are now several instances of transboundary dispersal (Cozzi et al., 2020; Davies-Mostert et al., 2012; Masenga et al., 2016). Of course, boundaries in this sense relate to those on Anthropocentric maps, and there are ecological boundaries that are more relevant to African wild dogs in these landscapes. Indeed, anecdotal data from long-distance dispersal forays often result in recursive movement, which may suggest that searches for potential mates and viable free territories are often fruitless, and that the benefits of remaining in the pack may outweigh going alone where dispersal opportunities are poor.

In common with mammals in general, male dispersing cohorts tend to settle further afield on average than do female cohorts (McNutt, 1996b), though a more recent dataset found the opposite (Cozzi et al., 2020). Despite the occurrence of long-distance dispersal, budding can occur in some instances, in that dispersing individuals carve out a range that partially overlaps with that of their source or natal pack, with females tending to be more philopatric (McNutt, 1996b), and the degree of relatedness between neighboring packs impacting the extent of annual home-range overlap that occurs between them (Jackson et al., 2017).

6.5 Social Dynamics Within Packs

After briefly considering the key inter-pack potential influences on African wild dog social dynamics, we now focus the remainder and majority of this chapter on within-group social behavior, particularly with respect to hunting and retaining food. While inter-pack dynamics no doubt shape the broader social landscapes on which hunting plays out, within-pack social pressures and conventions also play a considerable role. While focusing on these intra-pack aspects, we also consider potential heterospecific influences throughout this section.

6.5.1 Acquiring and Retaining Food

6.5.1.1 Hunting Behaviors and Strategies

No hunt is typical. Clearly the considerable range of scenarios inherently possible by combining variation in prey species, prey and predator decisions and movements, and considerable variation in the ecological and social landscape on which each hunt occurs combine to create near-infinite variation. Nevertheless, some steps are common to most or at least many hunts of typical prey and, by breaking hunts down into general phases, we provide a useful framework to describe the details and nuances of African wild dog hunting behavior and related social ecology. While there are variations within subpopulations in a given area, and between subpopulations in different parts of the species range, there is value in characterizing and summarizing frequently observed hunting techniques. In the text for each phase listed below (and in Fig. 6.1), we draw examples from across the extant range and as broad a range of environments as possible. While some phases do not apply to all hunts, the schematic is intended to provide an overview and, we think, encompasses all possible transitions.

Rallying the Hunters

Most hunting bouts begin with the transition of a resting pack to a collectively mobile state, and this commonly occurs through a collective “rally” or “greeting

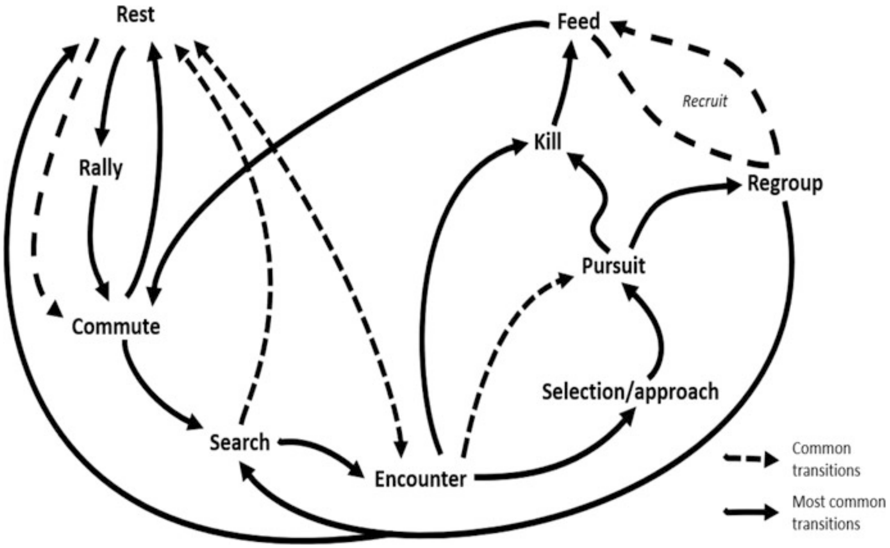

Fig. 6.1 Schematic of key stages typical to most African wild dog hunts, and common transitions between them. "Rest" state includes temporary rest sites, and resting at the den during the denning season, which often includes regurgitation to pups and other pack members there. Commuting includes non-searching movement back from the kill to a rest site (including back to the den in the denning season) and out from the rest or den site

ceremony" that has been described from across the extant range of the species (Creel & Creel, 1995; Robbins, 2000; Rütten & Fleissner, 2004; Walker et al., 2017). Although a captive study showed that rallies are more common during the gestation period (Rütten & Fleissner, 2004), such rallies appear year-round in free-living packs, suggesting that rallies are at least not exclusively related to breeding. While the function of these highly ritualized ceremonies has not been empirically tested, the accepted assumption is that they reinforce social bonds and promote cohesion within the pack (Estes & Goddard, 1967).

The underlying motivation to transition from rest may be driven by a combination of internal hunger state and external environmental conditions. The initial movement consists of one or more resting dogs rousing themselves and adopting a distinctive initiation posture (Fig. 6.2). Any dogs can initiate a rally in this way, and no clear patterns in which they do so have yet been identified. This is characterized by the dog dropping its head, with mouth open, and ears folded back (Robbins, 2000). The rally initiator(s) approach resting packmates in this posture (Estes & Goddard, 1967). When an approach has its intended effect of rousing the individual(s) in the vicinity, a sort of "social snowball" can ensue, whereby other dogs join in with the rally, they themselves then recruiting further resting dogs to join in the process. Sometimes, the rally quickly fizzles out and the dogs return to rest (~42% of rallies), but more frequently rallies facilitate the transition from rest to collective movement away from rest sites (Walker et al., 2017).

Fig. 6.2 Rallying the hunters. Three African wild dogs try to rouse a fourth to engage in a stereotyped and highly energetic pre-movement rally. Photo credit: Bobby-Jo Vial

Not all individuals participate in all rallies, but those that do so collectively engage in several stereotypic social interactions, including greeting, mobbing, mutual licking, urinating, and defecating, sometimes in combination and often while running in parallel or flank to flank. Participating dogs often also engage in a stereotypical tongue-curling display (Fig. 6.3), the function of which is not yet fully understood. Like most rally-related behavior, it is assumed to be affiliative in nature and is perhaps analogous to infantile-like appeasement or begging (Estes & Goddard, 1967).

Gradually this frenetic burst of collective social energy begins to wane and participating dogs may gradually return to rest and repeat the process at a later stage (Walker et al., 2017). If conditions are right, however, much of the pack may remain standing and ultimately leave the site and transition to the next stage of the hunt. The likelihood that rallies will result in collective movement away from rest increases as subsequent rallies occur (Walker et al., 2017). That is, the second attempt at rallying in a session is more likely than the first to result in collective movement, but whether this is due to changes in extrinsic conditions or intrinsic states is not yet known.

While the factors influencing the decision to move from a rest site are likely to be highly variable, the benefits to each individual from the pack remaining together as a cohesive social unit probably outweigh any inter-individual differences in the costs and benefits of moving or remaining resting in place. With the possible exceptions of both the denning season (when packs predictably return to a fixed point and the risks and costs incurred by losing the pack are considerably reduced), and when dogs

Fig. 6.3 Tongue-curling gesture typically adopted by African wild dogs participating in highly social rallies. Photo Credit: Hugh Webster

engage in pre-dispersal forays (when the potential direct fitness benefits of attaining a breeding position in another pack are considerable), the benefits of the pack staying together seem to outweigh any benefits of breaking away. Given these circumstances, and the extreme social reliance of the species, it is fitting that African wild dogs seem to have hit upon a semi-democratic solution to collective decision-making in this context.

In some parts of the species' range at least, post-rally decisions about when packs leave a rest site seem to correlate with distinctive rapid nasal exhalations or "sneezes." Specifically, in the immediate aftermath of a social rally, when packs seem to be deciding whether to return to rest or leave the site, a "sneeze" seems to signal an individual's intent to leave the rest site, with the number of sneezes required to reliably signal that the pack will move off depending on the participation, or not, of the dominant pair (Walker et al., 2017). Specifically, this quorum is reduced whenever dominant individuals initiate a rally, suggesting that dominant participation increases the likelihood of a rally's success, but this is not in itself a prerequisite. It is not yet known whether this nasal exhalation is a signal used by the dogs themselves, or whether sneezes correlate with other signals that the dogs may be using.

Whether "sneezing" post-rally—and the relationship between this and moving from the rest site—is a locally specific adaptation or a species-wide trait is also not yet known. In addition to the published study from the Okavango Delta region (Botswana) (Walker et al., 2017), anecdotal evidence from the authors of this chapter suggests that it has been observed in packs in the Linyanti region (Botswana) (B. Tshimilogo, pers obs) and the Savé Valley Conservancy (Zimbabwe) (J. Watermeyer, pers obs), but not in South Africa (D. Marneweck, pers obs) or the Samburu-Laikipia region (Kenya) (D. Ngatia, pers obs). This behavior does not appear to have been common in the historic Serengeti population either, as James Malcolm (pers comms with N. Jordan) noted that he had not witnessed this directly, and neither had it been noted in the extensive diaries made by Jane Goodall there. Further study would be necessary to determine the extent of this behavior, and potentially the social and ecological factors associated with it. It remains possible, therefore, that this behavior evolved in dense habitats where visual signals are less effective, or that it is a cultural trait in the sense that it may be confined to specific communities and potentially be acquired and retained through social learning, but to our knowledge no research has yet been published in this area.

While not all rallies culminate in collective movements, and not all collective movements are preceded by such highly social frenzied rallies (Walker et al., 2017), these rallies are ubiquitous across the extant range and are therefore an important aspect of African wild dog social behavior. Rallies have even been suggested to play key a role in establishing and maintaining pack cohesion (Rütten & Fleissner, 2004), and it is hard to watch a rally without coming to the same conclusion. Experimental work that might determine their explicit function is, however, hard to envisage within the bounds of feasibility and acceptable animal ethics considerations.

Commuting

Following a decision to move off, and assuming that prey is not encountered directly at the rest site, the next phase in a typical hunt involves commuting. In this phase, the dogs move as a unit, usually departing in a common direction at a casual-seeming pace (ca. 0.35 m/s; Fig. 6.4), before picking up speed to a trotting gait (ca. 2.5 m/s; Hubel et al., 2016b) at a variable later stage. Initial departure may also occur at a trotting or cantering pace in some instances. While they may not have made the decision to leave the site, dominants seem to assume the lead in this commuting phase, being found more often at or near the front of this line (N. Jordan, pers obs). The decision to transition from rest to commuting is not always unanimously complied, and resting individuals may display an apparent profound reluctance to follow, as described above.

During the approximately 3-month long denning period, packs are spatially anchored around a den site (Pomilia et al., 2015), with individuals commuting to and from this site approximately twice daily to hunt for food (Davies et al., 2016; Malcolm & Marten, 1982). During some hunts, some individuals remain at the den and do not participate in the hunt at all. Commonly this includes the dominant female, especially in the first several weeks following parturition (Courchamp et al., 2002; Malcolm & Marten, 1982), but other individuals may also remain either with or in lieu of the dominant female. It is believed that staying at the den might help the breeding female to guard the pups against predators, such as lions, leopards (*Panthera pardus*), and spotted hyenas (*Crocuta crocuta*). African wild dogs also attempt to reduce predation by selecting den sites in rugged areas of dense vegetation

Fig. 6.4 African wild dog packs commute through woodland to more favorable hunting grounds. This phase often occurs in single file. Photo credit: Krystyna Golabek

that facilitate lion avoidance (Davies et al., 2016; Jackson et al., 2014; van der Meer et al., 2013), or in areas sparse in prey and competitors (Mbizah et al., 2014), even when favored topography is absent in the landscape (Alting et al., 2021).

Outside of the denning season, rest site fidelity is generally low, since dogs departing to hunt do not return to that same site. This so-called fugitive state within the home range may result from inter-specific competition risk (Webster et al., 2010, 2012). For example, African wild dog scents accumulate at rest sites as a consequence of prolonged use through the heat of the day and through other suboptimal hunting periods (e.g., moonlit nights; Cozzi et al., 2012), and the communal dumping of scats and urine associated with social rallies (N. Jordan, pers obs). Such signals may directly attract the attention of lions at short distances, or indirectly over longer distances by the presence of coprophagous hooded vultures (*Necrosyrtes monachus*), which already attend to den sites (Reading et al., 2017). Rest-site fidelity would create a reliable food source (scats) for these visually conspicuous vultures, whose attendance may feasibly attract lions to African wild dog rest sites. Alternatively, observed rest-site transience could result from prey depletion, but there is currently no empirical evidence to support the notion that prey avoid areas recently frequented by packs (Mbizah et al., 2014). Similarly, placing African wild dog scents at waterholes changes prey vigilance but not their presence there (van der Meer et al., 2012, 2015), further suggesting that rest-site transience is not related to prey capture.

While commuting itself is not an active hunting phase, prey are also taken opportunistically whenever encountered. While this is true of all prey, it is perhaps most common for small prey to be flushed in the commuting (and the subsequent active searching) phase. Common small prey includes steenbok (*Raphicerus campestris*) and common duiker (*Sylvicapra grimmia*) in Botswana, and dik-dik (*Madoqua* spp.) in Kenya, in particular. When encountered in this context, prey may be dispatched and eaten quickly in situ without the hunters transitioning through the active searching/coursing and prey chase phases of a hunt. The act of killing and consuming prey can be extremely fast in this context and may be achieved without pursuit by a grab, a quick violent shake (Creel & Creel, 1995), followed by near instantaneous consumption by a quickly converging scrum of dogs. Such small prey may also be opportunistically chased if they bolt, but usually only over short distances. Indeed, chase distance positively correlates with both prey size and pack size, possibly resulting from the combination of prey size and stamina, and the suggestion that small prey hesitate and about turn at the edge of their (smaller) home ranges (Creel & Creel, 1995).

Given that pursuit and killing of prey can occur at any phase of the hunt, we suggest that mobile African wild dogs should generally be considered to be in hunting mode, with the possible exception of their commute on distended bellies from the kill site back to the den, or to a temporary resting site away from the kill (though half-hearted chases do also occur in these contexts).

Active Searching/Coursing

While opportunistic capture can occur in the commuting phase, packs commonly transition into a more active searching phase of the hunt before long, and this occurs more frequently as they reach more favorable hunting grounds. At this point, individuals begin to pick up the pace and fan out, trotting or cantering at speeds around 10 km/h, in a loose and criss-crossing fan formation spread over a range of 10–100 m (Creel & Creel, 2002). This approach likely increases the chances of flushing out prey. As commuting can occur at similar speeds, this fanning out distinguishes the active searching or coursing phase from the commuting phase and seems to be an effective method of flushing out small prey, such as dik-dik (Woodroffe et al., 2007). Indeed, in some areas, such as in Samburu-Laikipia (Kenya), African wild dogs are extremely successful at flushing small prey.

If prey is flushed out, the chase begins. If not, active searching continues or may culminate in an additional resting period (see Fig. 6.1 for common transitions). Both the commuting and searching phases may also be punctuated with stationary bouts, where members of the pack stand alert and appear to be listening attentively to their surroundings. Anecdotally, changes in the pack's direction of movement are common following these stationary attentive bouts. Whether such direction changes occur after hearing potential prey and moving in their direction, or hearing heterospecific competitors and moving away, is not always clear.

Prey Encounters

When potential prey is sighted, there are two main ways in which African wild dogs approach, both serving to reduce the distance from prey before it attempts to escape

Fig. 6.5 Although stalking-like, approaches by African wild dogs on prey seem to make no attempt at concealment, but nevertheless serve to reduce the gap between them and their intended prey. Photo credit: Bobby-Jo Vial

(Fanshawe & Fitzgibbon, 1993). There is no skulking around and taking up tactical positions, as lions do in setting an ambush (Stander, 1992); instead, African wild dogs try to close the gap between themselves and their prey before the pursuit begins. Typically (approximately 77% of prey encounters (Fanshawe & Fitzgibbon, 1993)), the dogs run directly toward prey. In other situations, the hunting packs halt, lower their ears back against their heads—which they also lower toward the ground—and slowly progress directly toward the prey (Estes & Goddard, 1967), keeping a fixed gaze on their quarry (Fig. 6.5).

While the reduced speed, hunched posture, and flattened ears make this appear like stalking, the dogs actually make little to no attempt to conceal themselves from prey. Approaches occur in plain sight of the prey, which often stand and watch them approach. While it has been suggested that the closer wild dogs got to their prey initially, the shorter the resultant chase (Estes & Goddard, 1967), and that the stalking style of approach reduced this initial distance between the pack and their prey (Fanshawe & Fitzgibbon, 1993), these effects are not expected to be significant determinants of hunting success.

Common prey such as impala, lowland nyala (*Tragelaphus angasii*), and greater kudu (*Tragelaphus strepsiceros*) do not respond with an alarm call to the presence or approach of African wild dogs—the predators can clearly observe that they have been seen and African wild dogs are not ambush predators that give up on the hunt when they have been detected (Fig. 6.6). Immediately pre-flight, some prey including impala (N. Jordan, pers obs), lechwe (*Kobus leche*) (Stevenson-Hamilton, 1947),

Fig. 6.6 African wild dogs approach a herd of alert impala. Photo credit: Megan Claase

and greater kudu (Selous, 1881) make a discernible and characteristic head movement, before performing a quick about-turn to flee. Like the shot of a starter gun, it seems that this first characteristic movement of the prey's head is the signal that triggers an explosion of speed from the dogs, and they all set off in pursuit.

Prey Selection

Prey preferences certainly occur at the species level, and may also be chosen/targeted individually within herds or groups, at least in some contexts. At the species level, previous work in the three core contemporary populations of free-ranging African wild dogs suggests that they usually select the most abundant medium-sized antelope in the environment (Creel et al., 2004; Hayward et al., 2006; Vogel et al., 2019). As such, while these studies represent what is occurring for the majority of the extant population (in terms of raw numbers of free-ranging African wild dogs), our understanding of prey selection in this species remains limited and somewhat skewed. There are likely to be local adaptations and exceptions to this particularly from the understudied populations, and smaller prey that are consumed quickly are likely to be underrepresented in the data.

Previous work in the three populations suggests that differences in diet between ecosystems are somewhat explained by the relative abundance of potential prey species in those ecosystems (Creel et al., 2004). Nevertheless, some broad patterns can be described, with packs focusing primarily on wildebeest, impala, greater kudu, gazelles (*Gazella thomsonii*, *G. grantii*), guenther's dik-dik (*Madoqua guentheri*), and warthogs (*Phacochoerus aethiopicus*) (Creel, 2001; Creel & Creel 1995; Fanshawe & Fitzgibbon, 1993; Fuller et al., 1995; Pienaar, 1969; Tshimologo et al., 2021; Woodroffe et al., 2007) according to availability and encounter rates. Broad prey selection analyses have been conducted using data from 4874 kills of 45 prey species collated from studies in East Africa (Kenya, Tanzania) and southern Africa (South Africa, Zambia, Zimbabwe), and demonstrated that African wild dogs have a bimodal preference by body mass, preferring prey in the ranges of 16–32 kg and 120–140 kg (Hayward et al., 2006). The commonly selected prey overlaps considerably with that provided above (Creel et al., 2004), with the exceptions that Hayward et al. (2006) identified duiker and steenbok as commonly preferred prey, and excluded wildebeest.

There is also some evidence to suggest that wild dogs select prey that may be less likely to cause injury when hunted (Hayward et al., 2006). In the Okavango region of northern Botswana, preferred prey are impala (Tshimologo et al., 2021), while data from Kenya, and particularly the Samburu-Laikipia region, suggest that dik-dik form the principal part of the diet there (Woodroffe et al., 2007). In contrast to this risk avoidance in prey selection, research from Mana Pools (Zimbabwe) suggests that chacma baboons (*Papio ursinus*) form a substantial part of the diet, and were preferentially predated (van der Meer et al., 2019). Of particular note is that dangerous adult male baboons formed a large proportion of the known demographics of baboon kills (van der Meer et al., 2019). In other parts of their range, such as central Africa, to our knowledge no published information exists on their diet, restricting our understanding of local dietary adaptations throughout the range.

Once prey have been detected, selection of target individuals within a herd then occurs. Such prey selection likely involves identifying and focusing on any individuals that may be compromised or otherwise less likely to escape. Each dog appears to act on its own in selecting an individual from a herd (Kuhme, 1965a), and this can result in a pack chasing several prey independently (Fanshawe & Fitzgibbon, 1993). Indeed, evidence from the marrow fat content of prey limb bones suggests that African wild dogs killed—and perhaps targeted—Thomson’s gazelles in relatively poor condition (Fitzgibbon & Fanshawe, 1989). Similarly, data from the Savé Valley Conservancy (Zimbabwe) demonstrated that prey killed were in poorer condition than individuals that were culled unselectively, which suggests that African wild dogs either targeted weaker individuals (Pole et al., 2004) or were more successful at catching them during hunts. Alarm calls serve to alert ambush predators that they have been seen and that the predator has lost the upper hand (e.g., Tilson & Norton, 1981), but some African wild dog prey species do not emit alarm calls in the presence of this cursorial hunter. Thomson’s gazelle, for example, are more likely to “stot” in the presence of African wild dogs than in response to stalking or ambush predators such as cheetahs, which is interpreted as an honest signal of condition (Fitzgibbon & Fanshawe, 1988). Similarly, springbok (*Antidorcas marsupialis*) that are approached by African wild dogs can respond by stotting, but such displays do not always guarantee survival. On several occasions, African wild dogs in Botswana’s central Kalahari Desert have been observed killing the stotting individual from a herd (B. Tshimologo, pers obs).

In contrast to smaller prey which tend to be run down, African wild dogs take a different approach to hunting large and dangerous prey. Large prey (e.g., wildebeest) often stand in a defensive “pinwheel,” facing outward, and will charge at dogs, often using their horns to defend themselves while retaining juveniles in the center of the group (Creel & Creel, 1995). Other solitary, horned prey (e.g., warthog, greater kudu males) can also stand and defend themselves and, in both of these situations, the pack encircles the herd or individual and attacks from multiple directions (Creel & Creel, 1995). The intended outcome of this testing appears to be to try to separate an individual from the herd—by inciting a charge—at which point other pack members can lunge at temporarily exposed hind quarters or juveniles in the center. Such harassment can also result in one or more of the prey bolting, and a high-speed chase ensuing (Creel & Creel, 1995). It is difficult to determine whether selection of specific individual animals occurs at this point, or whether the dogs respond purely opportunistically. Additionally, a lack of any relationship between pack size and kill frequency of prey species and demographic categories considered dangerous suggest that they are hunted opportunistically, perhaps as sick or injured animals are occasionally encountered (Creel, 2001).

In contrast to relatively intact or open range landscapes, African wild dogs can and do use boundary fences in fenced reserves to catch prey, running prey directly into them (Rhodes & Rhodes, 2004). As a result of utilizing these anthropogenic features, packs in these reserves are able to select more dangerous prey to pursue (i.e., adult male kudu, older aged prey, and prey in better condition) because they use these structures to catch them which likely reduces the risk (Davies-Mostert et al., 2013). Moreover, fencing helps increase African wild dog catch per unit effort (Davies-Mostert et al., 2013). Thus, in the fenced protected areas of South Africa in particular, wild dogs are able to select a diverse range of prey that includes potentially dangerous species and individuals that would be unattainable otherwise, and to catch these prey more efficiently than in unfenced areas.

Intuitively, the type of prey that can be tackled could also be influenced by pack size, with large dangerous prey potentially being only accessible to larger packs. Indeed, this is borne out in the data. In the Selous (Tanzania) for example, where the majority of hunting observations have been documented, small packs (up to ten adult individuals) relied principally on impala, whereas median and large packs fed mainly on wildebeest (Creel & Creel, 2002). Nevertheless, the authors have observed lone African wild dogs successfully catch and kill adult male impala in different regions (N. Jordan, pers obs in Botswana; D. Ngatia, pers obs in Kenya), and this presumably occurs elsewhere and with other prey.

Pursuit of Prey

Following prey selection, what happens next depends on a variety of factors, but usually transitions into active prey pursuit. While African wild dogs are arguably the poster species for endurance hunting, as noted above, prey encountered during coursing is often pursued only for a short distance or may even be dispatched rapidly in situ without a chase. The latter scenario may be particularly common when capturing small prey, for example dik-dik (D. Ngatia & D. Rabaiotti, pers obs), and during the calving season, when abundant impala (Botswana, South Africa) or

Thompson's gazelle (East Africa) calves can be taken simultaneously or in quick succession by the pack (N. Jordan, pers obs).

While the species has multiple adaptations to endurance running, particularly in muscular size and attachments (Koshy et al., 2020), and toleration of hyperthermia during exercise (Taylor et al., 1971), recent work suggests that popular descriptions of the distance over which African wild dog prey pursuits occur may be overstated (Creel & Creel, 1995; Hubel et al., 2016b). Data from two populations in mixed woodland savannah—a mosaic habitat that probably typifies that inhabited by the majority of the remaining core extant population (Creel et al., 2004)—suggests that the distance covered in the chase phase is not usually substantial. Chases leading to successful hunts in Selous (Tanzania) varied from 0.5 km in large packs (approximately 20 adults) to 1.1 km in small packs (approximately three adults) (Creel & Creel, 1995); though maximum distances noted elsewhere range from 50 m to 4.6 km (Creel, 2001). As data were derived there from direct observations, and packs may have been lost during longer chases, it is possible that the Selous (Tanzania) study may over-represent shorter runs. Indeed, direct observations of entire hunts in Moremi (Botswana), Hluhluwe-iMfolozi (South Africa), and elsewhere are extremely challenging to complete and consequently rare to document due to thick vegetation, making the volume of data from Selous (Creel, 1997; Creel & Creel, 1995, 2002) in somewhat similar habitat particularly impressive. As a result of a sampling bias toward shorter runs from direct observations, published data on chase distances are unlikely to reflect the full range occurring, and specifically would be expected to underestimate this metric.

Remotely derived data from animal-borne GPS would be expected to reflect chase distances more accurately and record higher mean chase distances because of extended and uninterrupted observations compared to human observers. Surprisingly therefore, data derived from GPS-IMU collars fitted to a small pack of dogs in Botswana showed a median individual chase distance of 324 m, with a maximum chase distance of less than 700 m (Hubel et al., 2016a, 2016b). While this overlaps with large packs from Selous, these values are at the lower end, not the upper end as predicted. These data are themselves limited, being derived from a single pack of six adults, but when considered together with direct observations from Selous (Tanzania) it is reasonable to conclude that while long-distance endurance chases may form part of the African wild dog hunting repertoire, endurance pursuit is not the preferred or common manifestation of hunting in this species.

Individual Roles

Popular depictions of hunting by this species also perpetuate the idea that specific dogs take on specific roles, and that these may be specialized and consistent as they are in lions (Stander, 1992). In safari-lore indeed, levels of cooperation of hunting African wild dogs are almost legendary (noted in Fanshawe & Fitzgibbon, 1993). In reality however, there is little evidence of this from empirical studies. This again includes the small pack of six dogs in the Okavango delta (Botswana) that were fitted with high-resolution GPS-IMU radio collars to record details of their movement, speeds, and locations (Hubel et al., 2016a, 2016b). Use of high-level cooperative chase strategies (coordination and collaboration) was not discernible (Hubel et al., 2016a). Instead, individuals appeared to work opportunistically during hunts, with the additive effects of their individual efforts increasing the packs' hunting success. While acknowledging the important caveat on generalizing the results of a study conducted primarily on a single pack and exclusively on one subpopulation of the species, the fact that no evidence of coordination or role specialization was apparent in this dataset is compelling.

Individual approaches to hunting, if not consistent role specializations, are likely to exist in African wild dogs. For example, in the Serengeti (Tanzania), the dominant male in the core study pack is described as often making the first grab at prey (Malcolm & Marten, 1982). In contrast, the dominant pair in a small core study pack in the Okavango delta (Botswana) had reduced hunting involvement, participating in fewer chases than subdominant pack mates (Hubel et al., 2016a, 2016b). Such lack of consistency in roles *between* packs according to rank does not negate the possibility that individuals consistently take on specific roles *within* their packs, or even the potential that particular roles may be shared or varied between individuals in different hunts depending on the circumstances and relative positions of individual dogs when those hunts begin. While such adaptive/flexible role performance might occur, there is no direct empirical evidence of this in the literature during the pursuit phase, and the consensus among the authors of this chapter is that hunts resemble an "uncoordinated mess," albeit often a highly successful one. Overall, and as has been pointed out previously, participation of individuals in a hunt is almost impossible to determine because the mere presence of additional individuals, even where they are not clearly actively participating, can affect prey behavior and influence the outcome of a hunt (Creel & Creel, 1995; Reich, 1981; Stander, 1992).

While there is little evidence of role specialization in the pursuit phase of hunts, a degree of role consistency or specialization may occur during the prey capture phase. This is likely to be most apparent in the subduing of large prey, which has previously been described in detail (Creel & Creel, 1995). Immobilizing dangerous prey with horns, or powerful kicks, carries with it a significant risk of injury, and deep cuts, broken teeth, and injured limbs are not unusual (Creel & Creel, 1995). In these circumstances, individuals attempt to restrain the head of the prey, while others circle around and attempt to disembowel it (Creel & Creel, 1995; Estes & Goddard, 1967). As noted above, while the dominant male in one core study pack was often first to grab at prey (Malcolm & Marten, 1982), and individuals are likely to somewhat specialize, evidence of strict consistency in roles is currently lacking. While there is no evidence that individuals specialize in roles at this stage of the hunt, nor is there published evidence to the contrary, as far as we are aware. Whether individuals behave opportunistically in this phase is not definitively known, but a combination of some degree of specialization and opportunistic involvement is possible.

In terms of increasing success by being together, and even working loosely together, it is hard to argue that wild dogs do not hunt cooperatively. In this context "cooperatively" relies on hunters gaining greater per capita returns by working together (Sibly, 1983). As per capita intake is greater in larger packs, up to a given pack size (Creel, 2001; Creel & Creel, 1995), wild dogs do technically hunt cooperatively, without necessarily working together in a coordinated manner. As noted in previous studies, it is difficult to determine whether such coordination or active collaboration occurs, especially where several individuals are running simultaneously over large areas (Creel, 2001). Ideally, what one would have are synchronous data on the decisions made by and movements of all members of the pack and all members of the prey. This is impractical to achieve in this study system through collars, but aerial footage of hunts could be used in the future, perhaps particularly as the use of drones in research expands (Koh & Wich, 2012).

Relay Running

Like gray wolves (see Tallian et al., Chap. 4), previous authors have noted that individual African wild dogs pursuing the same prey animal do not generally follow the same pursuit route. In combination with decisions that prey make, individual decisions made independently from different positions can result in one or more African wild dogs intercepting a prey animal after taking an apparent shortcut (Estes and Goddard, 1967; Fanshawe & Fitzgibbon, 1993). While the anticipation of prey movements is likely to occur to a certain extent, intentionality of shortcutting is not necessarily implied (Creel & Creel, 1995), and there is certainly no systematic evidence for relay running—in the strict sense—in African wild dogs. Unsurprisingly, researchers found no evidence of relay running in the Botswana pack with high resolution GPS-IMU collars (Hubel et al., 2016a), and we are not aware of convincing evidence of this having been gathered elsewhere.

Immobilizing and Killing Prey

The majority of work in this area has again been conducted on the Selous (Tanzania) population (Creel & Creel, 1995, 2002), but descriptions of killing methods here are summarized from various sources (Creel, 1997, 2001; Creel & Creel, 1995, 2002; Hubel et al., 2016a, 2016b; Malcolm & Marten, 1982). Single African wild dogs can pick up and kill small prey by shaking them ((Creel & Creel, 1995) such as dik-dik, adult steenbok or duiker, or impala calves), and while lone adult dogs can occasionally take larger prey such as adult male impala (N. Jordan & D. Ngatia, pers obs), there are significant risks to this in terms of potential injury during restraint and killing, and also through the risk of attracting heterospecific competitors through a prolonged struggle (and associated prey distress calls). More typically, kills involve one or more dogs grabbing the nose or ears of the prey in their mouths to restrain it, while others collectively disembowel the prey by simultaneously pulling in several directions. This can lead to small-bodied prey quickly being torn into pieces.

Again, detailed information on the hunting of large and dangerous prey (e.g., adult male impala, adult wildebeest, warthog, zebra (*Equus* spp.), red hartebeest (*Alcelaphus buselaphus*), southern reedbuck (*Redunca arundinum*), and waterbuck (*Kobus ellipsiprymnus*) comes primarily from Selous (Tanzania) (Creel & Creel, 1995, 2002). In this context, wildebeest herds for example tend to adopt a pinwheel formation (Fig. 6.7), and the pack encircles them with each dog attacking simultaneously. This tactic is described as an attempt to separate an individual from the herd, with dogs lunging in behind an individual that is enticed into a short charge

Fig. 6.7 Blue wildebeest adopt a loose pinwheel formation as they are harried by a pack of African wild dogs in Botswana. Photo credit: Dominik Behr

or lunge. If an individual is separated from the herd and begins to run, the chase resembles that for medium-sized prey such as impala. Once caught, prey are killed by collective disemboweling, and individual dogs assist to protect those involved in that aspect by feinting at the front and grabbing at the muzzle and head where possible to restrain it and reduce the risk of injury by horns and tusks. Such injuries are not uncommon (Creel & Creel, 1995), and even a single warthog represents a dangerous adversary. For example, a yearling male in a pack of 17 African wild dogs was tusked in the chest by a warthog and died instantly during a hunt in the Central Kalahari (Botswana) (B. Tshimologo, pers obs).

Particular features within landscapes may also aid or hinder prey capture by African wild dogs. While they do not need to drink to maintain water balance, African wild dogs access water where available. This brings them into contact with congregations of prey (and sometimes competitors) at these sites, and some prey, including red lechwe, may plunge into water to evade capture (Lent, 1969). African wild dogs may pursue them into water, but the risk of crocodile (*Crocodylus niloticus*) attack makes both the evasive tactic and subsequent pursuit risky. Approaches to prey immobilization in aquatic environments are not well documented, but, while prey may be killed in the water, they are usually pulled to land or vegetation for consumption.

In addition to natural landscape features, anthropogenic features can also impact hunting approaches and success. We have described the dogs' use of fences in hunting, and the increased success that these tactics result in small fenced reserves

(Davies-Mostert et al., 2013), but anecdotal accounts also suggest that tarred roads in Hluhluwe-iMfolozi and Kruger (South Africa) specifically may aid in prey capture by providing a surface that is slippery under hoof. It is not known whether African wild dogs deliberately herd prey toward sealed roads, as they appear to do with fences, but the opportunity for learning such a tactic exists, particularly as African wild dogs preferentially commute along roads (Abrahms et al., 2016). The use of anthropogenic structures may have a social learning component, but no research has yet been carried out to quantify whether roads are deliberately used in this way.

Regroup and Recruit to Kill

In a typical hunt of medium-sized and large prey, many if not most individuals undertake the chase, but others may remain close to the start point without participating. Commonly but not always this includes the dominant female—and perhaps particularly when she is close to parturition—and in some subpopulations the dominant male often remains with her (N. Jordan & K. Golabek, pers obs). This behavior may explain the reduced investment of dominants in hunts at the site in the Okavango delta (Botswana) (Hubel et al., 2016a), but it does not seem to be a behavior common to all African wild dogs. A lack of participation by the dominant male is not observed in the Savé Valley Conservancy (Zimbabwe) (J. Watermeyer, pers obs) or South African study populations (D. Marneweck, pers obs), and remaining at the origin of the chase does not seem to extend beyond the early period of pup dependency shortly after pups have permanently left their den sites.

In the Moremi (Botswana) subpopulation at least, any individuals that pursued prey but lost their chosen target and the rest of the pack will often return to a regrouping site close to the origin of the chase (N. Jordan, K. Golabek, & B. Tshimologo, pers obs; Fig. 6.8). Other stragglers sporadically appear and join the waiting pack, temporarily setting off a burst of excitement in their vigilant packmates, which soon appear to determine that the returnees were unsuccessful and so settle back to waiting. If all animals have returned, empty-stomached, the pack may rise and restart the process. Sometimes, however, they rest in place.

In contrast, when a pack member returns to the regroup site bearing the signs of a successful kill, including a distended belly, and blood splatter on the legs, head, and neck (Jordan et al. 2022; Fig. 6.9), the pack sets off in the direction from which it came, heading to the kill with the recruiter(s). Sometimes such recruitment is unnecessary, as satellite ears and associated acute hearing may allow the remnant pack members to hear the death-cry of the prey, or other signs of a kill taking place. In these circumstances, the pack quickly makes a beeline for the kill site without the need to be recruited.

One benefit of the involvement of multiple dogs in subduing a single prey animal is the speed with which it can be killed. This may reduce the vocal cues that otherwise could make the pack vulnerable to kleptoparasitism in the profitable early stages of consumption. While the scale of impact of kleptoparasitism on African wild dogs is somewhat ambiguous and under debate (Carbone et al., 2005; Gorman et al., 1998; Jongeling & Koetsier, 2014, Speakman et al., 2016; van der Meer et al., 2011), the likelihood of losing kills to scavenging competitors is affected

Fig. 6.8 Unsuccessful chasers return to the regroup site and wait, alert, for other pack members to return. If no kill is made, packs often reunite close to the origin of the chase. Photo credit: Bobby-Jo Vial

Fig. 6.9 A pack member returns to the chase origin or regroup site to recruit other pack members to the carcass. Photo credit: Bobby-Jo Vial

by pack size (larger packs may be better able to defend prey from spotted hyenas in particular (Carbone et al., 1997)), and scavenging risk is likely to affect behavior (Carbone et al., 2005; Webster et al., 2010). In areas with sympatric competitors such as lions and hyenas, timely attendance of the rest of the pack may be crucial to the pack retaining the kill (Jordan et al., 2022). Collaborative killing and some social nuances of their subsequent feeding strategy may be specifically adapted to reduce this risk, and we cover some of that in subsequent sections.

Consumption of the Kill

In African wild dogs, feeding may be argued to be part of the killing process, as prey are disembowelled by the hunters and some feeding therefore occurs during this process. Once dead, subsequent feeding by African wild dogs may appear chaotic, but it is generally systematic both in terms of the order in which parts are consumed and the order in which individuals access it.

Prey consumption patterns differ according to prey size. When considering common medium-sized prey, such as impala and female kudu, in the early stages of feeding when the carcass is relatively intact, individuals generally follow the patterns observed in other species, with feeders focusing on the most nutritional valuable parts, such as the liver (Jordan et al., 2022). Smaller prey is obviously devoured more quickly and observations on partitioning or preference of particular parts of the carcass are nearly impossible to observe and quantify with current methods. Consumption of small prey appears to be a chaotic free-for-all, with late arrivals missing out even after only a few seconds. Similarly, with larger prey, feeding begins often during the killing phase, with dogs disemboweling prey and beginning to feed from the organs. On departure from the carcass, pups may carry the skull or other parts of the skeleton with them, and adults sometimes do the same including delivering such to the pups at the den. This may, we speculate, allow pups to become familiarized with potential prey through play.

There are also fascinating social determinants of feeding access within packs. In contrast to many carnivore species, where access to kills is determined by an individual's ability to defend it from other group members (e.g., lions (Packer et al., 2001)), African wild dogs exhibit a youngest-feed-first system which was first alluded to in work from Kruger National Park in South Africa (Rosevear, 1974) and subsequently elsewhere (McNutt, 1996a) (Fig. 6.10). Feeding priority at carcasses is given exclusively to pups (Creel & Creel, 1995; Malcolm & Marten, 1982; Rosevear, 1974; Walker et al., 2017) and, while dholes (*Cuon alpinus*) may display some aspects of this system (Venkataraman, 1996), it is likely the exception in mammals.

When multiple age classes of offspring are present, it is suggested that the order of priority is extended to pups first in an age-based feeding hierarchy that may be socially reinforced by the dominant pair (McNutt, 1996b). Indeed, the details and consequences of this system have now been described and suggested to have profound implications on the hunting investment of individuals according to their access to food that is caught (Jordan et al., 2022).

Fig. 6.10 Young African wild dogs are given early uncontested access to carcasses, incentivizing prompt attendance at kills and reducing or diluting the risk of inter-specific competition with lions and hyenas. Photo credit: Krystyna Golabek

When prey is caught and killed, dogs that are in attendance and involved in the killing feed first, concentrating on the high nutritive value organs such as the liver. If other group members do not join them, one or more of the incumbents will usually leave the site and recruit others. Again, while this recruitment has not been directly witnessed in Hluhluwe-iMfolozi Park or Kruger National Park (South Africa), the prevalence of this behavior in Botswana and its potential utility suggest that this may be an overlooked trait rather than a subpopulation-specific adaptation. An exception is when small prey are captured and can be wholly consumed quickly by those present. Recruitment to kill sites is specific to kills that can be shared with more dogs than are involved in the kill, and in other situations the dogs feed quickly and return to the rest of the pack. Within the social constraints of the system, prey consumption must be conducted as swiftly and quietly as possible to reduce the losses should heterospecifics ambush their kill. Excited twitter vocalizations (Robbins, 2000; Robbins & McCreery, 2003) are emitted by the pack during feeding and, although they are not audible over a long range (Webster, 2009), playback experiments indicate that lions and spotted hyaenas are attracted to them (Webster et al., 2010, 2012), which may expose them to kleptoparasitism risk.

Recruitment of the rest of the pack to the kill site may be the wild dog equivalent of the so-called selfish sentinel in meerkats, where well-fed foragers are better off performing sentinel duty than investing further in feeding (Clutton-Brock et al., 1999). In this case, however, the feeder first must recruit the rest of the pack before

Fig. 6.11 An older subdominant African wild dog is left with slim pickings, after not participating in the kill itself. Photo credit: Bobby-Jo Vial

allowing them to feed. The result of recruitment is increased numbers at the kills, and the age-based feeding system means that non-feeding dogs provide vigilance and consequently provide safety in numbers around the carcass.

Following recruitment, or if all pack members have otherwise arrived at the site, the youngest animals tend to feed first, with older dogs milling around, and not contesting this order (McNutt, 1996b). The exception to this is the dominant pair, where they often feed immediately after the pups. Access then cascades down through older dogs, until the eldest subdominant pack members get access at the end (Jordan et al., 2022) (Fig. 6.11). This is critical as, for average size kills and packs, this results in older subdominants that did not participate in the killing failing to gain access to kills at the most profitable early stages of consumption. Such a system may incentivize older subdominants to participate in the most dangerous phases of the hunt, or risk receiving insufficient rewards for the pack's collective efforts (Jordan et al., 2022).

The youngest-feed-first system of priority of access to carcasses is likely to have broad implications on individual investment in hunting. Indeed, increased likelihood of direct involvement in the act of killing prey (measured by the proxy of prey blood on the legs) was found to be related to reduced access to the carcass (Jordan et al., 2022).

Losing Food to Others

Due to the high costs involved in catching food, and the narrow activity windows within which this can be economically attempted (Cozzi et al., 2012; Rabaiotti & Woodroffe, 2019; Woodroffe et al., 2017), African wild dogs have a number of social strategies and adaptations to avoid losing their kills to other species. Kleptoparasitism has been suggested to put African wild dogs on an ecological knife edge (Gorman et al., 1998; Speakman et al., 2016, but see Hubel et al., 2016b; Jongeling & Koetsier, 2014). When African wild dogs lose their kills, this is generally to spotted hyenas but lions are also drawn to and steal kills. This adds a mortal risk to the process, as lions are responsible for a high proportion of both African wild dog pup and adult mortality (Groom et al., 2017; Woodroffe & Ginsberg, 1999).

One key social adaptation to protecting kills from being stolen by heterospecific competitors is pack size, which has been related to a pack's ability to defend their kill from hyenas (Carbone et al., 1997). The ability of packs to defend kills from lions is also probably related to pack size, but African wild dogs seem to run at first sight of a lion. Kleptoparasitism impacts differ across ecosystems and are linked to hyena density (Creel & Creel, 1996) and habitat. In open habitats, kleptoparasitism is common and the ability to defend kills against hyena depends on pack size (Carbone et al., 2005). Where hyena densities and visibility are lower, or where hyenas do not forage in large subgroups, the potential impact of kleptoparasitism may be reduced (Creel & Creel 1995, 2002; Hubel et al., 2016b). While pack size likely reduces the risk of kleptoparasitism and ambush by heterospecific competitors, once most individuals have fed the pack will move off. In some situations, late-feeding subdominants may be left at the kill site when the rest of the pack has moved off, exposing them to the risk of ambush by inter-specific predators. We know of one such occasion—inferred by spoor and bones—when an older collared male was left at a kill site and was killed and eaten by spotted hyenas (N. Jordan & K. Golabek, pers obs).

While work in the Serengeti (Tanzania) showed that hyenas had a huge kleptoparasitic influence on African wild dogs, work in Selous (Tanzania) suggests kleptoparasitism is less important, with only 2% of African wild dog kills lost to hyenas (Creel & Creel 1995, 1996). Models also tend to discount the possibility that often only the least profitable parts are lost to hyenas. In Moremi (Botswana), hyenas travel in smaller subgroups than in the Serengeti (Vitale, 2018) and can be seen waiting in singles or pairs for the African wild dog pack to abandon a kill of skin and bones (N. Jordan, pers obs). Elsewhere too, African wild dogs are capable of protecting kills from hyenas (Estes & Goddard, 1967; Fuller & Kat, 1990; Kuhme, 1965a; Pienaar, 1969).

Another key strategy to reduce the risk of costly kleptoparasitism, and risky encounters with competitors, is to feed quickly and move on. Speed-feeding—or "wolfing"—a kill is a clear adaptation to this process. This does not seem to be driven by intense intraspecific scramble competition, as evidenced by their youngest-feed-first system described above. With a capacity of approximately 9 kg (Creel & Creel, 2002), which represents around 30% adult body weight, an adult African wild dog's stomach is used as a shopping bag to evacuate meat from the danger zone as quickly as possible.

After feeding, packs always retreat some distance from the kill site before resting, which is sometimes but often not necessary for shade. This suggests that post-feeding abandonment of kill sites is done in response to risk of encounters with their heterospecific competitors, particularly since more dominant predators such as lions do not display this combination of fast feeding and retreat behavior. Valuable insights would be provided by comparative analyses of kill consumption rates and the frequency of post-consumption retreat from kill sites in relation to habitat and heterospecific predator densities.

Distributing Food to Other Pack Members

In addition to allowing pack members access to kills, patterns of regurgitation away from the kill site have been documented (Forssman et al., 2018; Malcolm & Marten 1982). As noted above, the fast-food take-away approach to feeding adopted by African wild dogs is likely an adaptation to the risk of ambush and kleptoparasitism at kill sites. While lions and other large carnivores rest at their kill sites, feeding leisurely from the carcass, African wild dogs feed quickly and leave, carrying up to 9 kg in their stomachs (Creel & Creel, 2002) and digesting it in relative safety away from the kill site. During the denning season, stomach contents are ferried back to the den, where pups, the breeding female, and possibly other helpers can be provisioned through regurgitation (Forssman et al., 2018) (Fig. 6.12). These individuals solicit feeding from the returning pack (Forssman et al., 2018), and most regurgitation occurs within the first few hours of their return.

Patterns of provisioning by regurgitation have only been examined in detail in one subpopulation around Kruger National Park (Forssman et al., 2018). In large packs, dominants were less likely to provision pups, whereas they were more likely than subordinates to do so in smaller packs, highlighting the importance of subordinate helpers. In large packs, yearlings were also more likely to regurgitate than adults. Sex had no impact on provisioning in any pack (Forssman et al., 2018), and no evidence of sex-biased provisioning exists in this species (McNutt & Silk, 2008).

While previous literature has suggested that wild dogs are limited by heterospecific density (Mills & Gorman, 1997, Swanson et al., 2014), recent evidence has brought to light mechanisms of coexistence that allow wild dogs to persist in areas of high lion density. In Kruger (South Africa), high prey availability allows wild dog packs to spatially partition from areas of high lion density (Marneweck, Marneweck, et al., 2019). At another, highly heterogeneous site, Hluhluwe-iMfolozi (South Africa), wild dogs persist with a high-density lion population by utilizing landscape features or dense vegetation to avoid detection (Davies et al., 2021). Indeed, when considering sites for the managed metapopulation in South Africa, the availability of suitable prey is ranked higher than the density of competitors (Mills et al., 1998). Thus, while competitors are an important part of their ecology, at

Fig. 6.12 An adult African wild dog regurgitates food for the pups, after commuting back to the den with a full stomach. Photo credit: Krystyna Golabek

least in some landscapes, African wild dogs can coexist with other large carnivores in high densities if sufficient prey are available.

Acquiring Food from Others
In addition to losing food to other species, African wild dogs are occasionally—albeit rarely—also the beneficiaries of kleptoparasitism. Black-backed jackals may lose kills or carcasses they are currently consuming to African wild dogs (Frame & Frame, 1981). Also, anecdotal observations by the authors of this chapter suggest that African wild dogs occasionally scavenge food, including kleptoparasitizing from leopards and cheetahs. Previous studies mention the appropriation of kills from spotted hyenas by African wild dogs (Frame & Frame, 1981; Kruuk, 1972; Kruuk & Turner, 1967; Schaller, 2009) but see Mills, (1993) and even once from lions (Creel & Creel, 2002). Nevertheless, while it is clear that African wild dogs opportunistically scavenge, scavenging is not a substantial part of their diet.

6.6 Spatial and Temporal Patterns of Hunting

African wild dogs have a crepuscular activity pattern, with hunts occurring around sunrise and sunset, and little activity in the middle of the day (Cozzi et al., 2012; Creel, 2001; Creel & Creel, 1995, 2002; Estes & Goddard, 1967; Fuller & Kat, 1993; Kuhme, 1965b; McNutt et al., 2019; Woodroffe et al., 2017). Nocturnal activity also occurs and is positively related to moonlight intensity (Cozzi et al., 2012; Rabaiotti & Woodroffe, 2019); however, dawn and dusk forays still contribute to the vast majority of hunts (Woodroffe et al., 2017), indicating that hunting studies based on crepuscular patterns are probably representative (Creel, 2001).

Several factors impact the timing, duration, and intensity of wild dog hunts. The timing of diel peaks in hunting is likely to be driven primarily by thermoregulation, with dogs hunting in the cool morning and evening, and engaging in little activity in the middle of the day when temperatures are highest (Cozzi et al., 2012). Moreover, wild dogs are more likely to engage in nocturnal hunts when day-time temperatures are higher (Rabaiotti & Woodroffe, 2019). Denning also influences diel hunt duration, with packs in Laikipia (Kenya) more active during denning (Rabaiotti & Woodroffe, 2019). There have been conflicting findings as to whether denning also affects the likelihood of nocturnal hunting—work from Selous (Tanzania) suggested that denning packs were more likely to hunt at night (Creel, 2001), whereas in Laikipia (Kenya), nocturnal hunts were less likely during denning.

Wild dogs are more likely to engage in a third hunting period at night when moonlight levels are greater (Creel, 2001; Rabaiotti & Woodroffe, 2019). This is likely due to higher levels of visibility facilitating detection and pursuit of prey as well as detection of potential competitors such as lions and hyenas. In two populations in Zimbabwe (Hwange National Park and a farming area of Nyamandlovu), packs frequently hunt by moonlight (Rasmussen & Macdonald, 2012).

6.7 African Wild Dogs in the Anthropocene

Once distributed throughout much of Africa, and with ancestral lineages in Eurasia (Madurell-Malapeira et al., 2013; Martinez-Navarro & Rook, 2003), African wild dogs are somewhat emblematic of so-called pristine protected landscapes, even famously being sighted on the snowy peak of Mount Kilimanjaro (Thesiger, 1970). However, the species now inhabits a mere 10% of its former range, and populations across Africa continue to decline (Woodroffe & Sillero-Zubiri, 2020). With each pack occupying several hundred square kilometers (Marneweck, Marneweck, et al., 2019; Pomilia et al., 2015), and individuals and cohorts sometimes dispersing over vast distances (Cozzi et al., 2020; Davies-Mostert et al., 2012), securing protected areas that are sufficiently large and capable of sustaining viable subpopulations of the species thus presents a considerable challenge. Consequently, packs in many subpopulations may be increasingly reliant on human-dominated landscapes and the implications of this reliance can be profound (Woodroffe & Ginsberg, 1998). Here we consider some aspects of the African wild dog social system that impact upon the species' ability to adapt to life in these landscapes, and in the Anthropocene more generally.

6.7.1 Hunting in Human-Dominated Landscapes

Historically, African wild dogs were believed to thrive only in vast and undisturbed landscapes free of human activity (Davies & Du Toit, 2004). However, conservationists have been inspired by the realization that this species can coexist alongside people and their livestock (Frank et al., 2005; Woodroffe, 2011a; Woodroffe et al., 2007). In such areas, African wild dogs kill livestock (Gusset et al., 2009; Rasmussen, 1999; Woodroffe et al., 2005), and on small game ranches, they also use fences to increase hunting efficiency by up to 11 times (Romañach & Lindsey, 2008).

African wild dogs in Zimbabwe tend to scatter (rather than clump) while resting when compared to those in protected areas. This is interpreted as a strategy to increase vigilance for humans and reduce their own detection (Rasmussen & Macdonald, 2012), though differences in lion densities and other variables between the sites cannot be ruled out as alternative drivers. Humans also have clear impacts on wild dog movements; movements are faster and more direct when outside of protected areas, yet slower in areas of high human footprint (Creel et al., 2020). Even within protected areas, anthropogenic features such as tracks and roads vastly influence the movement ecology of the species (Abrahms et al., 2016).

Taken together, these factors may impact African wild dog hunting ecology and success in human-dominated landscapes where wild dogs have the extra burden of vigilance toward the direct threat of humans while attempting to obtain adequate food resources. However, the reward for more easily captured prey (such as livestock that tend to be easier to catch than wild prey) might offset such a cost of extra vigilance. In South Africa, very few African wild dogs survive outside of protected areas due to retaliatory killing, and attitudes toward them are overwhelmingly negative (Thorn et al., 2015). African wild dogs can also be framed as problem animals where they overlap with livestock, depending on the agendas, priorities, and values of stakeholders (Fraser-Celin et al., 2018). A contributory factor to this is that African wild dogs are perceived as killing and consuming prey at unsustainable rates.

Certainly, during the 3-month denning season, when packs are constrained to approximately 27% of their annual home range (Pole, 2000; Pomilia et al., 2015) and energetic demands may be highest due to pup provisioning, dens located close to livestock enterprises can lead to severe conflict. Where natural prey is scarce, African wild dogs focus on goats and sheep, and the impact that twice-daily hunts of multiple domestic animals can have on farmers may be economically devastating. Retaliatory killing occurs, and to curb this risk and maintain genetic diversity in the subpopulation, researchers have attempted pup translocation or “adoption,” which occasionally occurs naturally (McNutt, 1996a), with mixed results (McNutt et al., 2008). Pups captured from such problem packs in livestock areas and translocated to denning packs in nearby protected areas in Northern Botswana were successfully adopted and raised by their recipient packs, with natal packs moving on and reducing the conflict (McNutt et al., 2008). Similar translocations have failed in the same context, with pups that were accepted initially ultimately failing to survive (N. Jordan & K. Golabek, pers obs). Such data hint at the potential failure to recognize unknown kin, or perhaps the benefits of increased pack size in this species selects for acceptance of non-kin.

6.7.2 *Potential Impacts of Changing Climates and Land Use*

With the ongoing expansion of human populations and the wide-ranging behavior of African wild dogs, strategies for coexistence in human-dominated landscapes may be crucial to the ongoing survival of the species. In Kenya, a multi-year study showed expansion of the wild dog population (in terms of density) and suggested that African wild dogs could avoid anthropogenic threats and thrive in some human-dominated landscapes (Woodroffe, 2011b).

The general recovery of the African wild dog population was attributed to vigilant herding of livestock by traditional pastoralists, who also engaged in minimal hunting of wild prey (Woodroffe, 2011a). Wild dogs in the area have been found to engage in minimal depredation of livestock, with only one attack annually per 1000 km^2, and mostly occurring where wildlife was heavily depleted (Woodroffe et al., 2005). While wild dogs have higher mortality on community lands (typified by abundant human populations and livestock) when compared to commercial ranches (with lower human and livestock densities) (Rabaiotti et al., 2021), the population still increased from a single pack in 2000, to the 5th biggest population globally in 2017. The success of this population, which has persisted outside protected areas for over 20 years, might be replicated in other areas where traditional pastoralism is still practiced.

High temperatures impact African wild dog hunting behavior, with shorter day-time hunts at high temperatures, and lower activity levels over 24 h (Rabaiotti & Woodroffe, 2019). Elevated temperatures also impact several demographic variables. Across three separate sites—the Okavango Delta in Botswana, Savé Valley Conservancy, Zimbabwe, and Laikipia Kenya—African wild dog survival to adulthood was lower when temperatures were higher during the denning period (Woodroffe et al., 2017).

This issue was particularly acute in Botswana, where over the course of the study mean maximum temperatures had increased by 1 °C, and recruitment had also fallen over that time (Woodroffe et al., 2017). It is hypothesized that this is due, in part, to the constraints that high temperatures put on hunting (Rabaiotti & Woodroffe, 2019). In at least one of these sites, high temperatures have also reduced adult survival, and this appears to interact with other human pressures. In Laikipia (Kenya), high temperatures are associated with higher adult mortality from direct killings by people and disease, which spills over from domestic dogs (Rabaiotti et al., 2021).

African wild dogs reproduce seasonally across most of their geographical range (McNutt et al., 2019), but the peaks in nutritional requirements of the pack have not been neatly coupled with abundances in prey availability or vulnerability. In Botswana, for example, impala are the main and preferred prey (Creel et al., 2004; Tshimologo et al., 2021), but peaks in impala vulnerability—during rutting (April-May) and calving (November) specifically—do not coincide with the peak denning season (June-September (McNutt, 1996b)) when the energetic costs of the pack are likely to be greatest. In African wild dogs, the timing of reproduction seems therefore to be linked more closely to ambient temperature, and in captivity they have different median birth dates coinciding with the coolest parts of the year in whichever hemisphere they are in (McNutt et al., 2019). At the equator, wild dogs breed year-round, with a mean inter-birth interval of 11 months, as opposed to 12 at seasonal sites (Woodroffe et al., 2017). When temperatures during the previous denning period have been higher, the period between one breeding attempt and the next is longer (Woodroffe et al., 2017).

Demographic impacts due to climate change are of particular concern because they not only impact areas where habitat is being lost, but, since changes in climate will occur universally across the continent, they also impact African wild dog populations in protected areas, where they are generally shielded from other threats. Indeed, a recent study on the Moremi (Botswana) population showed that whelping dates are progressivey delayed each year, as packs track the coolest months in which to raise oups (Abrahms et al., 2022). Packs are now giving birth up to 20 days later than three decades ago, and the narrowing thermal window, and its predicted negative impact on pup survival is a major cause for concern. Overall, it seems likely that these combined impacts will put some wild dog populations at risk, and research should focus on using modern climate forecasting to predict suitable areas in the future and make them priorities for African wild dog conservation.

6.7.3 *Intensive Population Management*

Under natural circumstances, African wild dogs disperse from their natal pack in single-sex cohorts in search of an unrelated opposite sex cohort with which to form a new pack (Creel & Creel, 2002; McCreery & Robbins, 2001). However, increasing human populations and fragmentation of suitable areas in the landscape limit successful dispersal and subsequent settlement in some populations, with dispersers and newly established packs encountering several threatening processes including human–wildlife conflict. In South Africa, the managed metapopulation approach—where packs in several fenced reserves are managed as a single population—replaces the natural dispersal with human-mediated dispersal (Davies-Mostert et al., 2009). In this process, cohorts that have already dispersed, or are likely to soon disperse, are captured, socially integrated with an opposite-sex dispersal cohort, and transported to a suitable new location (Davies-Mostert et al., 2009). Because this process mimics natural processes with individuals that are already (or imminently likely to be) dispersing, the remaining pack is not unnaturally impacted and remains a viable social unit. This program of coordinated reintroductions that includes multistakeholder engagement, feasibility assessments of potential new sites, implementation of reintroductions and population augmentations, and subsequent monitoring has enabled the South African wild dog population to grow substantially and subsequently stabilize (Nicholson et al., 2020). This "managed metapopulation" approach (i.e., managing fragmented and isolated subpopulations as one population with human-mediated dispersal) has ensured high genetic diversity (Tensen et al., 2019), and consistently accounts for an high proportion of the total population in South Africa over the past 20 years. Indeed, the metapopulation is now considered the backbone of South Africa's wild dog population, and South Africa is now the only country on the continent with an increasing and expanding population of African wild dogs.

The metapopulation approach to African wild dog conservation is sometimes argued to only be relevant within highly fragmented landscapes consisting of small (and perhaps fenced) protected areas in an ocean of high human population density, where intensive management (e.g., removal of dispersing individuals, translocations) is necessary for population growth (Nicholson et al., 2020). However, the managed metapopulation approach can also be useful in other landscapes. For example, this approach has aided African wild dog population recovery in the large, unfenced Gorongosa National Park (Mozambique) (Bouley et al., 2021). As elsewhere, the rapidly increasing human footprint in Africa will lead to an increase in fragmented habitat, which is particularly challenging for this wide-ranging species. As such, increasingly active and intensive management (such as a managed metapopulation) approaches are likely to assume greater importance across and beyond the extant range of African wild dog populations in increasingly fragmented habitats. The efficacy of future approaches will need to consider the effects of active human-mediated dispersal on the source population and on the social structure and hunting behavior of African wild dogs in both the source and newly introduced population.

6.8 Conclusions

African wild dogs exhibit a range of social and behavioral adaptations to hunting and survival in their extant range. While some of these strategies are common across subpopulations, African wild dogs also show a great deal of flexibility in social ecology across their range. Local adaptations occur across a suite of behaviors including prey preferences and hunting techniques, and these may arise due to variation in extrinsic factors such as prey availability, anthropogenic features and threats, habitat structure, and climatic conditions. While typified by group hunting, which is "a force in the evolutionary maintenance of group-living in wild dogs" (Creel, 2001), collective individual actions rather than collaboration per se seem to explain hunting success. Nevertheless, with approximately 31% of hunts resulting in prey capture, hunting success is far lower than most popular accounts and perceptions, and far closer to equivalent metrics for other species.

While detailed behavior or even pack demographic information is lacking from important parts of their extant range, and particularly central Africa where populations are fragmented and vulnerable, data from several key free-ranging populations contribute to our understanding of this cursorial species. Data from the managed metapopulation in particular show how wild dogs are adapting to a changing world, utilizing fences to increase the success of hunting and broadening the prey species and demographics available to them. Similarly, in human-dominated areas in East Africa, a shift to small prey in the absence of abundant wild alternatives demonstrates flexibility and potential for coexistence where at least some suitable wild prey persists. Nevertheless, changing land-use practices and climate impacts are already having measurable negative impacts on reproductive success and recruitment. Ultimately, the survival of this iconic social hunter lies beyond the pack and is likely to require increasingly intensive management intervention across and even beyond its extant range.

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Chapter 7
Social Strategies of a Consummate Marine Predator: Mammal-Hunting Killer Whales

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Abstract *Wolves of the Sea* is a commonly used moniker for mammal-hunting killer whales, but they are more than that with unique and blended characteristics of mammalian social carnivores. These marine mammal hunters are not archetypical predators. On current evidence, mammal-hunting killer whales do not show territoriality or defense of kills but may exhibit dominance hierarchy to reduce mating competition. But like most social mammalian carnivores, the social unit is fluid and female dominated. Mammal-hunting killer whales also show parental care, social bonding, culture, and social learning. The exceptionality of mammal-hunting killer whales is their embrace of a community of related and unrelated killer whales that share kill and do not compete for the same resources. Although the evolution of mammal-hunting killer whale societies is an area requiring research, there are ecological factors that may explain the social tolerance. For instance, adult killer whales have no natural predators and dominate the world's oceans feasting on diverse and abundant prey. Their hunting effectiveness, marine mammal diet, and high prey accessibility may be enough to meet energy needs and prevent the need for resource defense. Further, the ability of mammal-hunting killer whales to traverse huge distances and maintain extensive home ranges allows them to be flexible in their dietary patterns—going where the food is plentiful. Killer whales in shared habitats have developed remarkably different hunting behaviors that are adapted to prey type and ecological factors. Hunting group sizes are variable and consistent for pinniped prey, especially pups and juveniles. However, with exceptions, there is insufficient evidence available to correlate group sizes by prey type or hunting success. Despite a wealth of data from certain regions, we remain unaware of the

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strength of social associations and competition within an apparent expansive social network. We also lack knowledge about their hunting success, group size variation throughout the hunt, and costs/benefits of participating group and non-group killer whale individuals. Mammal-hunting killer whales seem engineered to hunt. They rarely switch off from foraging mode and seek to intimidate, harass, and hunt a variety of prey wherever they occur. Killer whale prey are not naïve and unresponsive. Most killer whale prey follow antipredator strategies and tactics that help to evade killer whale attacks or make it challenging for the predators to succeed. In this predator-prey behavioral game, killer whale hunting strategies are still far from understood. And while there is increasing evidence of sublethal effects from killer whales on prey behavior, our knowledge is limited to a few systems with no substantive analyses of killer whale ecosystem roles in human-dominated seascapes. Finally, there is a growing realization that killer whale communities, beyond the immediate social group, may be conduits for information transfer and that within social units, vertical and horizontal transmission of various hunting behaviors is important for succession and survival. Conservation approaches must consider the preservation of killer whale social units as human perturbations and climate change alter the marine ecosystems in unprecedented ways.

Keywords Mammal-hunting killer whales · Culture · Social carnivores · Predation · Group hunting · Social structure · Conservation behavior · Social learning

Artistic rendering by Britney Danials. Original photo credit: Mridula Srinivasan (foreground), Danial Bianchetta (background)

Frozen Planet *Season 1 Episode 1 Transcript*

Killer whales, the ocean's top predator. Killers are like wolves, for they will hunt animals far larger than themselves. But even smaller prey are a problem if you can't reach them. The solution is teamwork. Swimming in perfect formation, they flick their tails in unison and create a wave that cracks the ice. They regroup and assess the damage. A more powerful wave is needed. The ice floe is breaking up. Now they are close enough to get a good look at their target. The seal is a crab-eater, sharp-toothed and feisty. Not their favorite. The wolves of the sea move on, in search of easier quarry.

Scammon. 1874. Marine Mammals of the Northwestern Coast Pages 89–90 and 92.

Three or four of these voracious animals do not hesitate to grapple with the largest baleen whales; and it is surprising to see those leviathans of the deep so completely paralyzed by the presence of their natural, although diminutive, enemies. Frequently the terrified animal—comparatively of enormous size and superior *strength—evinces no effort to escape, but lies in a helpless condition, or makes but little resistance to the assaults of its merciless destroyers. The attack of these wolves of the ocean upon their gigantic prey may be likened, in some respects, to a pack of hounds holding the stricken deer at bay. … in whatever quarter of the world the Orcas are found, they seem always intent upon seeking something to destroy or devour.*

Boaz. F. Jan–March 1898. Traditions of the Tillamook Indians. The Journal of American Folklore Vol. 11, No. 40. https://doi.org/10.2307/533608

A year had elapsed; the people did not know that the young ones were still alive. One day they went out hunting seals and sea-lions. When they came to the rock, the two Killer Whales came out and devoured all the people; only the chief's son escaped by hiding under the bailer of one of the canoes. Peeping out from it, he saw one of the monsters swallow his father. He cried for fear, and pushed his canoe out into the sea, hoping to make his escape. He had no paddles, and drifted about helplessly. After a while some people who had remained in the village saw the canoe drifting by, and went out to secure it. They found the chief's son, who was so badly frightened that he was hardly able to speak. When he had recovered he told them what had happened.

The legend and enigma of the mammal-hunting killer whale are illuminated by the excerpts above from a nature documentary, historic literature, and American folklore. Yet, through the fog of abstraction and imagination, mammal-hunting killer whales are like other powerful group-hunting carnivorous predators. But group-hunting strategy and ecological conditions may influence social identity and associations and not vice versa. The chapter to follow explores these aspects by analyzing killer whale predatory styles within a socio-ecological context.

7.1 Introduction

From their historic depictions as a "whale killer" to their exalted role today as consummate social predators, killer whales (*Orcinus orca*, Linnaeus, 1758) have left an indelible impression as one of the fiercest predators on the planet. Physically, they are the largest species (Dahlheim & Heyning, 1999) in the dolphin family with an unmistakable striking black and white and gray shaded appearance. Females can reach a maximum length of 7.7 m and males 9 m with a nearly 2 m dorsal fin (Ford, 2019; Yamada et al., 2007). Killer whales occur in every ocean but are more abundant in coastal, high-latitude, and cooler temperate waters (Baird, 2000; Ford, 2019; Leatherwood & Dahlheim, 1978) than in the tropics (Forney & Wade, 2006; Wade & Gerrodette, 1993).

Killer whales are specialist predators but can assume a generalist diet in resource-poor environments. They can hunt and consume multiple marine species from sharks, rays, herring, and salmon to a variety of marine mammal species, including at least 20 cetacean species, as well as occasionally hunt or harass a trespassing deer or seabird (Best et al., 2010; Bigg et al., 1987; Durban & Pitman, 2012;

Ford & Reeves, 2008; Jefferson et al., 1991; Vos et al., 2006; Weller, 2009). But within certain geographic regions, killer whales are distinguishable into obligate fish hunters, marine mammal specialists, or nondiscriminatory predators consuming fish, invertebrates, and marine mammals in resource-limited environments.

In the North Pacific, distinct killer whale ecotypes are known based on morphology and dietary specialization. These ecotypes consist of Residents—exclusive fish eaters, Transients/Bigg's whales—predominant marine mammal hunters, and Offshore killer whales—shark specialists. Transient and Resident ecotypes also occur in Far East Russia (Filatova et al., 2015), as well as near Hokkaido, Japan (Mitani et al., 2021). In the northeastern Atlantic, Foote et al. (2009) classified Atlantic killer whales into Type 1 and Type 2 forms using a combination of tooth wear observations, mitochondrial DNA diversity, and δ15N (delta-N-15, a measure of the ratio of two stable isotopes of nitrogen) values. Predation observations further substantiate that Type 2 killer whales are cetacean specialists, while Type 1 killer whales are generalists feeding mainly on herring or mackerel but with some Type 1 individuals consistently eating both herring and seals near Iceland and Norway (Bisther & Vongraven, 2001). Similarly, in the Southern Ocean, there are at least five such recognized ecotypes—Type A, Types B1 (large form) and B2 (small form), Type C, and Type D. Type A killer whale, the largest form, feeds mainly on Antarctic minke whales (*Balaenoptera bonaerensis*). Type B1 preys on ice seals and B2 on *Pygoscelis* sp. penguins and marine mammals, Type C (Ross Sea) mainly predates fish, and Type D killer whale diet is unknown, but they are suspected to prefer fish based on depredation of Patagonian toothfish (*Dissostichus eleginoides*) from longline fisheries (Berzin & Vladimirov, 1983; Durban et al., 2017; Pitman & Durban, 2012; Pitman & Ensor, 2003; Pitman et al., 2011).

At this writing, killer whales represent one species globally and taxonomically despite morphological and behavioral differences, although further species designations are being proposed. Presently, killer whale ecotypes or different forms are defined based on prey preference, behavior, and appearance in well-studied habitats, but not based on genotype (Hoelzel et al., 2002; Leduc et al., 2008). Although no species-level delineations are currently recognized, genealogical studies suggest that ecological differences have shaped prey specializations. The behavioral adaptations of killer whale ecotypes (which globally diverged about 250,000 years ago) could arise due to the combined effects of ecological, cultural, and genetic differences (Foote et al., 2016). Further, by using sophisticated and sensitive high-throughput sequencing of the entire mitochondrial genome of 139 killer whale samples from the North Pacific, Antarctic, and North Atlantic, Morin et al. (2010) recommended that pagophilic Type B and C killer whales in the Southern Ocean and Bigg's killer whales in the North Pacific should be designated as separate species and the rest of the genetically indistinguishable ecotypes as subspecies. Nuclear sequencing and mitogenomic analysis of additional samples from these regions and tropical oceans may provide the necessary lines of evidence to delineate separate killer whale species. But for now, we consider all killer whale ecotypes or forms to represent a single species.

Mammal-hunting killer whales offer the best marine equivalent of a superlative social carnivorous predator. They can chase and successfully attack prey larger than themselves, exhibit coordination and cooperation maintain permanent and ephemeral social bonds beyond their immediate social unit or group, and invest in extensive social learning and cultural specialization. Much like the terrestrial carnivores in this book, mammal-hunting killer whales provide for an ideal study animal to understand the evolution and persistence of sociality among large social mammalian carnivores that routinely and deftly attack prey larger than themselves. They are also a good test example to delineate whether social dynamics determine group hunting or vice versa. We evaluate these questions by exploring the complex layers of predating mammal-hunting killer whales across habitats marked by physiological and social traits, converging prey-specific hunting strategies, ecological differences, and culturally mediated behaviors. We also highlight the unique social systems of these killer whales that separate them from other terrestrial social carnivores and elevate our understanding of mammalian social evolution.

7.2 Anatomy of a Hunt

7.2.1 Physiological Demands

Bioenergetics may be a principal factor affecting killer whale prey choice to feed exclusively or occasionally on marine mammals (Lima et al., 2003). Most marine mammals have higher basal metabolic costs and therefore higher caloric demands compared to their terrestrial counterparts of equivalent size (Williams, 2006; Williams et al., 2001). Although the reasons are not fully known, an aquatic endothermic existence, carnivory, and a large gastrointestinal tract may elevate metabolic rates (Williams, 2006). Mammal-hunting killer whales that feed on minke whales in the Southern Ocean are larger than their fish-eating counterparts, which are 2–3 m smaller (Pitman, Perryman, et al., 2007); the same is true for Atlantic Type 2 killer whales that are cetacean hunting specialists (Foote et al., 2009). The large size and higher metabolic costs for killer whales equate to estimated daily energetic requirements of 193,000 kcal/day for an adult female and 287,000 kcal/day for an adult male killer whale (Williams et al., 2004).

Feeding on a large whale may allow a group of killer whales to meet individual daily energetic needs but may not always be a reliable option (Jefferson et al., 1991; Williams et al., 2004). Moreover, handling and processing times reduce the amount of salvageable carcass for the predators since most species of freshly killed whales can sink quickly and become inaccessible rapidly in deep waters. Thus, killer whales that specialize in hunting large whales favor consumption of the tongue (2.07 kcal/g, Williams et al., 2004) and portions of the blubber (4.0 kcal/g, Williams et al., 2004), which are also some of the most nutritious parts. Also, like other predators, killer whales may increase the diversity and quantity of prey consumed or, as an optimum foraging strategy, preferentially obtain nutritiously rich prey (Gomez et al., 2016; Spitz et al., 2012; Sutton et al., 2015).

Overall, hunting marine mammals is an expensive exercise for killer whales if the costs of prey searching, capture, handling, and potential injury while subduing larger and dangerous prey are programmed into overall foraging costs (Carbone et al., 2007). Moreover, these costs may be intensified when hunting marine mammal prey with similar sensory features. Killer whales frequently rely on stealth, stamina, and power in their hunting maneuvers to outwit and overpower prey. Consequently, these strategies add to foraging costs, and thus killer whales, like other large carnivores, maintain extensive home ranges, manage group size for maximum energy gain (Baird, 2000; Baird & Dill, 1996), and regulate activity levels to minimize energetic constraints (Kelt & Van Vuren, 1999; McNab 1963). For example, the predominant daily activity for Bigg's killer whales is foraging (63%) with only 2% of their time spent resting near Vancouver Island, British Columbia (Baird & Dill, 1995). Similarly, in Prince William Sound, Alaska, Bigg's killer whales spend 50% of their time foraging and 4% resting (Saulitis et al., 2000). However, Gulf of Alaska Bigg's whales rested more (43%) and foraged less (23%) in a study by Maniscalco et al. (2007), although they acknowledged that some predation events may have gone unobserved. Traveling and foraging behavioral states are difficult to tease apart in daily activity budgets and are sometimes best combined in analysis (Ford et al., 2013).

7.2.2 The Social Unit

Our understanding of mammal-hunting killer whale societies is sourced from the intensively studied Bigg's killer whales occurring near British Columbia, Washington, and southeastern Alaska. From long-term monitoring (Bigg et al., 1987; Ford & Ellis, 1999; Ford et al., 1998), we know that these killer whales have a fluid fission-fusion multilevel social structure that is not strictly matrilineal like their fish-eating sympatric Resident killer whales. All Bigg's (Transient) killer whales are composed of a single matriline compared to the 11 or so matrilines found in fish-eating Resident killer whales (Baird & Whitehead, 2000).

A typical group may include a female and her offspring. Both female and male offspring may leave their natal group as a juvenile or subadult and join other associates. Female offspring may occasionally return to the natal group for short periods but disperse again (Baird & Whitehead, 2000; Bigg et al., 1987). However, male offspring (especially, the firstborn) may stay with the mother for decades or turn into lone wandering males when the mother dies (Baird, 2000). Members within a group can form long-term and often everlasting social bonds and comprise a pod of mixed sex and age classes. Female-male associations tend to be stronger than female-female or male-male bonds (Baird & Whitehead, 2000), at least in Bigg's whales in the North Pacific. Near Galápagos Islands, Denkinger et al. (2020) found some adult male-male pairing to have strong associations, but these data could also be artifacts of the distinctiveness (human recognition) of male killer whales. However, Hoelzel (1991) also reported long-term bonding between a pair of genetically related adult males near Punta Norte, Argentina.

Post-reproductive females and older females may serve critical roles in killer whale social dynamics (see also Chap. 8, Black et al., in this book). Based on the evidence from fish-eating Northern Resident killer whales off British Columbia, Olesiuk et al. (2005) estimated a mean life expectancy of 46 years for female killer whales and about 31 years for male killer whales in the wild. Also, females reach reproductive senescence close to 40 years of age and continue to be part of the family unit. Recent work suggests that Bigg's whales may also have a long post-reproductive period similar to fish-eating Northern and Southern Resident killer whales, representing an important life stage for killer whale societies and providing substantial benefits to kin (Nielsen et al., 2021).

The social unit's size and composition may be largely determined by resource abundance, foraging specialization, and energetic demands. For example, both near the Galápagos Islands and Marion Islands, in the sub-Antarctic Indian Ocean, killer whales exhibit fission-fusion social dynamics (Denkinger et al., 2020; Jordaan et al., 2021) that may be partially influenced by localized prey resource availability and abundance. The "Goldilocks principle" may apply, where the size and the composition of the unit are exactly right to maximize hunting success (energetic gains) and avoidance of inbreeding (see Sect. 7.4 on group sizes).

In many geographic areas, members of mammal-hunting killer whales frequently intermingle with other groups, and these could represent a community or a large coalition with shared foraging needs (Baird & Whitehead, 2000; Black et al., 1997; Denkinger et al., 2020; Ford & Ellis, 1999; Guinet et al., 2000; Matkin et al., 1999). Some inter-pod interactions could be dictated by large prey size (Arnbom et al., 1987; Brennan & Rodriguez, 1994; Pacheco et al., 2019; Pitman, Fearnbach, et al., 2007), but they may also provide occasions for mating opportunities and social play (Baird & Dill, 1995). The associations are dynamic within this community, displaying no intraspecific aggression, territoriality, or defensive tactics despite overlapping ranges (Ford, 2009; Ford & Ellis, 1999)—unique relative to other social terrestrial carnivores compared in this book. While there is no discernible dominance hierarchy during feeding or niche segregation in killer whale society, it cannot be ruled out. Given physical attributes (oversized appendages), dominance may be exerted by male killer whales to improve reproductive success (Ford et al., 2011), but the exact biological mechanisms are not fully understood.

Bigg's whales may avoid encounters with fish-eating killer whales, due to examples of aggression displayed by fish-eating killer whales towards their mammal-hunting neighbors (Baird & Dill, 1995; Barrett-Lennard, 1992; Morton, 1990). Agonistic interactions between mammal-hunting killer whale groups are rarely reported during predation events. However, Baird and Dill (1995) noted that Bigg's whales in British Columbia associate often and closely with other whales that share similar foraging behaviors (e.g., foraging in open waters).

Again, unlike Resident killer whales, Bigg's whales, as well as mammal-hunting killer whales in other regions, show a limited acoustic repertoire, rarely use echolocation clicks, and exhibit population-specific calls (Barrett-Lennard et al., 1996; Deecke et al., 2005; Ford, 1984; Guinet & Jouventin, 1992). Killer whales can employ whistles (tonal signals) for social cohesion and short-range communication and pulsed calls (more often) to coordinate behaviors and group identification (Ford, 1989). However, mammal-hunting killer whales rarely produce pulsed calls, unless in a social context or after a hunt (Deecke et al., 2005). The limited range and frequency of vocalizations allow the killer whales to eavesdrop on potential prey and be acoustically inconspicuous to cetaceans and pinniped prey with high hearing acuity and overlapping communication ranges (Riesch & Deecke, 2011; Terhune, 1988).

Unlike the large groups formed by Resident killer whales, previous studies show that Bigg's whales usually travel in small hunting groups of six or fewer animals (Baird & Dill, 1995, 1996; Ford & Ellis, 1999), especially when hunting seals, sea lions, and sea otters (*Enhydra lutris*). However, recent data suggest that they may occur in much larger groups, ten or more, at times (Ford et al., 2013). Also, mammal-hunting killer whales can easily associate with related and unrelated killer whales to form larger group sizes, especially when hunting whales (Higdon et al., 2012; Pitman, Fearnbach, et al., 2007; Silber et al., 1990). The combination of acoustic crypticity and generally small group sizes elevates the importance of visual signaling and constitutes a fundamental foraging strategy (see Sect. 7.4 on group sizes). Based on the convergence of hunting behaviors influenced by ecological attributes and prey specialization in other less studied regions, the social composition and organization of mammal-hunting killer whales in other less studied regions may not be remarkably different.

7.2.3 Hunting Strategy

Mammal-hunting killer whales are remarkable hunters (Reeves et al., 2006). They use methodical and at times novel techniques to search and capture prey and transmit those learnings across generations. Yet a hunting strategy is not just the execution of the hunt but the rehearsals before to maximize hunting success. One such strategy is for predator movements to map with preferred prey densities, behavior, and temporal activity (Heimlich-Boran, 1988; Lima, 2002). The literature is replete with examples of mammal-hunting killer whale seasonal distribution coinciding strongly with preferred prey seasonality, breeding periods, and abundance. However, higher prey abundance does not automatically guarantee higher predation risk for their prey, and killer whales can be choosy.

Previously, Bigg's whale pods occur reliably each year near southern Vancouver Island nearshore haulouts during the harbor seal, *Phoca vitulina*, pupping (weaning to postweaning) season (Baird & Dill, 1995), but in recent times, their numbers have increased and are present daily around southern and eastern Vancouver Island with a great diversity in individuals and groups (Ford et al., 2013).

In coastal Norwegian waters, seal-specializing killer whale groups (Jourdain et al., 2017) have a high probability of occurrence during peak pupping and weaning times for harbor (June–July) and gray seals, *Halichoerus grypus* (September–October). The pattern repeats in Punta Norte, Argentina, where killer whale groups hunt weaned pups and juveniles of southern sea lions, *Otaria flavescens*, and elephant seals, *Mirounga leonina* (Hoelzel, 1991; Lopez & Lopez, 1985). In Western Australia, killer whales seasonally match the predictable presence of humpback whale (*Megaptera novaeangliae*) calves during austral winter (Pitman et al., 2015).

In tropical habitats in the southeastern Pacific, where killer whale studies are infrequent, evidence suggests that killer whales significantly overlap in distribution with humpback whales in Peru, southern Ecuador, and Galápagos (Capella et al., 2018; Testino et al., 2019). In Peruvian waters, killer whale attacks coincide with humpback whale breeding areas or near southern sea lion and southern fur seal (*Arctocephalus australis*) rookeries (Testino et al., 2019). Off Kaikoura, New Zealand, killer whale peak sightings coincided with the nearshore (<1 km) preference of dusky dolphins (*Lagenorhynchus obscurus*) during austral spring, summer, and late autumn, also when dusky calves are in abundance (Srinivasan & Markowitz, 2010).

Hunting habits can change with changing environmental states as witnessed in the Pacific Arctic (Stafford, 2019) and the eastern Canadian Arctic (Ferguson et al., 2012; Higdon & Ferguson, 2009, 2011). With ice-free habitats opening, mammal-hunting killer whales dominate in the Canadian Arctic and have a year-round presence seeking bowhead whale (*Balaena mysticetus*) calves, but largely monodontids (narwhals, *Monodon monoceros*, and belugas *Delphinapterus leucas*). Killer whales can also alter diel feeding cycles. Evidence from the northeastern Pacific (Baird et al., 2005, unpublished data) shows that mammal-hunting killer whales are rarely active at night, which is consistent with their daytime hunting of seals. However, in the Bering Sea, Newman and Springer (2008) reported higher killer whale feeding activity at night, matching the predominant nocturnal feeding of Pribilof northern fur seals (*Callorhinus ursinus*).

Habitat-specific prey specialization is another evolutionarily stable behavior for mammal-hunting killer whales in different geographic regions or within sympatric areas. For example, unlike their sympatric ecotype, some Bigg's whale pods off southern Vancouver hunt extensively on harbor seals and occasionally consume smaller porpoises, but in deeper open waters. In Alaskan waters, three subpopulations of Transient mammal-hunting killer whales are recognized (Barrett-Lennard & Ellis, 2001; Ford & Ellis, 1999) that include the West Coast Transients (around a range of 200 from California to southeastern Alaska), AT1 Transients (around 7 whales exist today, Muto et al., 2018), and Gulf of Alaska Transients (estimation of around 60 animals, Ford & Ellis, 1999). There is evidence of niche partitioning of prey among the sympatric Gulf of Alaska and Alaska AT1 whales near Kenai Fjords and Prince William Sound (Maniscalco et al., 2007; Matkin et al., 2005; Saulitis et al., 2000).

The Gulf of Alaska whales appear to selectively target Steller sea lions (*Eumetopias jubatus*) in this region even though harbor seal abundance is higher than that of sea lions. These killer whales may have a penchant for sea lions as they are observed hunting them in Kodiak, Alaska, during other times (Maniscalco et al., 2007), and this could be a cultural feature for Gulf of Alaska killer whales. The AT1 whales consume a separate set of prey, such as harbor seals (chiefly), Dall's porpoises (*Phocoenoides dalli*), harbor porpoises (*Phocoena phocoena*), and northern fur seals. Large whales are rare and are not part of the killer whale diet in coastal British Columbia and southeastern Alaska waters (Ford et al., 2005). The story is different in the Aleutian Islands, and near Unimak Island-Unimak Pass east, where gray whales (*Eschrichtius robustus*) migrate north through a shallow strip of water (about 70 m deep) and where calves and subadults become a regular target of California Bigg's whales in May. From June through September, killer whales shift to hunting northern fur seals to the west of Unimak Pass. Minke whales (*Balaenoptera acutorostrata*) and Dall's porpoises are also an important part of the diet, but harbor seals are notably missing from the diet (Matkin et al., 2007).

Off California, and especially near Monterey Bay, California Transients annually and seasonally attack migrating gray whale mothers with calves (see Chap. 8, Black et al., in this book). But killer whales have historically preyed on gray whale calves or subadults all through their migration corridor from Mexico to Alaska and in their feeding groups in the Bering and Chukchi seas. Gray whale calf attacks by killer whales date back to the 1840s near Baja California when commercial whaling for gray whales began in earnest (Scammon, 1874). Interestingly, connected with prey specialization is the employment and convergence of hunting techniques in Arctic and Antarctic waters and in tropical and temperate habitats. Some whales have developed sophisticated and sometimes risky maneuvers to hunt prey in given habitat topology and ecological constraints. In the sections below, we delve into the anatomy of a hunt or layers of a hunting sequence to fully grasp killer whale versatility and behavioral plasticity.

7.2.3.1 Prey Searching

Killer whales hunting marine mammal prey often use two searching patterns. The first involves traveling nearshore or heading into bays in tight groupings and maintaining erratic and often longer duration dive patterns while prowling the shoreline contour for mostly pinniped prey (Baird & Dill, 1995; Hoelzel, 1991; Morton, 1990). The second approach involves following open-water bathymetric contours to capture large groups of pelagic delphinid and sometimes adult pinnipeds, and often tracking the continental shelf or edge, especially when seeking large whales (Barrett-Lennard et al., 1996; Saulitis et al., 2000; Testino et al., 2019). With the exceptions of a few well-known hunting spots, it is unclear how killer whales reliably find patchy prey in open waters. Are they tracking the prey, the resource of their prey, or both (Lima, 2002)?

As game-theoretic approaches suggest, it is possible that killer whale prey encounter rate could be a function of habitat selection (discussed earlier), prey abundance, and encounter probabilities (Creel, 2010; Cressman et al., 2014; Lima et al., 2003). Another possibility is that the hunting whales maintain long-term spatial memories of successful hunting grounds, which may influence their search patterns, as suggested for blue whales (*Balaenoptera musculus*, Abrahms et al., 2019) and harbor seals (Iorio-Merlo et al., 2022).

Two other prey-searching strategies enhance the stealth hunting style of mammal-hunting killer whales. Bigg's whales spend >75% of their activity budget on foraging and traveling (Baird & Dill, 1995; Ford & Ellis, 1999; Morton, 1990). They can traverse extensive distances (Durban & Pitman, 2012), perform long-duration dives (Baird et al. unpublished data), and travel underwater over >1 km distance (Maniscalco et al., 2007). Goley and Straley (1994) recorded a Bigg's killer whale traveling a linear distance of more than 2600 km between Alaska and California. Matthews et al.'s (2011) satellite tracked a mammal-hunting killer whale, which traveled from the eastern Canadian Arctic (Lancaster Sound) into the open waters of North Atlantic covering a distance >5400 km in nearly a month—one of the longest distances measured for a killer whale. Their presence in the eastern Canadian Arctic coincides with the seasonal abundance of their mammalian prey and ice cover. In general, by dispersing across vast home ranges, they sustain an element of surprise and unpredictability, which is advantageous when hunting alert cetacean or pinniped prey.

Mammal-hunting killer whales are notoriously silent roving predators, as discussed before. The quiet searching serves two purposes: (a) to remain undetected by wary prey and (b) to listen for vocalizing cetaceans and pinniped prey that fall within their hearing range. However, silence does not always occur, for they may vocalize actively after a hunt, and often during social activity including play (Barrett-Lennard et al., 1996; Deecke et al., 2005). Passive listening is also an important part of the prey-searching arsenal when seeking elusive whales like beaked whales (*Mesoplodon* sp.) that usually vocalize at depth but are visually and acoustically cryptic at the surface. Beaked whales show some of the strongest fear responses of any cetacean to killer whales in playback experiments (Aguilar De Soto et al., 2020; Tyack, 2011).

We are remiss if we ignore the prey component of the predator-prey interaction. Prey behavior and antipredator strategies probably have a strong bearing on killer whale prey search modes and are not necessarily dictated by prey availability. We will discuss prey behaviors later in this section. We are dealing with sophisticated and behaviorally responsive predators and their prey, and they take cues from each other in the predator-prey shell game (Creel, 2010; Mitchell & Lima, 2002). Mammal-hunting killer whale foraging decisions (search patterns and prey selectivity) in open and nearshore systems, confronted with diverse types of prey with varied antipredator defenses, are a fascinating area for future research.

7.2.3.2 Prey Handling and Attack

Comprehensive observations of killer whale predation are possible in a few areas. Even in well-observed areas, researchers may arrive during or well after an attack, or miss the event entirely due to the nature of the attack and the prey species concerned. However, with time, the compilation of records from multiple researchers and through different platforms of observation reveals a pattern in killer whale hunting methods once a suitable prey type is found.

Great Whales: Baleen Whales and Sperm Whales

Baleen whales within the suborder *Mysticeti* range in size from the smaller sized minke whale (*Balaenoptera acutorostrata*, approximately 10 m, and over 9000 kg in weight) to the largest blue whale (approximately 33 m, and over 130,000 kg). There are smaller and larger forms of minke and blue whales depending on the region. Smaller forms are common in tropical areas (e.g., pygmy blue whales *Balaenoptera musculus brevicauda*), whereas the larger forms (e.g., Antarctic minke whale or blue whales) are found in the Southern Ocean. Also, baleen whales are sexually dimorphic, with adult females slightly larger in size than males of similar age—although sex is difficult to discern at sea without sustained photographic data or the presence of a calf. Besides mother-calf associations, the 14 whales in this suborder are solitary. Some species like humpback whales, minke whales, and Bryde's whales (*Balaenoptera edeni*) may form temporary aggregations and associations while feeding or mating (Bannister, 2009). Other than bowhead whales and a few tropical whales, most mysticetes engage in long-distance migrations between the tropics (breeding/calving habitat) and higher latitudes (feeding habitat). Mothers with calves make attractive targets for killer whales along the migratory route (Pitman et al., 2001; Reeves et al., 2006).

Sperm whales (*Physeter macrocephalus*) are the largest among the toothed whales or odontocetes, reaching maximum lengths of about 15–18 m (males) and 11 m (females). The males can attain weights of over 35,000 kg, and thus there is clear sexual dimorphism, as in killer whales. Sperm whales maintain strong social units comprised of females and calves in low to midlatitudes, while bull males largely roam alone in higher latitudes (Whitehead, 2009). Sperm whales are deep-water oceanic species, often found in waters deeper than 1000 m. They may show seasonal north-south migration between the higher latitudes (summer feeding areas) and tropical waters (breeding areas) or exhibit movements devoid of seasonality in temperate and equatorial waters (Whitehead, 2003).

Hunting large solitary whales or sperm whale clusters would appear impossible due to prey size and strength. Yet some killer whales have succeeded in developing clever techniques to subdue and consume or severely injure these great whales. Norman and Fraser (1949), in the section on whales and dolphins, describes an account of killer whales hunting baleen whales—(sic) *Killers hunt in packs varying in number from two or three to thirty or forty, and when attacking large baleen whales their behavior is comparable to that of a pack of wolves attacking a deer.* Also described is a hearsay account about killer whales cooperatively attacking baleen whales—(*Killers*) *… will lay hold of a whale's tail to keep him from threshing (sic) while others lay hold of his head and bite and thresh (sic) him; the* *poor creature being thus held lolls out his tongue and then some of the Killers catch hold of his lips and if possible of his tongue, and after they have killed him they chiefly feed upon the tongue and head, but when he begins to putrefy (sic) they leave him.*"

Similarly, Shaler (1873) provided a second-hand account of purported killer whale attacks on sperm whales and other great whale attacks—*Capt. Pease found a sperm whale nearly dead on the water with the lower jaw hanging by a single band of ligament a few inches through. The creature was being devoured by sharks and crustaceans, but the wrench which had crippled this whale must have come from one of his kind. Captain Pease has several times seen the killer attack right and humpback whales; they strike for the tongue if possible. They often jump many feet from the water and fall upon him. Many individuals, fifty or more, join in this attack. They tear out large pieces from the blubber, food being evidently the object of their attack. Their great activity makes the whale helpless against them, though he will struggle furiously before overborne. They sometimes drag down the whale after it has been killed by the whalemen*. While the accounts described above appear embellished, the fundamentals of the hunting sequence have been substantiated by several observations since then and are further illustrated below.

Select Prey

If killer whales come across a group of whales, their first task is to isolate a suitable target. For example, Whitehead and Glass (1985) witnessed killer whales moving between concentrations of feeding humpback whales before honing in on a group of three humpback whales. Usually, killer whales target calves, juveniles, or subadults (Jefferson et al., 1991; Weller, 2018), although they may also seek the weak and wounded animal amid the group (Jefferson et al., 1991). Adult whales are rarely chosen, but killer whales may still pursue them and grab chunks of flesh from them—although their motivations for these actions are not understood (Pitman et al., 2015; Tarpy, 1979; Totterdell et al., 2022; Whitehead & Glass, 1985)—or may scavenge carcasses (Pitman, Fearnbach, et al., 2007) as killer whales did during whaling times (Whitehead & Reeves, 2005).

Southern right whales (Eubalaena australis) (Cummings et al., 1972; Sironi et al., 2008), humpback whales (Pitman et al., 2017; Whitehead & Glass, 1985), and sperm whales (Pitman et al., 2001; Visser, 1999; Weir et al., 2010) possess some defense strategies that could frustrate killer whale attacks. Killer whales may prevail despite the sturdy defense not because of brute force but through a seemingly effortless execution of hunting strategies. Also, abandoned or failed hunts may involve younger animals (calves/juveniles) and therefore are occasions for social learning (Reeves et al., 2006).

Chase

Once the target is chosen, killer whales coordinate and cooperate to separate mom and calf (if present together) and drown the calf/subadult/juvenile. Killer whales may

Fig. 7.1 Killer whales travel with synchronous respiration. Photo credit: M. Srinivasan

reach speeds of 30–40 km/h when pursuing fast-swimming prey like fin whales, *Balaenoptera physalus* (Vidal & Pechter, 1989) or common minke whales (Ford et al., 2005). During chases, killer whales may exhibit synchronous dive or breathing patterns and be abreast or parallel to each other (Fig. 7.1), sometimes forming a crescent pattern (Ljungblad & Moore, 1983 (Fig. 7.2)). These synchronous dives are believed to reflect coordinated hunting tactics, with the principal objectives of tiring the prey and perhaps giving the appearance of a smaller hunting group than in actuality (Ljungblad & Moore, 1983).

Killer whales may maintain synchrony in their dive behavior regardless of age-sex differences during a hunt. In a limited study, Miller et al. (2010) found that adult males may be diving well within their aerobic limits, while the younger and smaller bodied animals may be stretching close to or past their maximum aerobic dive capacity. Thus, mixed age-sex killer whale hunting units may be compromised physiologically to maintain synchronicity. Fortunately, since their marine mammal prey also surfaces to breathe, there is less physiological competition between prey and predator. However, in prolonged and coordinated hunts in deep water, an adult male killer whale may have the advantage to stay deeper and longer to tire and attack prey, thereby reducing the burden on physiologically less able members of the hunting group. However, adult male killer whales may falter during a sustained chase due to their immense physical attributes, such as mass and length relative to female killer whales, and a nearly 2 m dorsal fin and pectoral flippers, potentially creating undue drag during high-speed chases (Ford et al., 2005).

Fig. 7.2 Killer whales in a crescent formation while hunting a gray whale mother-calf pair. Photo credit: M. Srinivasan

Once they catch up to the prey, animals take flanking positions on all sides to prevent animals from escaping and diving. Killer whale group sizes can be highly variable and might not necessarily increase proportionately with the size of the prey. Group size variability and hunting success are discussed in Sect. 7.4.

Ram, Suffocate, Drown

Testimonials of killer whale attack sequences indicate role specialization, coordination, and cooperative behaviors. Examples are of Bryde's (Alava et al., 2013; Silber et al., 1990), gray (Baldridge, 1972; Goley & Straley, 1994), southern right (Sironi et al., 2008), bowhead (Ferguson et al., 2012; Mitchell & Reeves, 1982; Young et al., 2020), blue (Totterdell et al., 2022), humpback (Flórez-González et al., 1994; Naessig & Lanyon, 2004), and minke whales (Ford et al., 2005; Guinet et al., 2000). In most cases, there are three aspects to a typical whale attack. The first is to immobilize the prey (biting skin and blubber from the dorsal fin/ridge, flanks, and caudal peduncle). The second is to suffocate and attempt to drown the animal by slamming on top of the rostrum/head and ramming the animal from the sides. Post-immobilization (when prey stops resisting), killer whales access the mouth (sometimes the jaw is removed) and consume the tongue and lips. The third is to prevent the whales from moving into shallow water depths.

These actions often take place concurrently, with different killer whales in the group assuming separate attack positions. While a few may block paths for escape,

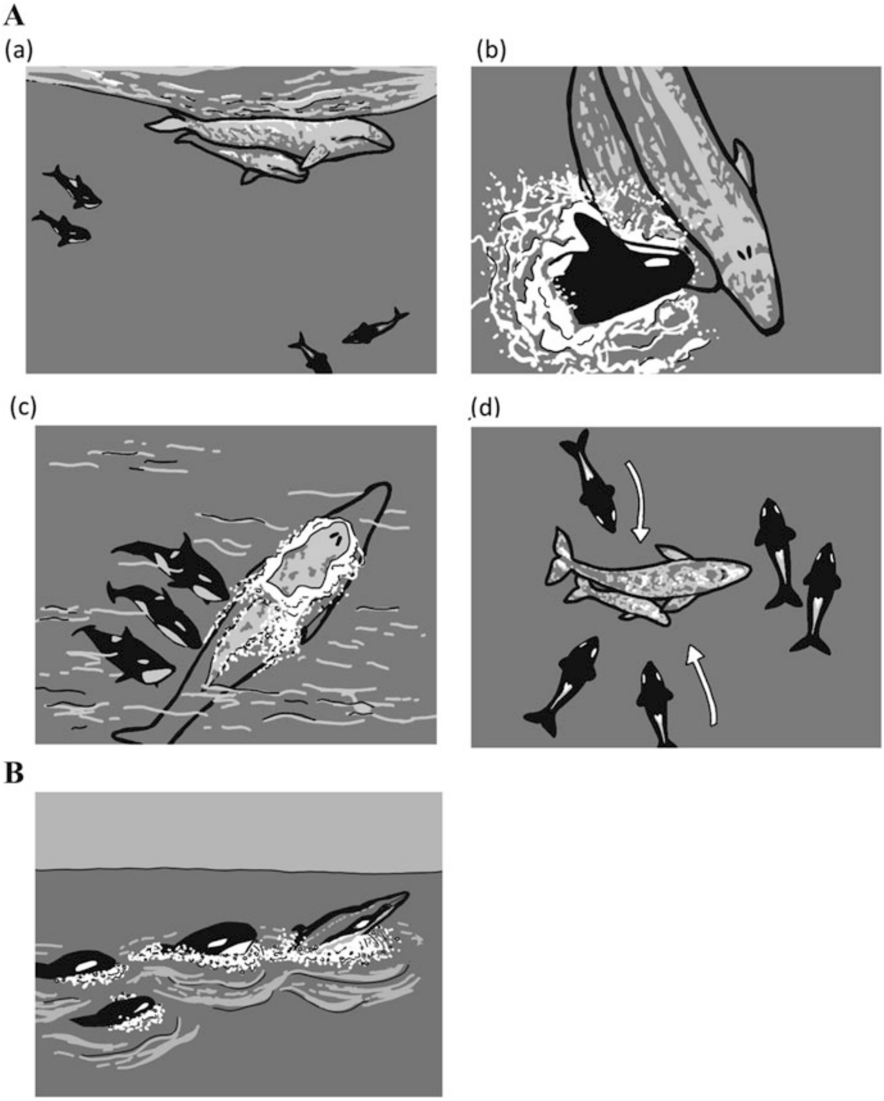

Fig. 7.3 (**A**) A hypothetical example of killer whales attacking a gray whale mother and calf pair by first (**a**) tracking and targeting a specific pair, then (**b**) separating the mom from calf, (**c**) ramming the whales on the flanks synchronously, and (**d**) attempting to block escape. (**B**) A hypothetical scenario of killer whales in pursuit of a fast-swimming minke whale. Illustrations by Hannah Rappoport

others may get on top of the whale to suffocate and drown the animal, while the rest may bite the mouth, jaw, flanks, tail fluke, or tug at the pectoral fins or tail flukes (e.g., Fig. 7.3). Still, others may act in unison by lining up parallel to each other and

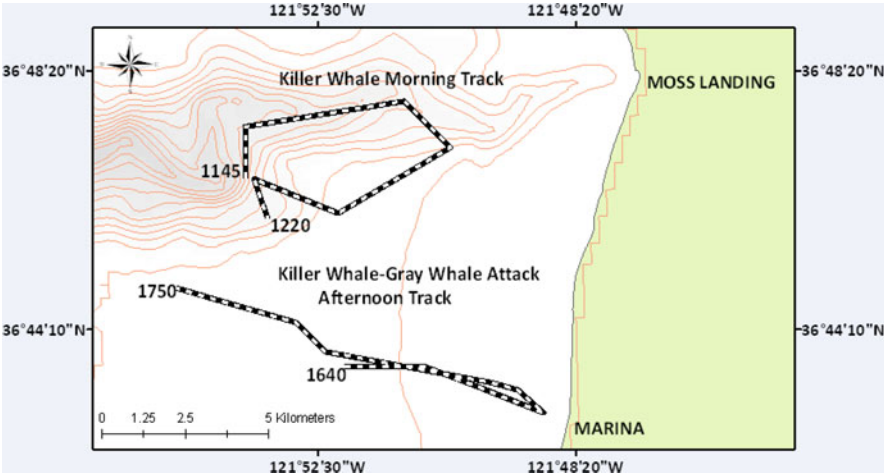

Fig. 7.4 Mammal-hunting killer whale group GPS tracks along the eastern edge of the Monterey Canyon in the morning and later in the afternoon when attacking a gray whale mom and calf pair. Data source: M. Srinivasan, unpublished data

perpendicular to the whale and ram the whale together. The hunting sequence and division of labor indicate abundant coordination and cooperation among the animals (Jefferson et al., 1991 and references therein). If the acquisition of the prey is prolonged, killer whales may take turns attacking.

Figure 7.4 shows GPS tracks of killer whales hunting a gray whale mom and calf pair. The gray whale pair eventually escaped by moving into shallower waters <15 m deep. The figure also provides a glimpse into the canyon shelf edge patrolling by these same killer whales earlier in the day to detect the potential passing of gray whale cow/calf pairs.

Killer whales may not always attack calves and juvenile baleen whales. Sironi et al. (2008) provided several case studies from Patagonia, Argentina, wherein most killer whale attacks (a total of 12 attacks) targeted adult (including mothers) southern right whales and were often orchestrated by male killer whales either in association with other killer whales or by themselves in four of the attacks reported. The authors commented on the segregation of roles by age-sex classes. For example, male killer whales would grab the pectoral fin of the adult whale and charge and bite the right whale while the females charged but did not bite, and the juveniles remained afar from the prey under attack to presumably avoid potential injury. Still, in another incident, the juveniles mainly engaged in pursuing adult right whales although adult killer whales remained in the vicinity. During the hunt, killer whales aimed attacks at the flanks, pectoral fins, jaw, genital area, and flukes. Interestingly, during some predation events, killer whales switched between hunting elephant seal pups and attacking right whales. Again, as with most attacks on large whales, the killer whales also coordinated behaviors to keep the whales in deep water. Male killer whales patrolled the shore while group attacks occurred, perhaps to prevent escapes to shallow depths. A remarkable feature of killer whale societies is their cooperative nature. Killer whales may be joined by other killer whales from the surrounding area, cooperating fully in the hunt without antagonistic displays (Barrett-Lennard et al., 2011; Guinet et al., 2000).

Hunting sperm whales is a unique proposition for killer whales. In this scenario, we have highly social hunters attacking large and tightly knit social groups. Usually, these sperm whale social units are comprised of subadults or mothers with calves, newborns, and juveniles (Arnbom et al., 1987). Observations of sperm whale predation are rare (Jefferson et al., 1991). Most evidence comes from stomach contents of stranded killer whales in the Southern Ocean (Best et al., 1984; Visser, 1999; Yukhov et al., 1975) or is based on sightings of wounded sperm whale prey (Dufault & Whitehead, 1995). Arnbom et al. (1987) and Pitman et al. (2001) provide descriptions of killer whale attacks on sperm whales, including a lethal episode (Pitman et al., 2001).

Sperm whales form a "marguerite" or rosette formation (Nishiwaki, 1962; Palacios & Mate, 1996; Weller et al., 1996) in response to cetacean harassment—from pilot whales, *Globicephala* sp., or false killer whales, *Pseudorca crassidens*. The formation involves animals positioning their heads to the center with flukes outwards, allowing them to slash at harassing predators with their powerful tails (Fig. 7.5a). On other occasions, sperm whales switch to a spindle formation or are horizontally huddled up with the calf in the middle (Fig. 7.5b). Confronted with such defensive maneuvers, the principal objective of attacking killer whales is to break up the formation. They do this by conducting several random attacks on multiple individuals, slashing and biting animals, targeting their sensitive heads, and avoiding tail flukes. Pitman et al. (2001) labeled this the "wound and withdraw" strategy—this approach has two functions. The first is to force the whales apart, and the second is to isolate vulnerable individuals that could be killed (Pitman et al., 2001).

In nearly all cases of attacks on baleen or large whales, e.g., sperm whales, females and subadults are the primary instigators and hunters. Male killer whales are usually on the periphery but may engage in the end, as noted when attacking gray whale calves (Reeves et al., 2006) and sperm whales (Arnbom et al., 1987; Pitman et al., 2001). Like African lions, the presence or participation of adult male killer whales is not a prerequisite for hunting large whales nor achieving hunting success. It could be that adult male killer whales may not have the maneuverability around large whales during a hunt or they serve as an intimidating deterrent to escaping prey. How much the mere presence of a male killer whale aids hunting success during whale attacks is unknown.

Pinnipeds: Seals, Sea Lions, and Walrus

A wealth of information exists about killer whales predating seals or sea lions. Pinnipeds (eared and earless seals, sea lions, and walrus) constitute a significant part of mammal-feeding killer whale diet, especially in temperate environments, near or in the Arctic, and in the Southern Ocean (Ford, 2009; Higdon & Ferguson, 2011;

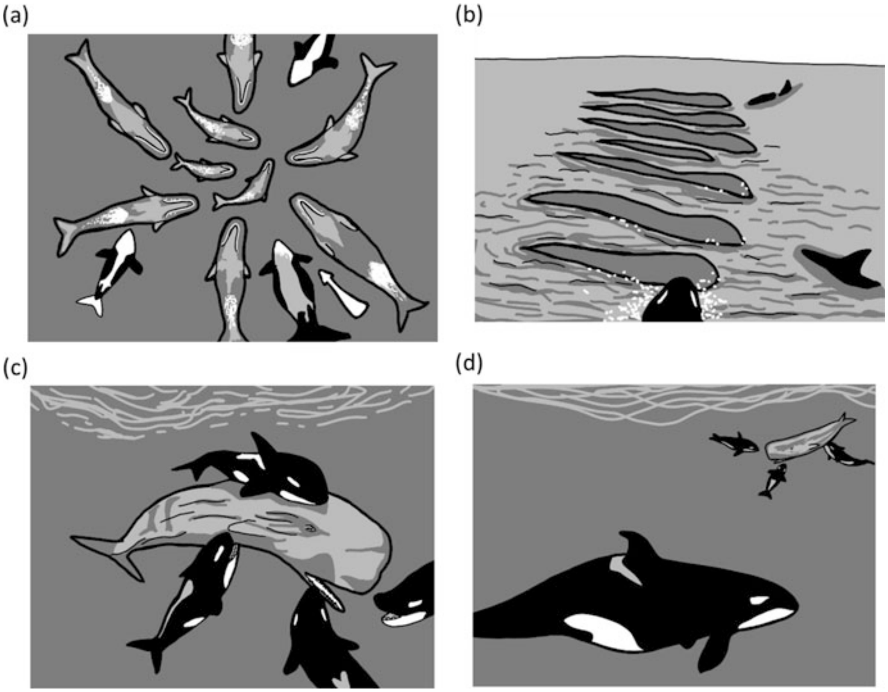

Fig. 7.5 A depiction of sperm whale cooperative defense strategy in response to killer whale predation threats or harassment. (**a**) Rosette "marguerite formation" and (**b**) parallel tight-knit group structure with short nearest-neighbor distances, (**c**) killer whales attacking calf/juvenile by biting in concert, and (**d**) killer whales scoping out and separating a target individual from the group. Illustrations by Hannah Rappoport

Pitman & Ensor, 2003; Weller, 2018). Most seal and sea lion species are attacked and eaten by killer whales. Like predation on whales, killer whales prefer smaller sized females, pups, subadults, and weak adults (Baird, 1994; Barrett-Lennard, 1995; Hoelzel, 1991). However, killer whales can attack and kill larger pinniped males, such as adult sea lions (*Zalophus californianus)*, elephant seals (*Mirounga* sp.), walrus (*Odobenus rosmarus*), Steller sea lions, and bearded seals (*Erignathus barbatus*). Prey-handling time varies with size, with the least amount of time spent (~2 min) on harbor seals and young sea lions and almost an hour or more longer when handling adult sea lions and elephant seals (Baird, 1994). However, prey-handling time can be confounded by animals engaging in play behavior or social learning occasions for calves and juveniles in the social unit (Baird & Dill, 1995).

Pinnipeds come in many shapes and sizes, from the smallest southern fur seals (multiple species, with females potentially weighing 20–50 kg and males 100–200 kg) to the largest male southern elephant seals (*Mirounga leonina,* which can weigh >3 tons). In general, pinnipeds encompass three families and 33 extant species. They are abundant and widely distributed in almost every part of the globe and make attractive and easy targets for roaming killer whales.

Typical hunting sequences when killer whales hunt pinnipeds are illustrated below. It is possible to predict the arrival of mammal-hunting killer whales in the area. As described in earlier sections, they time their visits to haulout sites or rookeries coinciding with pupping or weaning times and abundant prey hotspots (Ford & Ellis, 2014). Although they can be a predictable presence in some regions, when and how they start an attack on abundant pinniped prey is uncertain since they constantly wander and maintain acoustic crypticity. Most attacks of pinnipeds occur underwater (Baird & Dill, 1995; Condy et al., 1978; Saulitis et al., 2000), in both nearshore and offshore areas. Exceptionally, killer whales can also intentionally beach themselves to grab seals and sea lions on land in certain areas such as Peninsula Valdés, Argentina (Hoelzel, 1991; Lopez & Lopez, 1985); the Crozet Archipelago in the Indian Ocean (Guinet et al., 1992; Guinet & Jouventin, 1992); and near both poles. For the latter, they use a coordinated wave generation to dislodge seals off ice floes, e.g., in the Southern Ocean (Pitman & Ensor, 2003; Smith et al., 1981; Visser et al., 2008) and eastern Canadian Arctic (Ferguson et al., 2012). These predation strategies are further deciphered below.

Prowl, Hide, and Capture

A common tendency for killer whales hunting nearshore animals on haulout sites is to silently (Deecke et al., 2005, 2011) patrol the area (headlands, rocky shores, bays) in small tight hunting units of three or four animals without surfacing (Baird & Dill, 1996; Barrett-Lennard et al., 1995; Beck et al., 2011) (Fig. 7.6). They are on the lookout for pups in the water. Harbor seals are typically killed underwater, and blood, blubber pieces, and oil slicks are usually the only indicators of predation (Barrett-Lennard et al., 1995). Also, hunting killer whales display coordination and cooperation when harbor seals hide under rock crevices and actively work to prevent the seal from escaping by taking turns to stay underwater (Baird & Dill, 1995).

Killer whale search mechanisms in open water are unknown, and any preferred prey encounters could be due to chance or dictated by seasonal pinniped foraging hotspots. However, given killer whale tendencies to avoid echolocation use even when not in active hunting mode, they could be in a perpetual search-and-hunt mode seeking opportunistic targets (Barrett-Lennard et al., 1996; Barrett-Lennard & Heise, 2006). Once a suitable pinniped prey is acquired, killer whales give chase and quickly overcome the prey, with time of hunt depending on size.

When chasing harbor seals, the time lag between detection and consumption can be extremely short (Ford et al., 1998). Therefore, harbor seal attacks are mostly silent kills with minimal surface activity. Conversely, as the prey size increases, killer whale surface behaviors, such as leaps and splashes, are prominent (Barrett-Lennard et al., 1995). Thus, when adult sea lions are attacked, killer whales may throw the animal in the air, and different whales may repeatedly slash at the animal with their tail flukes and from all sides to weaken and wound the animal (Fig. 7.6).

In Far East Russia, killer whales often hunt walruses (Kryukova et al., 2012; Melnikov & Zagrebin, 2005). Kryukova et al. (2012) provided a detailed description of a predation event on a group of walruses near the Sea of Okhotsk. A killer whale

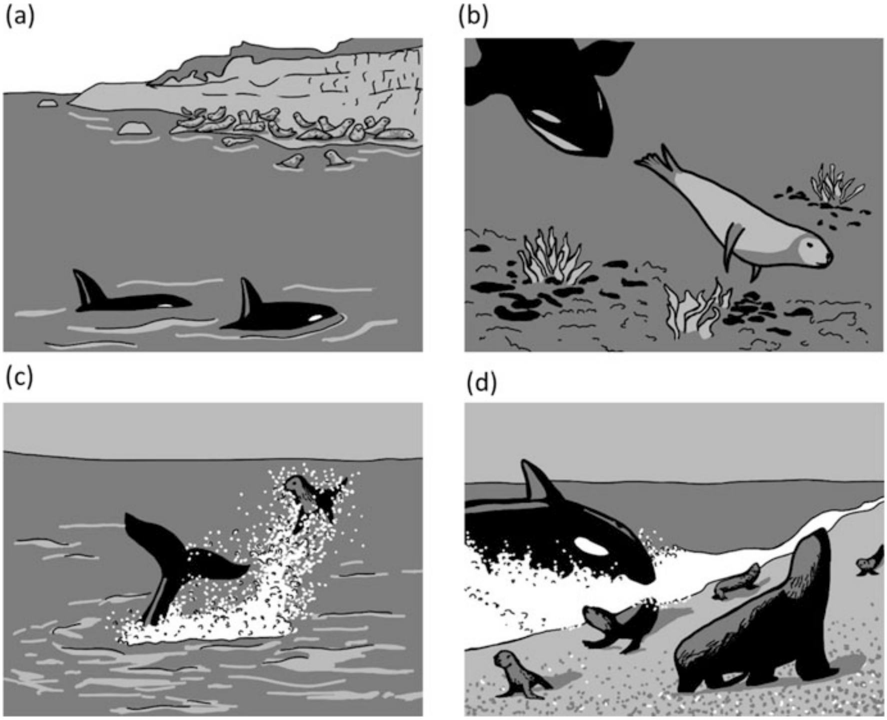

Fig. 7.6 A representative example of killer whales (**a**) patrolling the coastline before a potential hunt, (**b**) chasing and potentially consuming a seal underwater, (**c**) using the powerful tail fluke to flip the seal into the air, and (**d**) intentionally stranding on the beach to capture sea lion or seal pups. Illustrations by Hannah Rappoport

group of about seven adults and two calves participated in the attack. After patrolling the shoreline, the killer whales eventually split a group of 30 walruses into two groups and then isolated an individual for the primary target. The attack took place nearly 3.5 km from the haulout site. The target animal was attacked 55 times by the killer whales. The male killer whale did not play an active role in the event. Killer whales primarily used fast and erratic movements to assault the walrus with their flukes and tried to submerge it using their body weight. The head was at times attacked but mostly by adult killer whales while calves and juveniles refrained from striking the walrus head, possibly due to increased risk of injury.

Near Punta Norte, Argentina, Lopez and Lopez (1985) and Hoelzel (1991) provided extensive accounts of the social organization and hunting strategies of killer whales deliberately beaching themselves to capture southern sea lion and elephant seal pups and juveniles during the pupping and weaning season (Fig. 7.6d). Killer whales preferentially targeted sea lion pups and could distinguish pups from subadults. Occasionally, adult sea lions were hunted and captured by killer whales.

About 30 odd killer whales were observed in the area (Lopez & Lopez, 1985), but about three killer whale pods comprised of 13 whales were distinguished by Hoelzel (1991) in a later study. Most hunts took place near a deep channel surrounded by reefs that remained unexposed during low tide, although killer whales avoided accessing the area during low tide—this was also the point allowing maximum capture rate per stranding (Hoelzel, 1991). Southern sea lion pups regularly crossed the channel within and below the surf zone in both north and south directions.

Adult males usually hunt alone, but it is extraordinary that despite the size and large dorsal fin (~2 m high), they engage in this hunting method. Most beaching attacks are cooperative and coordinated hunts and involve a minimum of two killer whales (Lopez & Lopez, 1985). In a typical hunt, often one killer whale charges and corrals the seal while the rest create a wall of water to prevent the seal from escaping. After initial patrols that run parallel to the beach, killer whales charge at prey directly in the surf zone and all attacks tend to happen in the surf zone or as the wave advances from the beach. One whale is focused on securing the prey, while the rest may mill close by, possibly to prevent the seal from escaping. Sometimes, the captured seal is tossed to other killer whales in the area and thrown into the air several meters away and eventually shared (Hoelzel, 1991).

Killer whales were rarely fully stranded and used the waves and frequent sideways motion to grab the seal and return to deeper water with considerable skill. Immature or juvenile killer whales employing these hunting techniques were usually accompanied by another adult killer whale actively hunting alongside or watching closely from a distance (see Sect. 7.5 on social learning). Immature killer whales would typically intentionally beach extremely close to the prey and remain beside the seals for several seconds before possible capture (Lopez & Lopez, 1985).

Near Possession Island, Crozet Archipelago, mainly female killer whales use intentional beaching techniques to hunt weaned southern elephant seals that are headed to sea to feed (Guinet, 1991. Unlike in Argentina, male killer whales in this study site did not engage in this hunting mode and remained offshore, perhaps due to the unsuitable shallow gradient and sandy topography.

Charges at prey occurred within 3–10 m from shore, and killer whales were stranded in the sand behind the surf. Interestingly, some whales were pushed and stranded by another whale or multiple whales (Guinet, 1991). Also, only adult female killer whales here engaged in non-predatory beaching that represented social play activity to enhance bonding and refine hunting techniques. Calves participating in hunts were always accompanied by adult females not necessarily their mothers (Guinet, 1991). Like Argentina, usually one whale instigated the hunt while the rest milled nearby and were provisioned afterward when the prey was secured.

Another well-established pinniped hunting technique in ice waters of both hemispheres is the wave-washing technique (Fig. 7.7), where Arctic seals (e.g., ringed seals *Phoca (pusa) hispida*, harp seals *Pagophilus groenlandicus*) and Antarctic seal species (e.g., Weddell seals *Leptonychotes weddellii*, leopard seals *Hydrurga leptonyx*, southern elephant seals, crabeater seals *Lobodon carcinophaga*) are removed from ice floes through a series of exquisitely synchronized movements by hunting killer whales.

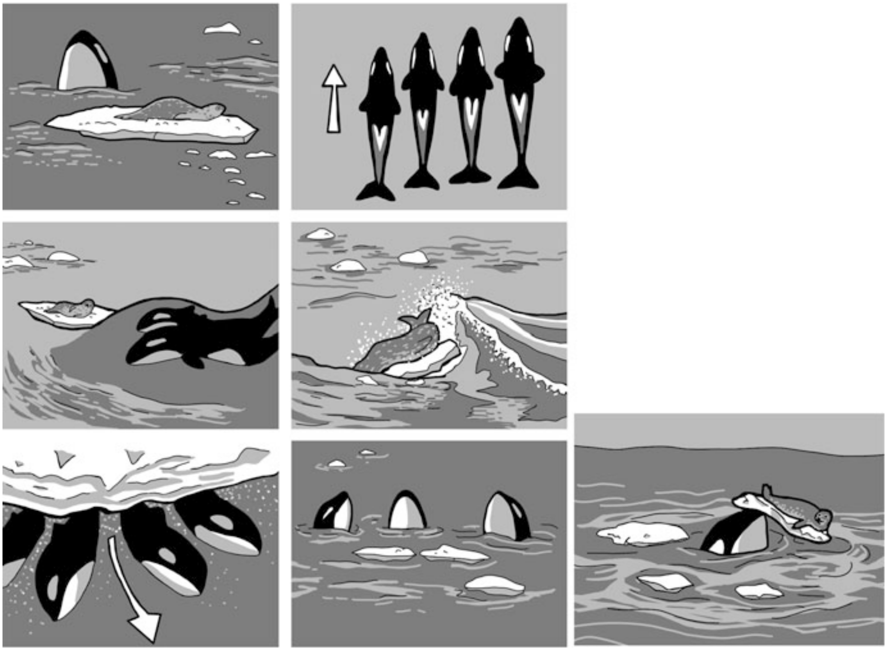

Fig. 7.7 A typical sequence of events during which killer whales successfully dislodge a seal from an ice floe through cooperation and coordination. See text for details. Illustrations by Hannah Rappaport

Smith et al. (1981) provide one of the earliest accounts of coordinated wave production by killer whales (Type B1 killer whales, Pitman & Ensor, 2003) to displace a crabeater seal from an ice floe. Others have narrated similar incidents (Ferguson et al., 2012; Pitman & Durban, 2012; Pitman & Ensor, 2003; Visser et al., 2008), wherein killer whales exhibit the following hunting sequence (Fig. 7.7): (a) one or more killer whales spy-hop (vertically raising their heads above the water surface and scanning) around the edge of ice floes and identify suitable ice floe with hauled-out prey; (b) two or more killer whales then attempt to move the ice in a specific direction, break up the ice into smaller fragments, and isolate the floe with the seal; (c) several whales arranged in parallel synchronously charge underwater with powerful tail fluke strokes, closing in on the target ice floe, and once within striking distance of the ice flip on their sides to avoid the ice; and (d) the outcome is the creation of turbulent wave action that tips the ice floe and dislodges the seal on it.

Sometimes as noted by Pitman and Durban (2012), the whales assumed different group structures in open water (tightly grouped with close spacing between individuals) vs. near pack ice (split into smaller units, mother-calf pairs). When near pack ice, individual killer whales would investigate (spy-hop) different ice floes, taking multiple looks around larger ice floes.

Hunting killer whales generated various levels of turbulence to achieve different objectives whether to break up the ice (smaller wave action) or displace the prey (stronger wave action) (Pitman & Durban, 2012; Visser et al., 2008). Depending on the wave action generated, killer whales could first move the ice floe with the seal into open water, thereby limiting escape routes for the seal, and then with more deliberate and forceful wave generation initiate tipping of the ice floe to displace the ice floe-restricted prey. On occasion, killer whales can also lift irregular pieces of ice floe from below the water with their rostrum and remove a hauled-out seal (Fig. 7.7e), a behavior that was also described in Fraser (1949) near the British Antarctic.

Often killer whales do not kill the seal immediately, and seals may be displaced and returned to ice floes, with repeated previous actions to dislodge the seal (Visser et al., 2008). The predators' sole purpose is to exhaust and drown the seal. Once the seal is in water, killer whales try to ensure that the seal is unable to return to another ice floe and then pull the prey underwater by the hind flippers. Kills happen underwater with limited surface evidence. And almost immediately, killer whales resume searching and pursuing other prey (Pitman & Durban, 2012).

Pitman and Durban (2012) also recorded that first-year ice floe is <1 m thick, flatter, and preferred by seals to haul out on. Although they found that seals hauled out on higher and thicker (1–3 m) older ice floe, uneven undulations made it more difficult for killer whales to detect and successfully hunt seals using the wave-washing technique.

In the Canadian Arctic, especially around southern Baffin Island, Inuit have observed killer whales using powerful tail fluke action to create waves and dislodge ring and harp seals off ice floes irrespective of ice floe thickness (Ferguson et al., 2012). In northern Baffin Island, killer whales can raise the ice floe from underwater (usually a single whale) to knock the phocid seal into the water (Higdon et al., 2012), similar to reports from the Antarctic Peninsula (Pitman & Durban, 2012).

Dolphins, Porpoises, and Other Cetaceans

Mammal-hunting killer whales hunt dolphins and porpoises opportunistically or perhaps when their desired pinniped or large whale prey options are unavailable for a variety of reasons. Smaller cetaceans are no match physically with the disproportionately larger and more powerful killer whales. However, hunting dolphins is a challenging prospect for killer whales since most pelagic dolphin species occur in large behaviorally coordinated pods; exhibit speed, endurance, and maneuverability; and have high hearing acuity and pervasive social networks allowing them to be extremely vigilant of potential predators. Nevertheless, killer whales have developed expertise in hunting both smaller agile dolphins and porpoises (typically less than 3 m in length) as well as cryptic or other midsized cetaceans (over 3 m long) in both shallow and deepwater habitats.

In the northeastern Pacific, researchers have noted opportunistic attacks on Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) (Dahlheim & Towell, 1994) and Dall’s and harbor porpoises (Barrett-Lennard et al., 1995, 1996; Ford et al., 1998; Saulitis et al., 2000) likely due to localized seasonal abundance, chance encounters, or absence of primary prey, harbor seals.

In Prince William Sound, Alaska, Dall’s porpoises are attacked frequently since harbor seals are fewer in numbers, but elsewhere in southeastern Alaska and off British Columbia, harbor seals are the preferred species. Attacking Dall’s porpoises is no easy feat and involves prolonged high-speed chases and much surface activity (Saulitis et al., 2000). In low-productive environments, such as Hawai’i, Baird et al. (2006) have observed that melon-headed whales (*Peponocephala electra*) and pantropical spotted dolphins (*Stenella attenuata*) exhibit evasive behaviors towards killer whales that do not exclusively feed on fish. In similar low-productive but tropical environments, e.g., the Bahamas, killer whales attack a variety of cetacean species. Dunn and Claridge (2014) observed killer whale predation events involving Atlantic spotted dolphin (*Stenella frontalis*), Fraser’s dolphin (*Lagenodelphis hosei*), dwarf sperm whale (*Kogia sima*), and pygmy sperm whale (*K. breviceps*). Unlike the spotted and Fraser’s dolphins, *Kogia* sp. are slow-swimming, deep-diving, cryptic species and possibly modify habitat use patterns in response to prey shifts and predation risk from nomadic killer whales. It is theorized that in prey-scarce or tropical environments, killer whales are generalist predators and not restrictive to consuming marine mammal prey, although they may employ similar hunting tactics.

In another example of resource-scarce marine environments, off New Zealand, Constantine et al. (1998) provided some of the most detailed accounts of killer whale attacks on dusky dolphins over several days. Killer whales have also been known to capture river dolphins, such as Franciscana dolphins (*Pontoporia blainvillei*) (Santos & Netto, 2005) in Brazilian waters and spinner dolphins (*Stenella longirostris*) (Pitman et al., 2015) in Coral Bay, Australia.

Killer whales also attack other midsized or larger cetaceans, false killer whales, which themselves can harass and mob other cetaceans (Visser et al., 2010; Weller, 2018). Visser et al. (2010) reported an incident of multiple killer whales attacking a nursery group of false killer whales associated with offshore bottlenose dolphins (*Tursiops* sp.) in New Zealand. The killer whales relied on endurance and speed to mount multiple ramming attacks on the whales but perhaps with the primary aim of separating and hunting calves in the group. Apart from hunting a variety of dolphin species (Jefferson et al., 1991), there is sporadic evidence of predation on *Mesoplodon* spp. or beaked whale species (Gualtieri & Pitman, 2019; Wellard et al., 2016). Beaked whales are largely solitary, deep-diving, and cryptic species. Based on their habitat use patterns, it is assumed that most beaked whale predation events happen offshore, and possibly at depth with scant evidence of predation. General hunting techniques are elaborated further below.

Stealth, Stamina, Speed, Corralling

There are common threads in hunting tactics that killer whales employ to attack dolphins and porpoises. Again, it is unclear if the encounter is random like other prey encounters in pelagic environments or whether they seek dolphin foraging hotspots

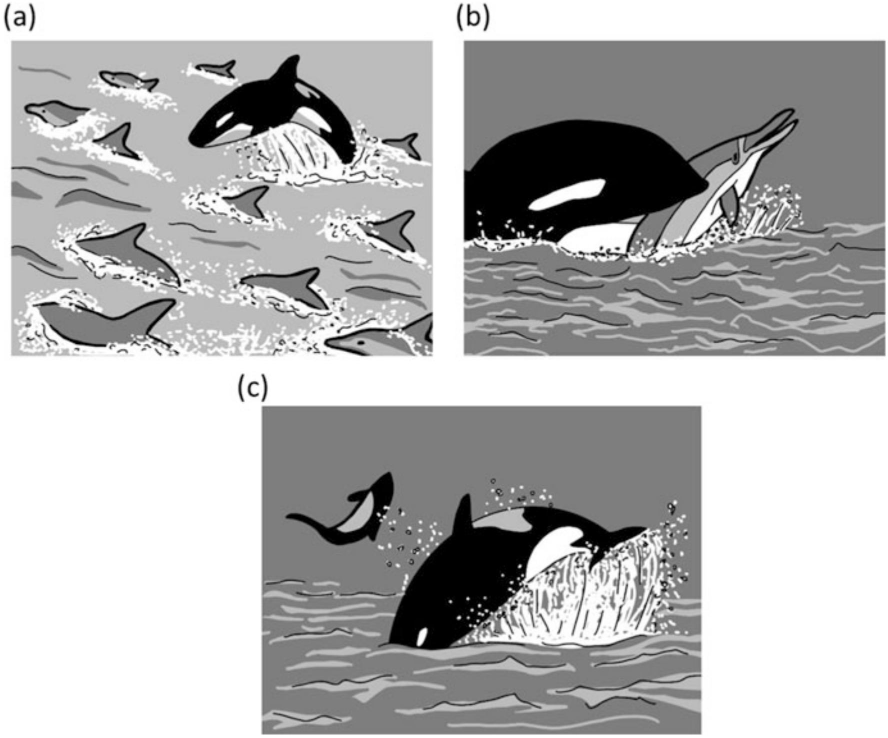

Fig. 7.8 A glimpse into some parts of an elaborate killer whale attack on (**a**) large school of pelagic dolphins, (**b**) a killer whale with a dolphin in its mouth, and (**c**) a killer whale flipping a Dall's porpoise once the killer whale has chased down the exceedingly fast-swimming porpoise. See text for additional details. Illustrations by Hannah Rappoport

or areas of high seasonal abundance (e.g., posing a heightened risk to dusky dolphins during austral summer and autumn near Kaikoura, New Zealand, or in open waters to capture Dall's porpoises near British Columbia).

In open waters, predation events are marked by ambush attacks on unsuspecting dolphins. If a large school of dolphins is involved (e.g., Pacific white-sided dolphins, dusky dolphins, common dolphins), killer whales flank the animals, attacking from behind and below, causing the prey to split into smaller groups, cutting escape routes, and engaging in high-speed pursuits (Fig. 7.8a). Once grasped, the animals could be flung in the air, torn to pieces, and consumed quickly (Rice & Saayman, 1987) (Fig. 7.8a). Dall's porpoises usually occur in small groups or can be solitary; they are also among the fastest swimming cetaceans. Thus, hunting killer whales must engage in prolonged and speedy chases when pursuing Dall's porpoises. If killer whales successfully catch up to the animal, they will ram the animal from below, tossing the porpoise high into the air (Ford et al., 1998) (Fig. 7.8b). Therefore, there is considerable surface activity visible during predation events. Alternatively, the smaller harbor porpoises are quietly attacked from behind by a chasing killer whale and consumed quickly—these predation events are of short duration with little surface activity (Dahlheim & White, 2010; Ford et al., 1998). Thus, most harbor porpoise attacks could go unnoticed (Ford et al., 1998).

Off Monterey, California, large concentrations of Pacific white-sided dolphins seasonally occur in response to intermittent killer whale threats (Black, 1994), predominantly in shelf-break waters. In contrast, in southeastern Alaska waters, Dahlheim and Towell (1994) report small groups of Pacific white-sided dolphins successfully hunted by mammal-eating killer whales found in shallower inland waterways. In British Columbia, Ford et al. (1998) documented rare attacks on Pacific white-sided dolphins with one successful kill between 1973 and 1996. Ashe et al. (2021) did a review of anecdotally reported killer whale and Pacific white-sided dolphin predatory interactions and photographic records of presumed killer whale attacks in British Columbia waters. They estimated that 9.5% of all killer whale mammal attacks involved Pacific white-sided dolphins, suggesting that predation from killer whales may be more significant than previously assumed. Most attacks involved killer whales chasing, dividing the pod of dolphins into smaller groups, corralling them into a confined space, ramming them from below or throwing them into the air, and then breaching on top of the dolphin.

Herding, tail slapping individuals, and tossing behavior are also common when dusky dolphins are attacked both near Kaikoura, New Zealand (Constantine et al., 1998), and Patagonia, Argentina (Coscarella et al., 2015). Coscarella et al. (2015) also documented another cooperative hunting tactic, which involved killer whales herding a common dolphin (*Delphinus delphis*) to a companion killer whale, which captured the animal.

Killer whales appear to be capable of hunting dolphins both in shallow and deep water. A lone male killer whale killed a probable single adult Franciscana dolphin with evidence of the dolphin being thrown up in the air and eventually drowned and consumed (Santos & Netto, 2005). Killer whales in southern Brazil are usually observed in deep waters, but the river dolphin predation incident occurred in 8–12 m water depth.

Hunting techniques do not vary much when killer whales hunt beluga whales or narwhals, with main differences due to habitat variability. The killer whales first corner the belugas into the shallows by herding them and then holding the beluga whale from the caudal peduncle, tossing them upwards and backward into deeper water, or thrashing them around from side to side before multiple whales feed on the killed prey (Frost et al., 1992). Additionally, in Arctic waters, Inuit descriptions of killer whale hunting techniques suggest that killer whales may circle, ram, and bite midsections of the belugas and toss them around causing severe internal damage (Ferguson et al., 2012). Like African lions, killer whales may also engage in surplus killing based on evidence from Inuit hunters of 100s of belugas killed without being eaten (Ferguson et al., 2012).

Shelden et al. (2003) reported predation events in Cook Inlet, Alaska, where killer whales regularly predate beluga whales but are constrained by severe tidal variations, which the belugas use to their advantage. On occasion, killer whales become stuck on shallow mudflats while herding and chasing belugas. But despite tidal variations, strong currents, and seasonal ice, killer whales adapt their distribution to successfully chase, corral/strand, and eat beluga whales.

Narwhals could be risky prey for killer whales given the presence of tusks in the male adults. However, much like belugas, killer whales do not appear to be deterred from attacking narwhals with or without tusks (Ferguson et al., 2012). Typical hunting strikes involve herding the animals into confined zones or shallow areas, circling the target animals, and tiring them before commencing attacks. Like belugas, killer whales may cause severe internal damage to narwhals by forcefully ramming, biting, and holding them in the mouth, or flipping the animal into the air before consumption. Before the attacks, killer whales use slow and deliberate movements as they silently search for suitable targets. Laidre et al. (2006) recorded a predation event where a minimum of four narwhals were killed by 12–15 killer whales in about 6 h—thus, killer whales can attack narwhals with efficiency.

7.2.3.3 Prey Consumption

Killer whales have made consumption of the carcass an art form. Pitman and Durban (2012) shared evidence of how feeding killer whales, perhaps acting in concert, stripped the entire skin leaving the seal body intact. Prey sharing is a widespread practice for killer whales. And often, multiple groups (including those not part of the hunt) arrive at the scene after a kill to consume the carcass, without aggression from the original hunters. Baird and Dill (1995) estimated that killer whales shared 51% of harbor seal kills in British Columbia waters, including transferring prey items to a neighboring killer whale after the kill. Hoelzel (1991) also observed similar behaviors in killer whales off Argentina where one killer whale passed a caught seal to another killer whale that fed on it. Jourdain et al. (2017) also described the sharing of three seals among three groups of killer whales during a 6-h period.

Intergroup sharing of prey is frequently observed when large whales are killed (Pitman & Chivers, 1999; Silber et al., 1990; Totterdell et al., 2022). The arrival of faraway groups of mammal-hunting killer whales is speculated to help with preventing the whale carcass from sinking and maximizing foraging opportunities in the available window (Guinet et al., 2000). Other killer whale groups are probably attracted to the kill by heightened killer whale vocalizations after an attack, and potentially by alarm signals emanating from debilitated prey. In most cases of baleen whale attacks, as previously noted, killer whales are fixated on consuming the tongue and lips or taking out chunks of flesh from the flanks and jaw—they strive to quickly consume the most nutritious parts before the carcass sinks. The exclusivity of these body parts is not a new phenomenon. There are records from the nineteenth century where whalers have documented killer whale consumption habits after a whale kill (Mitchell & Reeves, 1982).

In shallow water depths, killer whales could return to feed on submerged carcasses post-kill as described by Barrett-Lennard et al. (2011) near Unimak Island, Alaska. The authors observed killer whales returning to slick sites to retrieve gray whale carcass fragments, including killer whales that were not part of the original hunting group. Around Unimak Island, interestingly, intergroup carcass sharing did not occur immediately, but neither were there any antagonistic or affiliative reactions to the presence of outside members postattack. There is currently no evidence that killer whales defend carcasses from non-group members.

7.3 Prey Response

Killer whale predation strategies are emblematic of predator-prey shell games (Mitchell & Lima, 2002), wherein predators return to the same areas where they found prey previously, and the prey attempt to be elusive and unpredictable spatiotemporally while striving to manage state-dependent risk and energetic demands (Lima, 1998). Simultaneously, both predator and prey are engaged in behavioral games, and evolving behaviors to adapt to changing habitats and population dynamics, e.g., Houghton et al. (2015).

Antipredator decision-making among killer whale prey runs across the gamut and can be divided into acute and chronic antipredator behaviors. Among whales, Ford and Reeves (2008) neatly classified baleen whale defensive strategies (acute response) into two modes *fight* and *flight* when confronted with immediate danger. An example of a *fight* species is the humpback whale. Humpback whales can unleash their formidable 4 m long pectoral flippers during direct combat with killer whales (Pitman et al., 2015, 2017). Humpback whales when under attack from killer whales may also produce distinct “wheezing” or trumpeting blows (Whitehead & Glass, 1985). And when interfering with other marine mammal predation events involving killer whales, humpbacks will also produce loud trumpeting sounds (Pitman et al., 2017), a possible antagonistic or gesture of annoyance.

Minke whales, in contrast, are a *flight* species. During imminent predation risk, minke whales rely on speed and stamina to outrun chasing killer whales (Ford et al., 2005; Guinet et al., 2000). But once whales are within the gauntlet of a killer whale group assault, they exhibit repetitive behaviors. During their northward migration from the tropics, gray whales accompanied by calves are vulnerable to killer whale predation. On these occasions, gray whale mothers maneuver between the attacking killer whales and their calf, vigorously thrash their tail flukes, and always seek to make a straight-line exit towards shallower water, sometimes <10 m deep (Morejohn, 1968). At other times, young gray whales may give up entirely and roll onto their backs or roll repeatedly to prevent killer whales from steadfastly grasping their pectoral flippers (Barrett-Lennard et al., 2011; Goley & Straley, 1994). When multiple gray whales occupy an area, they may group during elevated predation risk (Ljungblad & Moore, 1983). Blue, fin, and sei whales (*Balaenoptera borealis*) and Bryde’s whales also count in the *flight* category (Alava et al., 2013; Ford & Reeves, 2008).

Southern right whales employ a melded defense strategy. In the calving grounds near Patagonia, Argentina, and like sperm whales, groups of southern right whale mothers with calves under attack can arrange themselves in a rosette formation with their heads towards the center and weaponize their flukes to inflict injury on predating killer whales (Sironi et al., 2008). Generally, southern right whales can adopt a hybrid approach where they fight by slashing and hitting killer whales, increasing group size and aggregating, chasing their predators, or fleeing from the area (Best, 1982; Best et al., 2010; Sironi et al., 2008).

Male sperm whales are not immune to attacks. Sperm whales show sex-specific segregation with adult male sperm whales generally remaining solitary and occurring at high latitudes. But Cure et al. (2013) found that spatially separated adult male sperm whales can cluster in response to playback of killer whale vocalizations. Sperm whales consisting of female pods with calves or juveniles rely exclusively on cooperative defense against equally cooperative predators. They do not dive or flee, and despite the risk of injury from being attacked on all sides, they organize into rosette or parallel formations (Gemmell et al., 2015; Pitman et al., 2001). At times, sperm whales in the vicinity (several kilometers away) may come to the aid of sperm whale groups troubled by killer whales probing and testing sperm whale group defenses (Pitman et al., 2001).

In high latitudes, for cetacean and pinniped species, ice association in winter can be a natural barrier to ice-wary predating killer whales. Bowhead whales, belugas, narwhals, and ice-associated seals often use the ice as a refuge. With climate change and loss of sea ice, killer whales are making excursions into previously dense ice areas and becoming an enhanced threat to various cetacean and pinniped species in the Arctic (Matthews et al., 2020; Stafford, 2019).

For most pinnipeds, acute escape responses to mammal-hunting killer whale presence are to seek refuge under rocks and crevices, on land, or in extremely shallow water. If predating killer whales are detected earlier, harbor seals may dive to depth and travel out of the area into nearshore waters as an antipredator response (Barrett-Lennard et al., 1996; Womble et al., 2007). Social delphinids occurring in large groups scatter and flee during an attack, aiming for the shallowest water depths, sometimes <1 m water (Würsig & Würsig, 1980). The maintenance of large group sizes and the subsequent acute response of scattering and splintering into different directions can be effective antipredator strategies through the dilution and confusion effects (Milinski, 1977; Turner & Pitcher, 1986).

From a behavioral ecology perspective, perhaps most interesting are the intrinsic antipredator behaviors cultivated and perfected with time to react to intermittent or predictable predation risk from killer whales. From playback experiments (reviewed in Deecke, 2006), on beluga whales (Fish & Vania, 1971), gray whales (Cummings & Thompson, 1971), *Mesoplodon* spp. (Tyack, 2011), Pacific harbor seals (Deecke et al., 2002), northern bottlenose whale *Hyperoodon ampullatus*, humpback, long-finned pilot whales, *Globicephala melas*, and sperm whales (Miller et al., 2022), there is definitive evidence of strong avoidance and frightened reactions, such as rapid and uncontrolled surfacing from depth in beaked whale species exposed to killer whale sounds. These studies also show that cetacean and pinniped prey are acutely discriminatory to mammal-hunting killer whale vocalizations.

Hearing sensitivities attuned to predatory killer whale sounds are evolutionarily stable traits that are vital for survival. Conversely, it is presumed that some cetacean species (e.g., *Kogia* sp. and Franciscana dolphins) are devoid of certain vocalization types (e.g., whistles) in their acoustic repertoire to be less detectable by extant killer whales (Morisaka & Connor, 2007) or in the past from extinct ancient killer whale-like predators (Galatius et al., 2019), and thus succeed in maintaining acoustic crypsis. Acoustic signaling through alarm calls (Rankin et al., 2013) can be effective for alerting neighboring species or conspecifics about killer whale presence, while aerial behaviors such as acrobatic leaps among social delphinids may be essential for maintaining social cohesion and vigilance (Würsig & Whitehead, 2009).

Nevertheless, most cetacean decision-making in response to variable predation risk and by extension the fear of predation is through optimal behavioral choices manifested through foraging decisions, changes in movement and distribution patterns, and maintaining reliable communication and vigilance networks through group living (reviewed in Connor, 2000; Srinivasan, 2010). In some cases, there may be trade-offs between reducing risk and maximizing foraging; in other baseline scenarios, prey availability and access may not skew the balance. For example, dusky dolphins off Kaikoura seasonally occupy shallower habitats during heightened killer whale predation risk and resort to nearshore-offshore excursions to feed in deep water but choose deeper habitats during low predation risk and consequently close to their prime food source (Srinivasan & Markowitz, 2010). These long-term habitat-use decisions by age class may not be consequential under minimal predation risk but could result in severe ecological costs, especially for energy-compromised lactating dolphin mothers (Srinivasan et al., 2018).

For two species of beaked whales, Aguilar de Soto et al. (2020) found that individual foraging whales maintained strict dive synchrony and vocal foraging time 98% of the time in conjunction with long, silent ascents to the surface that compromised foraging opportunities. The authors postulated that the fear of killer whale predation triggered these synchronous antipredator dives and vocalization rhythms. Bowhead whales appear to react to killer whales more than 100 km away, possibly relying on low-frequency communications from conspecifics with knowledge of killer whale presence (Matthews et al., 2020). During nonpeak killer whale season, bowheads seek profitable open-water ice-free habitats, consuming more energy than required. However, once killer whale threats increase, they choose shallow, ice-dense habitats, exhibiting clear avoidance and reduction in activity. The authors speculate that the differential habitat choice could disproportionately affect calves, juveniles, and lactating mothers with higher energy needs and represent nonconsumptive risk effects (Matthews et al., 2020).

Killer whale-directed antipredator behaviors and their potential ecological consequences are discussed in depth by Srinivasan (2019) and are not covered further here. However, the key point is that marine mammal prey—like terrestrial prey—can make optimal or suboptimal choices related to foraging, interspecific associations, or calving in response to varying or indifferent predation risk and are not mute spectators in the behavioral game. Moreover, prey behavior can induce predators to modulate responses and hunting strategies (Creel, 2010; Dill, 1987; Lima, 1998; Lima & Dill, 1990), and remains an exciting area for further investigations.

7.4 Group Sizes and Hunting Success

Adult killer whales have no natural predators, and thus, predation risk is generally not a confounding factor for observed group sizes (Gowans et al., 2008). Predator group sizes are expected to be managed to maximize hunting success (Krause & Godin, 1995). Indeed, studies show that hunting success is correlated with prey group size, such that success diminishes as prey group size increases (Pulliam & Caraco, 1984). Mammal-hunting killer whale group sizes generally align well with their daily activity budgets (i.e., maximum time spent foraging or feeding), foraging methods, and target prey.

Baird and Dill (1995) found that Bigg's killer whale group sizes were larger during social and play behaviors than when foraging on harbor seals off southern Vancouver Island, British Columbia. Social behavior was higher during the seal pupping period than during depleted feeding opportunities. Further, smaller groups consisted of related individuals compared to larger groups that aggregated for social activities. According to Baird and Dill (1996), from an energy acquisition perspective, a group size of three was an ideal hunting group size for Bigg's whales when hunting harbor seals. However, since 2000s, annual average group sizes are typically >4 and maximum group sizes can exceed 10 regularly with temporary aggregations of 30 animals, which is indicative of increasing Bigg's killer whale populations in the area (Ford et al., 2013).

Group sizes can be biased towards fewer individuals when killer whales are searching and hunting pinnipeds. Near Macquarie Island, Australia, Travers et al. (2018) have reported on a median group of three killer whales often seen hunting weaned elephant seal pups. Near Marion Island, in the southern Indian Ocean, Condy et al. (1978) found that the most frequent herd/group size was two individuals, composed of females with their calves or pairs of subadults. Adult males operated alone or could be seen in a trio with a female and her calf or with subadults. The group size corresponded with the prey species of interest, southern elephant seals that were caught mostly in shallow waters near the beach. The killer whale dorsal fins remained visible when farther away but switched to surreptitious submerged mode closer to the beach to catch unsuspecting seals. Likewise, off Punta Norte, Argentina, single animals or groups of two killer whales precipitated attacks on sea lion pups, with some killer whales from the group staying a short distance away—group size was not correlated with prey group size. Similarly, near Scotland, Atlantic killer whales had a mean group size of about 5.8 (SD = 3.0) based on systematic and opportunistic predation events on seals (Beck et al., 2011). Interestingly, these same killer whales operating in Icelandic waters feeding on herring (*Clupea harengus*) maintained larger group sizes (mean = 14.8; SD = 12) and stronger associations within the social network relative to seal-hunting killer whales in Scotland waters. Thus, ecological conditions can have a critical impact on associations and predation group sizes.

It is theorized that in unproductive tropical waters, killer whales are generalist predators eating a combination of fish and marine mammals and maintaining smaller group sizes. For example, Weir et al. (2010) reported killer whale group size of 5.2 in West African waters, Bolanos-Jimenez et al. (2014) estimated a group size of 3.7 in the Caribbean Sea, and Baird et al. (2006) and Dunn and Claridge (2004) calculated a group size estimate of around 4.2 for killer whales near Hawai'i and Bahamas, respectively.

Based on a mariner survey ($n = 126$ respondents) near British Columbia and Alaska, Barrett-Lennard et al. (1996) reported a median group size of 4 (range 2–20) during predatory attacks on Steller sea lions (the largest sea lion species) in Alaska waters. However, while most of the attacks reported involved small adults (potential sampling bias), approximately 15–20 killer whales were involved when a single bull sea lion was attacked. In another study, Dahlheim and White (2010) provided group size variability by prey type using predation data from southeastern Alaska. They reported group size ranges of 3–25 for attacks on Dall's porpoise, 7–15 for Pacific white-sided dolphins, 2–5 for harbor porpoise, 1–6 for harbor seals, 6–15 for Steller sea lion, and 5–10 for minke whales. But they could not correlate hunting group sizes by prey type due to low sample sizes. Conversely, Ford et al. (1998) found significant differences in group sizes corresponding to prey type with killer whale maintaining smaller mean group sizes of about 3.5 for harbor seal prey and about 5 when hunting Steller and California sea lions and smaller cetaceans in coastal British Columbia and adjacent waters. In the Canadian Arctic, the median group size of killer whales was 4 for pursuing bowhead whales, 2 for phocid seals, and 7 for narwhals and beluga whales (Higdon & Ferguson, 2011). In Antarctic waters, Type A killer whales foraging on Antarctic minke whales had an average group size of 13.6 individuals and a range of 1–38 (Pitman & Ensor, 2003).

Killer whale group sizes are highly variable across regions and prey types—a non-exhaustive list of group sizes from numerous studies is shown in Table 7.1 in Appendix. Even within the same area involving the same species, consistent grouping patterns are not the norm (e.g., minke whales or gray whale calf attacks; Table 7.1 in Appendix).

When large prey are involved, estimating hunting group sizes can be notoriously difficult for mammal-hunting killer whales for several reasons. (1) The number of killer whales pre-, during, and postattack can be vastly different; (2) observers could easily miss killer whales pre-attack due to the furtive approach of the whales and their ability to travel undetected; (3) when large animals are hunted, killer whales from far away can arrive in the area further confounding hunting sizes and participants; and (4) observation of a full predation event can be rare and observers may only witness portions of an event and thus may not have a credible estimate of group sizes.

With repeated observations and in highly studied areas like the Pacific northwest, group size estimates are reliable and correlate with prey type (e.g., Baird & Dill, 1995; Ford et al., 1998). However, whenever possible, future observers of predation events should endeavor to record group sizes throughout the predation event before, during, and after an attack and distinguish between hunting members and late arrivals coming to savor the spoils of another pod or group.

Within studies with a high observation of attacks, the success percentage can be 100% for harbor seals in British Columbia waters but as low as 15% in Peninsula

Table 7.1 Representative examples documenting variability in mammal-hunting killer whale group sizes by study, location, and prey species during predation events. In some studies, the authors presented descriptions of multiple predation events involving the same species and associated killer whale group sizes. The data underscore discernible patterns in group sizes for pinniped pup hunts (i.e., small group sizes <4 individuals) but less so for other marine mammal species, including adult pinnipeds

Citation	Location	Killer whale group size	Prey species
Alava et al. (2013)	Bolívar Channel, western region of the Galápagos Archipelago	6 during the attack	Bryde's whale
Arnbom et al. (1987)	Galápagos Islands, Ecuador	10 before, 15–25 during (2–7 in subgroup)	Sperm whale
Ashe et al. (2021)	British Columbia	8	Pacific white-sided dolphins
Baird et al. (2006)	Kauai, Hawai'i	6	Humpback whale
Baldridge (1972)	Point Lobos State Reserve, south of Carmel, California	5–6 (during)	Gray whale calf
Barrett-Lennard et al. (2011)	West of Ikatan Peninsula, Alaska	4–5 (2 KW—during attack on calf)	Gray whale
Barrett-Lennard et al. (2011)	East side of the Ikatan Peninsula, Alaska	8	Gray whale
Barrett-Lennard et al. (2011)	East side of the Ikatan Peninsula, Alaska	8 in each (2 groups)	Gray whale calf
Barrett-Lennard et al. (2011)	East side of Ikatan Peninsula, Alaska	3	Gray whale calf
Barrett-Lennard et al. (2011)	Ikatan Peninsula, Alaska	4	Gray whale calf
Barrett-Lennard et al. (2011)	East side of Ikatan Peninsula, Alaska	4	Steller sea lion
Barrett-Lennard et al. (2011)	South of Unimak Island, Alaska	25 (4 groups)—0.5 km separation	Gray whale
Best (1982); Best et al. (2010)	Close inshore at Melkbosstrand, north of Cape Town, South Africa	2	Southern right whales
Best et al. (2010)	Rooikrans, False Bay, South Africa	1	Unidentified (possibly, humpback whales)
Best et al. (2010)	South-East Coast near Plettenberg Bay, South Africa	3	Bryde's whale calf
Best et al. (2010)	South of Cape Point, South Africa	1	Fur seal
Laidre et al. (2006)	North of Kakiak Point, Admiralty Inlet, Nunavut, Canada	12–15	Narwhal
Lopez and Lopez (1985)	Punta Norte, Argentina	Mode = 2; mean = 3.2, SD = 3.6	Southern Elephant seals and Southern sea lions

(continued)

Table 7.1 (continued)

Citation	Location	Killer whale group size	Prey species
Campbell et al. (1988)	Koluktoo Bay near Milne Inlet	9	Narwhal
Constantine et al. (1998)	Kaikoura, New Zealand	4	Dusky dolphins
Dahlheim and Towell (1994)	Club Rocks, SW Ketchikan, Dixon Entrance, Alaska	15	Pacific white-sided dolphins
Whitehead and Glass (1985)	Newfoundland	10–12	Humpback whale
Whitehead and Glass (1985)	Newfoundland	17	Humpback whale
Flórez-González et al. (1994)	Gorgona Island, Colombian Pacific	10	Humpback whale
Ford et al. (2005)	Johnstone Strait, British Columbia	2	Minke whale
Ford et al. (2005)	Glacier Bay, Alaska	13	Minke whale
Ford et al. (2005)	Cormorant Channel, British Columbia	9	Minke whale
Ford et al. (2005)	Ganges Harbor, British Columbia	4	Minke whale
Ford et al. (2005)	Juan de Fuca Strait, British Columbia	4	Minke whale
Ford et al. (2005)	Blackfish Sound, British Columbia	4	Minke whale
Ford et al. (2005)	Glacier Bay, Alaska	2	Minke whale
Ford et al. (2005)	Juan de Fuca Strait, British Columbia	6	Minke whale
Ford et al. (2005)	Shoal Harbour, British Columbia	2	Minke whale
Frost et al. (1992)	Lower Naknek River, Alaska	9	Beluga whale
Goley and Straley (1994)	Monterey Bay, California	17	Gray whale
Grandi et al. (2012)	Isla Pan de Azúcar, Argentina	3	South American sea lions
Gualtieri and Pitman (2019)	Southwest of Cape Verde Islands	7	Gervais whale
Guinet et al. (2000)	Crozet Archipelago (southern Indian Ocean)	Pods 1–6 Pods 2–5 (post-hunt) Pods 3–3	Minke whale calf
Guinet et al. (2000)	Crozet Archipelago	Pods 1–6 Pod 2—unidentified 5–6 killer whales (post-hunt)	Elephant seal pup
Jourdain et al. (2017)	Orskjera, Møre, Norway	3 (minimum)	Harbor seal
Jourdain et al. (2017)	Ona, Møre, Norway	3 (minimum)	Harbor seal

(continued)

Table 7.1 (continued)

Citation	Location	Killer whale group size	Prey species
Jourdain et al. (2017)	Andenes, Norway	4 (minimum)	Harbor seal
Jourdain et al. (2017)	Andenes, Norway	3 (minimum)	Harbor seal
Jourdain et al. (2017)	Vestfjord, Norway	5 (minimum)	Harbor seal
Jourdain et al. (2017)	Andenes, Norway	10 (minimum)	Harbor seal (1), gray seal (1), undetermined (1)
Jourdain et al. (2017)	Senja, Troms, Norway	5 (minimum)	Harbor seal (1) and undetermined (1)
Kryukova et al. (2012)	Retkyn Spit, Chukotka	8	Walrus
Ljungblad and Moore (1983)	Northern Bering Sea	16	Gray whale
Lowry et al. (1987)	West side of Amaknak Island, near Dutch Harbor, Alaska	7	Minke whale
Naessig and Lanyon (2004)	Near Green Cape Lighthouse, New South Wales, Australia	7	Humpback whale
Totterdell et al. (2022)	Offshore Bremer Bay, Western Australia	12–14 (50 whales post-hunt)	Blue whale
Totterdell et al. (2022)	Offshore Bremer Bay, Western Australia	25 (40 during attack, 50 post-hunt)	Blue whale (calf 10–12 m approximately)
Totterdell et al. (2022)	Offshore Bremer Bay, Western Australia	12 (2 subgroups)	Blue whale juvenile/yearling (12–14 m)
Pitman et al. (2015)	Coral Bay, Australia	7–8	Spinner dolphins
Pitman et al. (2015)	Coral Bay, Australia	6 (median group size of killer whales attacking humpback whales)	Humpback whales
Silber et al. (1990)	Gulf of California, Mexico	15	Bryde's whale

Valdés, Argentina, for southern sea lions (Vila et al., 2008), where the predators intentionally strand to procure pups. But in the same area, a previous study by Lopez and Lopez (1985) estimated hunting success to be 29% (although prey included both southern elephant seal pups and sea lions). In both studies, the number of observations was over 500. Lopez and Lopez (1985) also observed that cooperative killer whale attacks (~94%) were more frequent and resulted in higher captures (~31%) than when solitary males launched individual attacks.

From studies in the Pacific Northwest, we know that harbor seals seem to be easily catchable and managed by just three Bigg's killer whales. But in the same region, Bigg's killer whales require larger group sizes to secure more challenging prey, such as Dall's and harbor porpoises and Steller and California sea lions (Ford et al., 1998), and encounter higher failure rates. For large whale attacks, Pitman et al. (2015) recounted a humpback whale kill success percentage of 64% for killer whales in Western Australia, and in Alaska, gray whales were successfully pursued 18 times with one failure (Matkin et al., 2007). Some examples of hunting success reported in studies are summarized in Table 7.2.

Overall, there are only few studies that provide clues to killer whale hunting competence. The limited data are unsurprising given the paucity of predation events witnessed globally. Also, the data are skewed towards coastal areas where predation studies are feasible but still sporadically observed from start to finish (but see Chap. 8, Black et al., in this book). However, even with limited success rates (which is desirable for maintaining prey populations), mammal-hunting killer whales may achieve the necessary daily energetic demands and more (an adult killer whale requires 51–59 kcal/kg/day) (Baird & Dill, 1996; Doak et al., 2006; Williams et al., 2004) by targeting catchable prey, consuming nutritious and large prey items, and diversifying their prey type. They even make energetic gains through failed predation attempts of taking down the entire animal (e.g., through the wound and withdraw strategy, Pitman et al., 2001; Whitehead & Glass, 1985).

7.5 Hunting Through Social Learning

The fluid social structure in mammal-hunting killer whales (composed of both ephemeral and permanent social bonds) can stimulate cultural traits and potentially be a reason for the prevalence of different killer whale ecotypes globally (Foote et al., 2016; Whitehead, 2017). Group-specific hunting behaviors, like wave washing, intentional beach strandings, capturing cryptic species or certain prey types, and systematically dismantling large whale defensive maneuvers, are emblematic of killer whale cultures that are transmitted through social learning from conspecifics or inherited from the mother and shaped by ecological forces (Cantor & Whitehead, 2013; Foote et al., 2016; Rendell & Whitehead, 2001; Riesch et al., 2012; Whitehead, 2017).

Some of the best elucidated examples of observational social learning in killer whales come from studies by Lopez and Lopez (1985), Hoelzel (1991), Guinet (1991), and Guinet and Bouvier (1995). In Argentina, Lopez and Lopez (1985) observed adult killer whales stranding simultaneously but about 4 m apart from a juvenile animal. On occasion, the adult would fling prey towards the juvenile, which may or may not have captured a pinniped already. Such interactions are difficult to interpret as active teaching and may be a case of young animals observing, imitating, and learning prey-handling skills.

Table 7.2 Select examples of mammal-eating killer whale hunting success by study and species. Blank spaces refer to those areas where no data were available

Citation	Prey	Number of attacks	Number of successful attacks	Success %	Number of unsuccessful attacks	Unsuccessful %
Baird and Dill (1995)	Harbor seals	130	130	100		
	Harbor porpoise	3	3	100		
	Dall's porpoise[a]	2	0	0		
	Elephant seal	1	1	100		
	Unidentified sea lion	2	2	100		
Pitman et al. (2015)	Humpback whales	22	14	64	8	36
Matkin et al. (2007)	Gray whale (May–June only)		18		1	
	Dall's porpoise		0		3	
	Steller sea lion		1		0	
	Humpback whale		1		0	
	Northern fur seal		4		1	
	Minke whale		2		0	
Ashe et al. (2021)	Pacific white-sided dolphin[b]		12		30	
Ford et al. (1998)	Harbor seal	80	72	90	8	10
	California sea lion	8	4	50	4	50
	Steller sea lion	20	8	40	12	60
	Dall's porpoise	18	7	36.8	11	61.1
	Harbor porpoise	16	16	100	0	0
	Pacific white-sided dolphin	4	1	25	3	75
	Gray whale	2	0	0	2	100
	Minke whale	1	0	0	1	100

(continued)

Table 7.2 (continued)

Citation	Prey	Number of attacks	Number of successful attacks	Success %	Number of unsuccessful attacks	Unsuccessful %
Lopez and Lopez (1985)	Southern elephant seal and sea lion pups[c]	568	164	29		
Melnikov and Zagrebin (2005)	Gray whale	61	23	38	6	62
	32[d]					
	Walrus	24	5	21	2	79
	17[d]					
	Steller sea lion	1	1	100		0
	Bowhead whale	1			1	100
	Beluga whale	2	1	100		0
	1[d]					
Vila et al. (2008)	South American sea lion	585	88	15		

[a] Two successful Dall's porpoise attacks observed locally were by larger groups (four and eight individuals)

[b] Two unknown outcomes

[c] Includes corralling and intentional beaching hunting strategies

[d] Unknown outcomes

The beaching technique produced higher capture rates (~34%) of pinnipeds than cooperative hunting (~21%) and is riskier than cooperative hunting in deeper water—corroborated by Hoelzel (1991) in a later study. Hoelzel (1991) also noted the higher success rate when a pair of killer whales coordinated to hunt sea lion pups during deliberate strandings. Thus, despite the risk involved, killer whales may maximize hunting success through the beaching technique and may transmit those capabilities and knowledge to their young or conspecifics. The killer whales occurring in the area also appeared to maintain strong long-term associations that persist despite dispersal patterns and changes in group membership (Iniguez et al., 2005, unpublished report to the International Whaling Commission).

Off Possession Island, Crozet Archipelago, where killer whales use the same hunting technique, Guinet and Bouvier (1995) provided the only clear evidence of teaching and learning progress in young killer whales over a 5-year period. Up until year 6, juvenile killer whales engaged in practice strandings accompanied by an adult female, not necessarily the mother. After year 6, the same juveniles could conduct hunts on their own but still required their mother to help them return to deep water. Their observations suggest that older females, including the mother, provided encouragement, guidance, and instruction throughout the formative years to help refine their maturing young's hunting skills. The heavy parental investment and the close and lengthy bond between mother and offspring unlike in other areas could explain the low reproductive rates for killer whales in Crozet Archipelago. Guinet (1991) considered the alloparental teaching to afford inclusive individual fitness through kin selection (Hamilton, 1972) and by assuring long-term hunting success for social unit members.

In other regions, mammal-hunting killer whales may abandon kills or toy with prey (Jefferson et al., 1991; Jourdain et al., 2017; Reeves et al., 2006), harass but not attack (Ford et al., 1998), and selectively involve calf/juveniles in different tasks during large whale attacks and engage in surplus killing (Ferguson et al., 2012; Gaydos, 2005)—these incidences hint at potential learning opportunities for the young but are probably examples of failed attacks.

7.6 Conclusions

The social organization and structure of mammal-hunting killer whales are poorly studied in most regions of the world. Our knowledge may be incomplete, but there is increasing evidence that the predation success of mammal-hunting killer whales, and killer whales in general, is dependent on the fabric of their matriarchal society. Several studies, e.g., Beck et al. (2011), Jordaan et al. (2021), and Denkinger et al. (2020), have emphasized the fission-fusion nature of killer whale associations that markedly changes with ecological conditions, and uniquely among social carnivores, foraging strategies define and enhance social networks, and not the other way around (Denkinger et al., 2020; Jordaan et al., 2021). Further, the fluid social system and the attendance and tolerance of related and non-related individuals at feeding sites indicate that killer whales may operate as divergent groups within a democratic community. Thus, establishing artificial geospatial boundaries to mark management units is unlikely to be adequate for overall conservation strategies of both predator and prey. We need conservation models to account for the specialized hunting behaviors and associations within and among sympatric groups. Further, the evolution and persistence of hunting techniques through two centuries or more elucidate the importance of information transfer and cultural traits. The survival of mammal-hunting killer whales is dependent on the continuation of these key skills that enhance foraging success—a large part of which is achieved through social learning and consequently retention of cultural traits (Brakes et al., 2021).

Disruption of social units could have cascading tremors in the population and impact the viability of discrete groups. Evidence from Busson et al. (2019) on the loss of individuals from multiple social units due to lethal interactions with fisheries created demographic stress and impeded adult survival. The authors noticed weaker strength of associations within and among socially disrupted groups. Additionally, the loss of post-reproductive females and matriarchs could have profound effects on group resilience to man-made stressors. Like many social mammalian carnivores, female killer whale groups are the lynchpin for initiating and succeeding in an attack on large or small prey. Females carry the added responsibility of calf defense, extended parental investments in sharing hunting skills, providing nutrition during lactation, and alloparental care. At a minimum, we need to better elucidate every aspect of mammal-hunting killer whale predatory behaviors within a socioecological and evolutionary context in areas where they can be intensively studied over time. As Lima (2002) so eloquently and strongly argued, we need to accept that predator-prey behaviors are dynamic and interactive. For killer whales, we need to comprehensively unravel the anatomy of a hunt from prey search to consumption and modulation of behavior in response to multiple prey availability and behavior.

Despite the charismatic position that killer whales occupy in human perception, we remain uneducated about much of their lives and their ecosystem role. As impressive unmatched predators in the ocean, they can exert control in the marine environment through myriad direct lethal and indirect sublethal pathways (Reeves et al., 2006). Also, through the power of their expansive social network and hunting efficiency and tenacity, which continually evolves to align with changing ecological conditions, mammal-hunting killer whales could impact discrete populations and restructure ecosystems by influencing prey behavior and eliciting risk effects (Frid & Dill, 2002, summarized in Kiszka et al., 2015). Finally, by understanding and articulating the role of killer whales—an apex predator in marine environments—we can be prepared to address the challenges of human-dominated seascapes that can forever alter the resilience of animal societies.

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Chapter 8
Mammal Hunting Killer Whales off Monterey, California: A 30-Year Synthesis

Nancy A. Black, Colleen M. Talty, Alisa Schulman-Janiger, and Mridula Srinivasan

Abstract Bigg's (Transient) killer whales (*Orcinus orca*) display incredible cooperative hunting techniques and a complex social organization. We describe the predation behavior of Bigg's killer whales in Monterey Bay, California, over a 30-year period. These killer whales are marine mammal foraging specialists, with aspects of their occurrence, habitat use, association patterns, hunting strategies, and communication calls influenced by this ecological specialization. This population encompasses at least 193 individuals and 44 different matrilines. Bigg's killer whales off Monterey, California predate 12 different marine mammal species. Within this population, there are six key matriarchs that have played a significant role over the past three decades in 85% of gray whale calf (*Eschrichtius robustus)* predation events—an important prey in spring. Some killer whales gather in large groups during gray whale hunting season, where they jointly participate in attacks and engage in multi-group socializing for several days. When hunting smaller prey such as seals, sea lions, dolphins, and porpoises, they generally travel in separate matrilines composed of a mother and her non-dispersed offspring. Based on extensive observations, we believe that their prey-specific hunting techniques and their communication calls are likely transferred to subsequent generations through social learning, primarily through imitation. This culturally transmitted information results in sustained knowledge and enhancement of hunting techniques in successive generations. Despite apex predator status and lack of natural predators, Bigg's killer whale populations are vulnerable to the effects of climate change through potential

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changes in their marine mammal prey abundance and distribution, and the effects of persistent contaminants such as DDTs and PCBs that could negatively affect their reproductive success and immune system. The current chapter is a descriptive summary of the social dynamics and hunting prowess of mammal hunting killer whales in Monterey Bay. Future investigations are necessary to analyze observed patterns on hunting success, group size dynamics, predation risk effects, and social association patterns.

Keywords Matrilines · Generations · Cooperative hunting · Social structure · Foraging specialists · Cultural transmission · Bigg's killer whales · *Orcinus orca* · Predator–prey · Mammal hunters

Artistic Rendering by Britney Danials. Original Photos Credit: Daniel Bianchetta

It was Halloween 2020 when we took an all-day trip to look for whales and other *marine life in Monterey Bay. Nancy Black was captaining the trip and had several friends along. As we traveled south along the canyon towards Carmel Bay, we spotted splashes in the distance and several short quick blows with black dorsal fins, a sure sign of killer whales. Everyone on board was thrilled, as most people hope to see killer whales, but they are very unpredictable, especially in October, away from their peak sighting period during spring.*

We soon caught up to the action and immediately recognized the individual whales: adult female CA140B Louise and her offspring, CA140B1 (Stinger), CA140B2 (Bee), and CA140B3 (Buzz). There was also another female killer whale, CA23A2, who was traveling with this group, as her mother disappeared a few years earlier (likely died). We found these whales as they were right in the middle of hunting sea lions! As soon as we caught up to them and stopped, Louise literally came flying out of the water within several meters of our boat—so close that photos of her filled the frame. She was chasing a sea lion and leaped several times to catch it. Louise finally corralled the sea lion and then began to hit it with her fluke but did not kill it; instead, it looked like she was instructing the younger whales how to catch a sea lion while allowing them to imitate her actions. It looked like her first born, 7-year-old Stinger, was most involved in the lesson, and used her flukes to begin hitting this subadult sea lion. Both whales also knocked the sea lion with their heads, but predominantly used flukes. They could have easily taken this sea lion down quickly, as it was just lying on the surface taking a beating. Instead, this prolonged attack lasted just over an hour, while Louise and Stinger took turns hitting the sea lion. The other three whales watched nearby, with 10-year-old CA23A2 participating to a lesser extent. Stinger's siblings Bee (4-years-old) and Buzz (less than a year old) were likely too young to participate.

Louise, who is Emma's (CA140's) daughter, has learned these incredible skills from her mother, who now is continuing the transmission of knowledge to her own offspring. Emma is an extremely proficient hunter whose family, which included Louise at the time was involved in 10 predation events during spring of 2017, sometimes on consecutive days. Louise's kids have traveled with Emma for most of their lives, learning from her and their likely great-grandmother, CA40 (Xena). Louise recently dispersed from Emma, but still joins up with Emma and her other relatives periodically, and often during gray whale hunts. While the killer whales took turns hitting the sea lion, we were surprised by two humpback whales who came charging in, while loudly trumpet blowing. They headed straight for the killer whales and sea lion and interfered enough to cause the killer whales to eventually abandon the sea lion. To our amazement, one humpback whale swam underneath the sea lion and lifted it onto its back, as the humpback whale swam away! As luck would have it, we had a drone in the air. The drone footage captured the humpback carrying the sea lion away on its back, but soon the sea lion slipped off. Humpbacks are known to exhibit this type of interference behavior with unexpected benefits for targeted prey. We often see humpback whales appearing to come to the rescue of any prey the killer whales are trying to catch, as well as trying to prevent the killer whales from feeding on dead prey. After about 30 minutes the humpbacks moved away, and Louise and her family came back in and quickly killed the sea lion, ending this incredible encounter with a meal for her family. YouTube Video Link - Killer

Whales Teach Young to Hunt Sea Lions While Humpbacks Interfere https://www.youtube.com/watch?v=sxZDHTeoUvo

–Nancy Black

8.1 Introduction

Killer whales (*Orcinus orca*) are exceptional animals with unique characteristics such as their appearance and sexual dimorphism, matriarchal social structure, complex communication system, and predation behavior. Killer whale studies have greatly expanded since Michael Bigg and colleagues first discovered different ecotypes in the Pacific Northwest over 50 years ago (Bigg et al., 1987). Although killer whales are top predators and feed on a wide variety of marine animals (Jefferson et al., 1991), distinct populations show prey specialization and communicate in complex ways with different vocal dialects (Deecke et al., 2000; Yurk et al., 2002; Filatova et al., 2012).

Killer whales occur worldwide and in all major oceans (Leatherwood & Dalheim, 1978; Forney & Wade, 2006; Ford, 2009). They live in matriarchal groups or in groups with close family or social bonds that cooperate to hunt prey (Ford, 2019). In addition, they are long-lived, with some females living 65 plus years (Olesiuk et al., 1990; Ford et al., 1996). They are among the few known animals with a post-reproductive period after around age 45, when grandmothers and perhaps great-grandmothers still associate with their families, transferring knowledge to the young (Ward et al., 2009; Riesch et al., 2012; Ford, 2019; Nattrass et al., 2019). The natural history and behavioral ecology of killer whales globally are covered in Chap. 7 (Srinivasan, 2023) of this book and not elaborated further here.

8.1.1 Marine Mammal Predation Events: Monterey Bay, California

Monterey Bay is located along the central California coast, 145 km south of San Francisco, and is part of the Monterey Bay National Marine Sanctuary. Its main feature is a submarine canyon that bisects the bay and approaches within 0.4 km of the shore (Greene et al., 2002). This is the largest and deepest canyon along the west coast of the United States that approaches close to shore. It is structured somewhat like the Grand Canyon, with steep edges and several canyon offshoots (Fig. 8.1). The canyon topography allows deep-water species of whales and dolphins to approach relatively close to shore. Because of the high abundance and diversity of marine mammal species, Monterey Bay is often referred to as the “Serengeti of the Sea” (Monterey Bay National Marine Sanctuary/montereybay.noaa.gov). The area is located within a major upwelling zone, where deep, cold, nutrient-rich waters are driven to the surface by a combination of strong spring northwest winds, the California Current, rotation of the earth, and the geography of the coastline

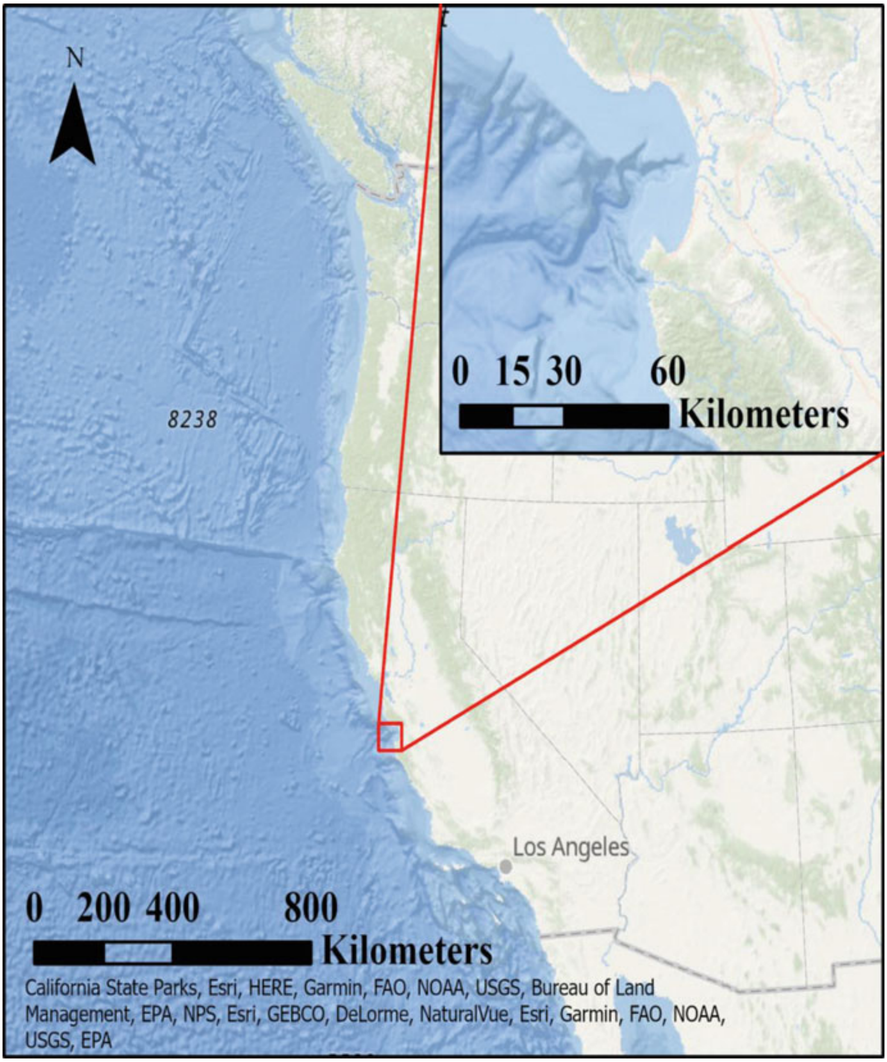

Fig. 8.1 Study area of Monterey Bay, California and its deep Monterey Submarine Canyon (map credit: Mason Donny)

(Rosenfield et al., 1994). There are only four other areas of coastal currents associated with the world's major upwelling areas as part of the five gyres. Besides the California Current (western coast of North America), these include the South Pacific Gyre (Humboldt Current/Peru and Chile), North Atlantic Gyre (Canary Current/ Northwest Africa), South Atlantic Gyre (Benguela Current/Southwest Africa), and the South Indian Ocean Gyre (West Australian Current/Western Australia) resulting in high productivity along the coastal areas of these currents (Munk, 1950; McClain et al., 2004). These five regions produce 25% of the total global marine fish catches but occupy only 5% of the total ocean area (Jennings et al., 2001). These unique oceanographic features result in high productivity that provides food sources for an abundance of marine life: for the Monterey Canyon, at least 26 marine mammal species and 94 species of seabirds have been documented.[1]

We have recorded Bigg's (Transient) killer whales' predatory behaviors in this region and observed longitudinal changes in predator–prey interactions within a socio-ecological context over several decades. Similar to groups of lions and wolves taking down prey (Scheel & Packer, 1991; Muro et al., 2011), there is extensive cooperation among individual killer whales and uniquely, transmission and refinement of hunting strategies across multiple generations.

In Monterey Bay, all three recognized North Pacific killer whale ecotypes—Residents (fish hunters, primarily salmon), Offshores (shark and fish hunters), and Bigg's killer whales (marine mammal hunters, Bigg, 1982; Bigg et al., 1987; Ford & Ellis, 1999; Morin et al., 2010), have been encountered in our study area. Occasionally, we encounter Offshore killer whales (Dahlheim et al., 2008; Ford et al., 2011), which are usually in groups of 25–60 (occasionally up to 100) and spread out over several kilometers. We have observed Offshore killer whales feeding on a seven-gill shark (*Notorynchus cepedianus*) and a blue shark (*Prionace glauca*). We encountered Southern Resident killer whales nine times between 2000 and 2023 in Monterey Bay, as they have seemingly expanded their range southward while searching for Chinook salmon *(Oncorhynchus tshawytscha*), which have become depleted along the Pacific coast (Walters et al., 2019).

Off Monterey, we mainly observe Bigg's killer whales. Bigg's killer whales have been genetically separated into four putative populations in the North Pacific, with each having prey differences (Ford et al., 1998; Saulitis et al., 2000; Heise et al., 2003; Matkin et al., 2007, 2012; Barrett-Lennard et al., 2011). They are: (1) West Coast Transients that range from southern California to Southeast Alaska (Goley & Straley, 1994; Black et al., 1997), (2) AT1 Transients in Prince William Sound, AK, (3) Gulf of Alaska Transients, and (4) Eastern Aleutian Transients (Barrett-Lennard, 2000; Parsons et al., 2013).

Monterey Bay is one of the few places where killer whales occur on a seasonal basis preying on gray whale (*Eschrichtius robustus*) calves, as well as year-round on pinnipeds, delphinids, and porpoises. Our study in Monterey Bay represents an open-ocean habitat and is quite different compared to mammal hunting Bigg's killer whales in inland waters of Washington State, British Columbia, and southeast Alaska (Baird & Dill, 1996; Ford & Ellis, 1999; Matkin et al., 1999; Dahlheim & White, 2010).

We see different matrilines and individuals than those commonly seen in the Pacific Northwest, although some Bigg's killer whales sighted in Monterey Bay have been observed off Washington, Vancouver Island, BC, in the inner and outer waters of the Queen Charlotte Islands, BC, and one group in southeast Alaska (Black et al.,1997; Towers et al., 2019). The habitat type is the main difference, as killer whales in the outer coastal waters off California live in exposed conditions, near the

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[1] https://montereybay.noaa.gov/intro/mbnms_quickfacts.html

shelf edge, that often include strong winds and swell that may impact their hunting abilities. The prey are also more diverse and abundant off California, compared to the northern inland waters of the Pacific Northwest. The inland waters of Washington, British Columbia, and southeast Alaska provide sheltered conditions, with harbor seals (*Phoca vitulina*) as the main prey, compared to the larger California sea lion (*Zalophus californianus)*, which is the main prey off California (See Chap. 7, Srinivasan, 2023). We also witness seasonal predations on gray whale calves off California, which are not part of the normal diet of Bigg's killer whales in the Pacific Northwest. However, gray whale calves are predated on a seasonal basis in the eastern Aleutians, another open ocean habitat along the gray whale migratory route (Barrett-Lennard et al., 2011).

We can comprehensively study Bigg's killer whale behaviors and social dynamics in Monterey Bay because we can observe them year-round for long periods of time in relatively mild weather conditions—often unattainable in other research sites. Hunting group sizes, as well as prey type and relative abundance, are different from the Pacific Northwest. Ford and Ellis (1999) reported 3–6 whales (1–2 matrilines) as the most encountered hunting group size, but these group sizes have become larger over the past two decades (Ford et al., 2013). In Monterey Bay, killer whales often congregate in large groups of 15–30 (3–5 matrilines) when hunting gray whale calves.

In the following sections, we discuss the foraging specializations of mammal hunting killer whales in Monterey Bay, and how their specialized marine mammal diet influences their movements and seasonal occurrence, social structure and organization, hunting strategies, and communication. We also discuss the importance of multigenerational information transfer through social learning on foraging success and survival. We also highlight some urgent threats to these apex predators from contaminant and toxin accumulation and the potential effects of climate change that may disrupt their top-down control of ecosystems (Baum & Worm, 2009). Most data presented here have never been published in the scientific literature, and therefore offer a foundational perspective on the lives of Monterey Bay mammal hunting killer whales. However, additional work is necessary to unravel individual facets of the foraging ecology of killer whales, including predation risk effects.

8.2 Survey Methods and Data Collection

Our survey methods included both opportunistic surveys aboard Monterey Bay Whale Watch vessels (which operate year-round on up to two daily trips of 3–4 hours each, and some 8–12-hour trips, weather and logistics permitting), as well as dedicated research surveys with our team (California Killer Whale Project, 501c3), focused on killer whales. These dedicated trips to survey Monterey Bay occurred periodically throughout the year. Killer whales are an unpredictable presence in Monterey Bay and along the coast, and most surveys are conducted opportunistically when killer whale sightings are reported. Despite extensive searches, they are not easily located in this large Bay, so we often rely on sighting reports from fishermen, naturalists, researchers, recreational groups, etc. In addition, we operate all-day boat surveys during April and May to coincide with peak killer whale sightings, when northbound gray whale cow/calf pairs migrate past the Bay. During these months, we conducted standard search patterns along the canyon edge, particularly on the north side of the canyon where most predation events occur. Some surveys were conducted under permit (1998–2004) to biopsy the killer whales and collect skin and blubber samples to analyze levels of chemical contaminants and genetics (Krahn et al., 2007).

When killer whales were sighted, we photographed all individuals for identification. We took perpendicular photos of both the left and right sides of their bodies, prioritizing the dorsal fin, saddle patch, and eyepatches. We noted killer whale group GPS positions at every surfacing or every half hour, group structure (tight vs. dispersed, or line abreast—parallel positioning of individuals), and general behavior (traveling, feeding, socializing, milling (non-directional movement), or resting). We also gathered data on the number of whales, water depth, sea conditions, dive times, and when possible, recorded predation behavior with photographs and a video camera. Since 2016, we have also used a drone to capture aerial views of behavior, group structure, and predation events. We stayed with the whales until the commercial trip time ended, sea conditions became poor, darkness fell, or we lost sight of the whales.

The time spent with each killer whale group encounter varied greatly, from an average of 1–2 hours on opportunistic trips to up to 14 hours on some dedicated surveys. We identified individual killer whales based on the ID numbers from our killer whale catalog (Black et al., 1997), which we have updated to document new calves, new individuals coming to the area, and suspected deaths. We analyzed videos and photographs of predation behaviors closely for some events. We collaborate with many other researchers who also identify killer whales along the west coast, to look for photographic matches of animals sighted in both areas.

8.2.1 Naming System

All Bigg's killer whales have catalog numbers; many also have nicknames. We follow the same naming system used by Ford and Ellis (1999) with Bigg's killer whales in the Pacific Northwest. All killer whales in our study have ID numbers that start with CA (for California). If these killer whales have been sighted in the Pacific Northwest, they will also have a designated T number. Our assigned IDs begin with CA1. For example, when female CA51 had offspring, they were assigned consecutive letters: CA51A, CA51B, CA51C, and so on. When her daughter CA51A had calves, they were assigned consecutive numbers: CA51A1, CA51A2, and so on. This tradition continues through multiple generations linking back to the original matriarch (Fig. 8.2).

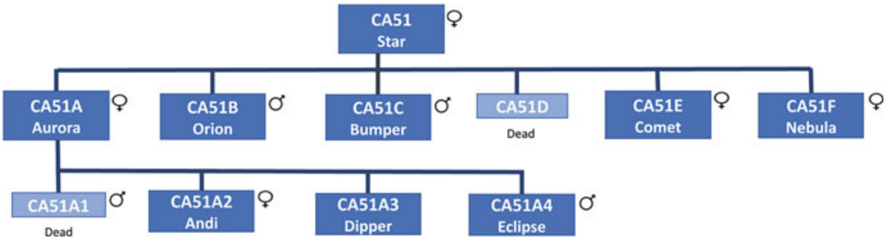

Fig. 8.2 Naming system for killer whale individuals in matrilines. This figure shows one of our most encountered matriarchs, CA51 (Star), and her offspring; this includes the now-dispersed female CA51A (Aurora) and her offspring

8.3 Social Dynamics

The California Bigg’s killer whale population most frequently seen in Monterey Bay, consists of 193 individuals, many of whom belong to 44 different matrilines (a female traveling with one or more offspring). Females can potentially give birth as young as 10 years old; most have their first calf between ages 12–15 years, and can continue having calves into their early 40 s. A male’s dorsal fin usually begins to “sprout” (grow taller and straighter) between ages 12–15 years; a few males in our population have started to sprout as early as 9–10 years old. A male is physically mature at 20 years old (Olesiuk et al., 1990). We encounter many groups annually, while others can go several years without being sighted in Monterey Bay.

Within our study population, we have demographic data (Towers et al., 2019) on 183 killer whales: 72 (39.3%) are mature females (20+ years old, unless reproductive at a younger age), 28 (15.3%) are mature males (20+ years old), 36 (19.7%) are subadults (ages 10–19, both sexes), and 47 (25.7%) are juveniles and calves (ages 0–9). Older killer whales that are at least 40 years old include 24 of our 72 mature females (33.3%), and 8 of our 28 mature males (28.6%). These counts are like data collected by Dahlheim and White (2010) on a different population of Bigg’s killer whales found in southeast Alaska. They identified 155 individuals (compared to our 193, with 153 used for demographics), 41 matrilines (compared to our 44), and 29 adult males (compared to our 28).

When female killer whales reach the age of about 45, they no longer have calves and experience menopause (Olesiuk et al., 1990; Ward et al., 2009; Foster et al., 2012; Brent et al., 2015; Croft et al., 2017), which is rare in mammals. Humans, short-finned pilot whales *Globicephala macrocephalus* (Kasuya, 1984), belugas *Delphinapterus leucas*, narwhals *Monodon monoceros* (Ellis et al., 2018), and false killer whales *Pseudorca crassidens* (Photopoulou et al., 2017) also experience menopause, although there may be more mammals for which such information does not exist. Researchers (Muller & Harris, 2022) recently found that female giraffes also experience menopause: they live about 8 years (~30% of their lives) after their reproductive window closes, helping to raise other giraffes’ calves.

Killer whale social structure and organization among matrilines in our study have been shaped by their foraging specializations. The social structure of Monterey Bay killer whales (Fig. 8.3) differs slightly from other Bigg's killer whales in the Pacific Northwest and Alaska and could be due to differences in main prey and habitat between these locations (Ford & Ellis, 1999; Baird & Whitehead, 2000). We have documented a few dispersals and are still gathering data on this shift in social groupings. All male offspring (with one exception) have stayed with their mothers and have not dispersed. When the daughter of a matriarch starts to have calves, she may split off to form her own family group after having one or two offspring. Only one female offspring in our Monterey population has stayed with her mom for a longer period even after having five calves. Males whose mothers die may travel by themselves or join up with another lone male; if the male is younger, he may be more likely to join another matriarch and her family. If the mother of a female dies before her daughter has her own calves, that daughter may join up with another matriarch and family and may associate for various time periods with a few different families.

Older post-menopausal females whose daughters have dispersed with their own offspring will continue to travel with their son (or sons). If her son dies, then these older females may join other lone post-menopausal females and periodically join other matriarchs and their families. Post-reproductive females are very important contributors to their population. Nattrass et al. (2019) found that in Resident killer whales, groups with grandmothers are more successful in foraging than those with no grandmothers. These grandmothers possess extensive memories about prey (i.e., where to find prey in difficult conditions) and can help provision youngsters (Nattrass et al., 2019), which is advantageous compared to matrilines with no older females. Similarly, in Monterey Bay, Bigg's killer whale matrilines with multiple generations have higher hunting success during gray whale calf predation and produce more surviving offspring than killer whales with smaller family groups and no grandmothers (see Sect. 8.5).

These are the core social groups found most of the year, except during the spring season when some whales prey on gray whale calves; then several of these core groups will often join in temporary aggregations to hunt, share killed prey, and socialize.

In Monterey Bay, we often see several matrilines that gather in temporary large groups (usually composed of >16 killer whales) when hunting or feeding on gray whale calves in the spring (Fig. 8.4).

When killer whales in Monterey Bay gather temporarily in larger groups to hunt, not all group members may be involved in prey capture. However, they share in eating the carcass (Fig. 8.5). Feeding events usually bring several matrilines together, creating a social gathering. We have observed several different matrilines sharing in the same kill, mostly with gray whale calf carcasses but sometimes with smaller prey.

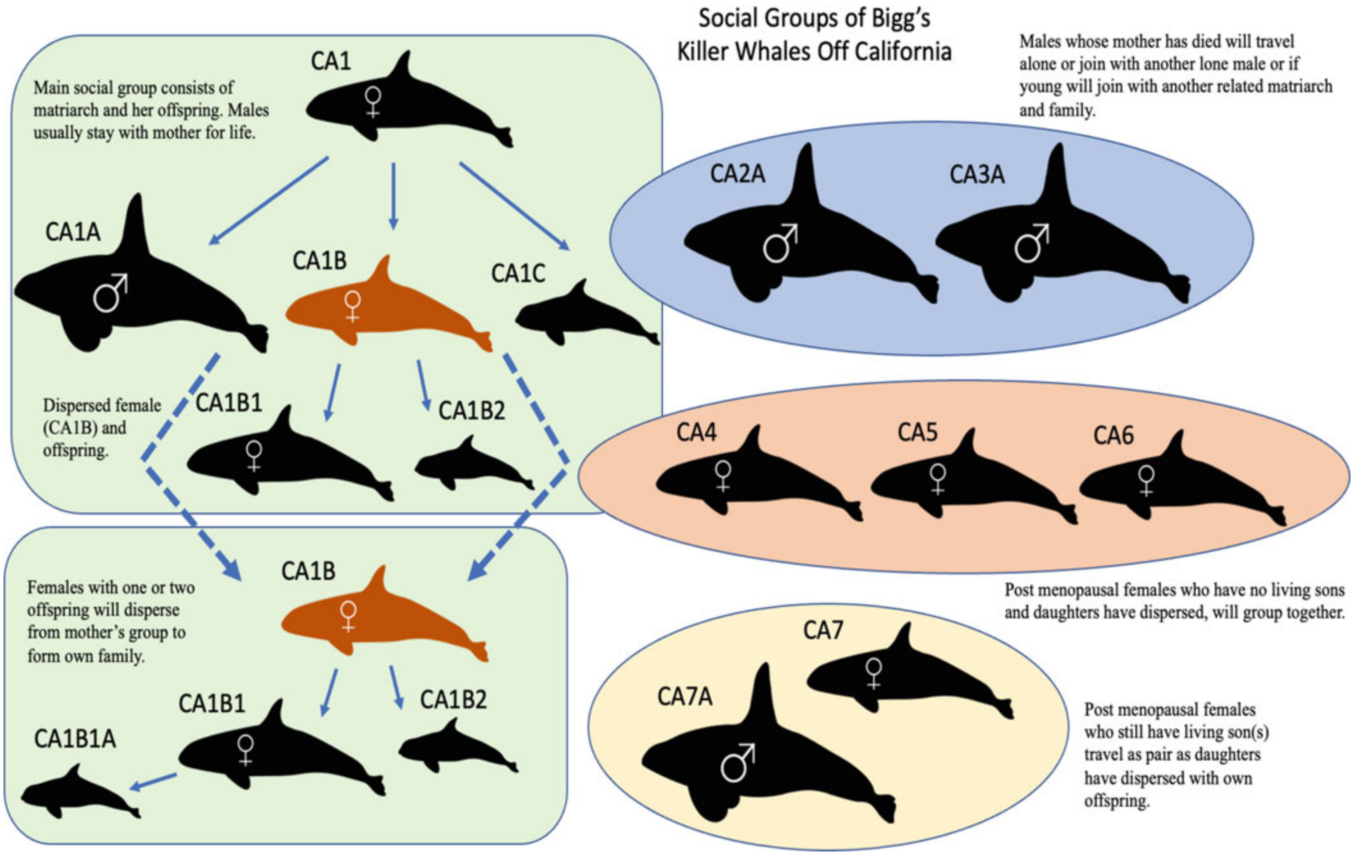

Fig. 8.3 Social structure of Bigg's killer whales off California. The primary social unit is a matriarch (adult female) and her offspring. A female offspring of the matriarch (tan color) will often disperse and form her own family after she has one or two offspring. A male usually remains with his mother for life; occasionally a son may disperse. Males travel alone, join other lone males, or join other matrilines after their mothers die. Post-menopausal females whose offspring have dispersed or died will often travel with each other. ID numbers shown here are for illustration only; they do not represent actual individuals

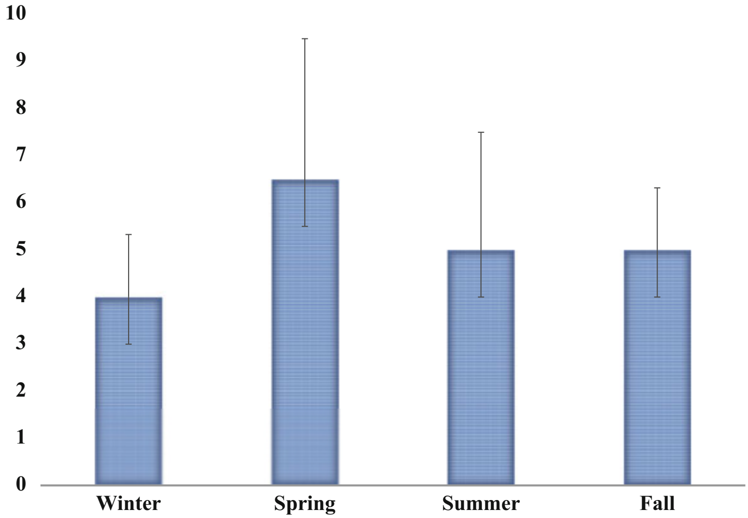

Fig. 8.4 Killer whale median group sizes by season (2002–2021) show the largest group sizes in spring when killer whales hunt gray whale calves. Error bars signify calculated standard deviation values from the median for each season (N=1,076)

Fig. 8.5 Killer whales sharing blubber from different predation events. (**a**) Killer whales sharing a pinniped carcass and (**b**) Killer whales sharing a gray whale carcass. *Photo credits:* ***a****. Evan Brodsky,* ***b****. Colleen Talty*

8.3.1 Seasonal Occurrence and Inter-Group Interactions

Encounters with mammal hunting killer whales occur most often in Monterey Bay during April and May when gray whale cow/calf pairs are traveling north to Alaska (Fig. 8.6). Killer whales also seasonally frequent pinniped pupping areas, especially when the pups are weaned and foraging at sea. There are several pinniped pupping areas around Monterey Bay, including an elephant seal (*Mirounga angustirostris*)

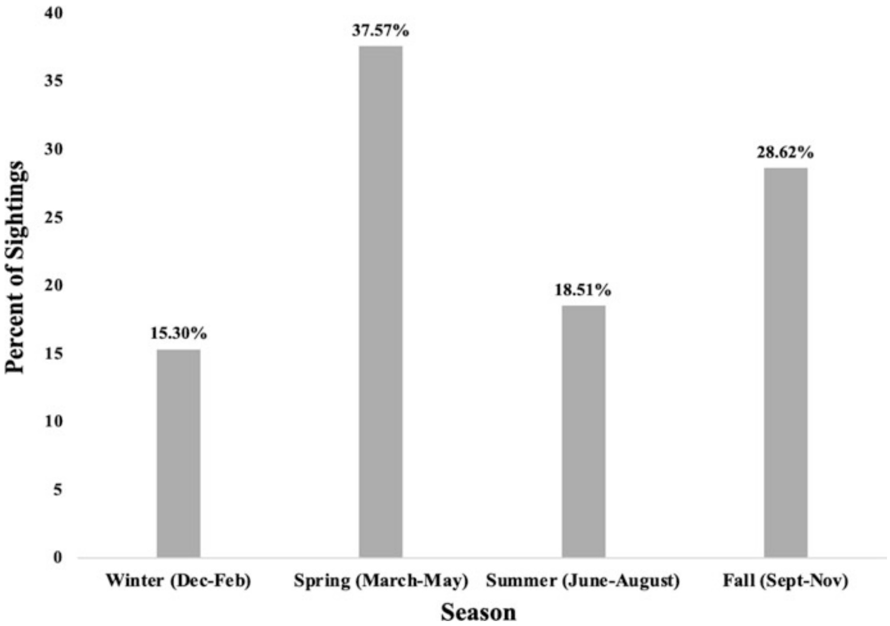

Fig. 8.6 Percent of seasonal sightings between 1997 and 2021, including April and May, which corresponds to the peak northbound gray whale cow/calf migration (N=1,345)

rookery at Año Nuevo to the north, an elephant seal rookery in San Simeon to the south, and a few harbor seal (*Phoca vitulina*) pupping beaches. California sea lions haul out throughout Monterey Bay and their primary pupping areas are in the Channel Islands in southern California during summer. Most sea lions, except some juveniles, leave Monterey Bay in the summer for the breeding areas, which could explain why fewer killer whales are seen during summer. The most current population estimates for pinnipeds off California include approximately 31,000 harbor seals, 180,000 northern elephant seals, and 250,000 California sea lions (Carretta et al., 2022). Mammal hunting killer whales have access to abundant pinniped prey in this area.

The maximum number of killer whale encounters (Fig. 8.6) and maximum photo-identification of individual killer whales (Fig. 8.7) in Monterey Bay also occur during spring. Typically, we observe one group of several matriarchs and sometimes with a male attempting to attack a gray whale calf. Occasionally, there may be 40 whales present in an area with only a few of them involved in the actual attack.

Killer whales are at least acoustically aware of other killer whales in the area. Killer whales can hear each other from at least 16 kms away (J. Ford, personal communication, 2012). On one occasion, we observed a group of killer whales leave the gray whale carcass suddenly after a kill and head at high speed to a location about 20 kms away, where another killer whale group was attacking another gray whale calf. The two groups joined forces and were able to kill that calf. Similarly, in 2020,

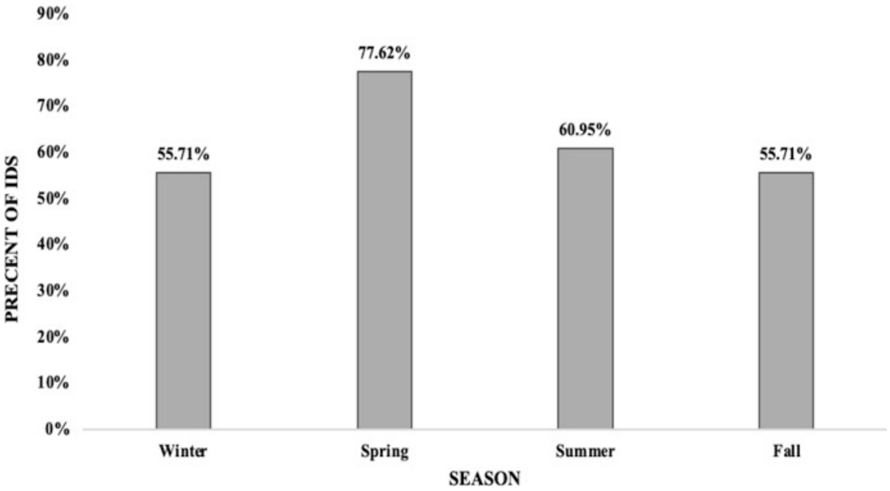

Fig. 8.7 Percent of individual killer whales observed per season from 2009 through 2019. This represents the seasonal occurrence of killer whales, with a greater number of individuals identified in Monterey Bay in spring (N=2,010)

we observed a family of Bigg's killer whales (the CA140s) in the northern part of the Bay suddenly pick up speed. We then received a report of an attack 15.3 km away (by her daughter, head of the CA140B matriline). By the time we arrived, the original killer whale group we had been with (the CA140s) was already at the attack site. These examples suggest that killer whales may either detect gray whale vocalizations or sounds from attacking killer whales from at least 15 km away during a predation event. When large killer whale groups converge at a predation site, there is no animosity or competition among them, and the whales fully cooperate with each other. We do not know if there is a dominance structure during intergroup interactions during or after a feeding event, but we have seen seemingly unrelated matrilines feeding together on a carcass. In addition, some matrilines appeared to wait their turn and only fed after other matrilines left the carcass.

8.4 Movement Patterns

Bigg's killer whales are often associated with the edge of the canyon (shelf-edge) in Monterey Bay, where the water is an average of 183 m deep, and marine mammal prey may be more concentrated due to oceanographic and bathymetric features, as discussed in Sect. 8.1. We have also observed killer whales closer to the coast in shelf waters, where they typically hunt harbor seals and harbor porpoises (*Phocoena phocoena*).

A small number of Bigg's killer whales from Monterey Bay were photographically matched with animals south of the Mexican border, and several others as far north as southeast Alaska. In southern California, Bigg's killer whales usually target California sea lions and large schools or "superpods" (over one thousand) of common dolphins (*Delphinus delphis*); in other areas such as the Channel Islands off southern California, they sometimes seek large aggregations of pinnipeds near haul-out locations. Bigg's killer whales prey on northbound gray whale cow/calf pairs as they head toward their Alaska feeding areas.

8.4.1 Short-Term Movements inside Monterey Bay

Bigg's killer whales strategically avoid staying for long periods in one area and remain undetected by wary prey. Potential marine mammal prey may be unaware of killer whale presence unless there is a predation event. Killer whales are ambush predators that hunt in stealth mode. Even if prey are alerted to predator presence, killer whales can still be successful in their hunts (See Sect. 8.5).

After a predation event, killer whales may leave immediately but may linger for a few days in Monterey Bay. At times, lone males or small family groups may be encountered for a few weeks. Sometimes lone males target harbor seals near one of their main haul-out sites inside the Bay, and we might encounter these males just 3–5 km from shore. A well-known group of killer whales, the CA51s—and their daughter's family (the CA51As)— often mill near the head of the canyon off Moss Landing (Fig. 8.8), and patrol back and forth (east and west) for several miles along the shelf-edge in that area while targeting harbor seals, sea lions, and young elephant seals. The CA51s and 51As also patrol inside Carmel Bay to catch seals near-shore, and gray whale calves, which is adjacent to the deep drop-off of Carmel Canyon. Since the canyon bisects Monterey Bay, they usually travel close to the edge around 200 m water depth (Fig. 8.8). We typically do not see other matrilines traveling and hunting so close to the canyon head, but other groups will also patrol the shelf-edge in the east-west direction. We assume that CA51A learned about these different hunting areas through her mother, CA51.

Killer whales traveling in Monterey Bay are often tightly grouped, frequently swimming in a line abreast formation. Sometimes they spread out, encounter prey, and either attempt to catch it or continue traveling. At other times, they may spread out over 2 km in singles, pairs, or trios—likely indicative of foraging behavior similar to the open-ocean foraging killer whales off Canada (Ford et al., 1998).

Killer whales exhibit a consistent dive pattern, with typical dives of 3–7 minutes and surfacing intervals of 1–2 minutes, taking several breaths before diving again. The whales can maintain this pattern for hours without catching prey. During traveling or foraging mode, they can pass by potential prey with no visible interest—either because they have been detected by vigilant prey or they are not in hunting mode. We hypothesize that the most abundant and easiest to hunt prey are captured regularly, unless more nutritious prey (e.g., a gray whale calf) is available (see Sect. 8.5).

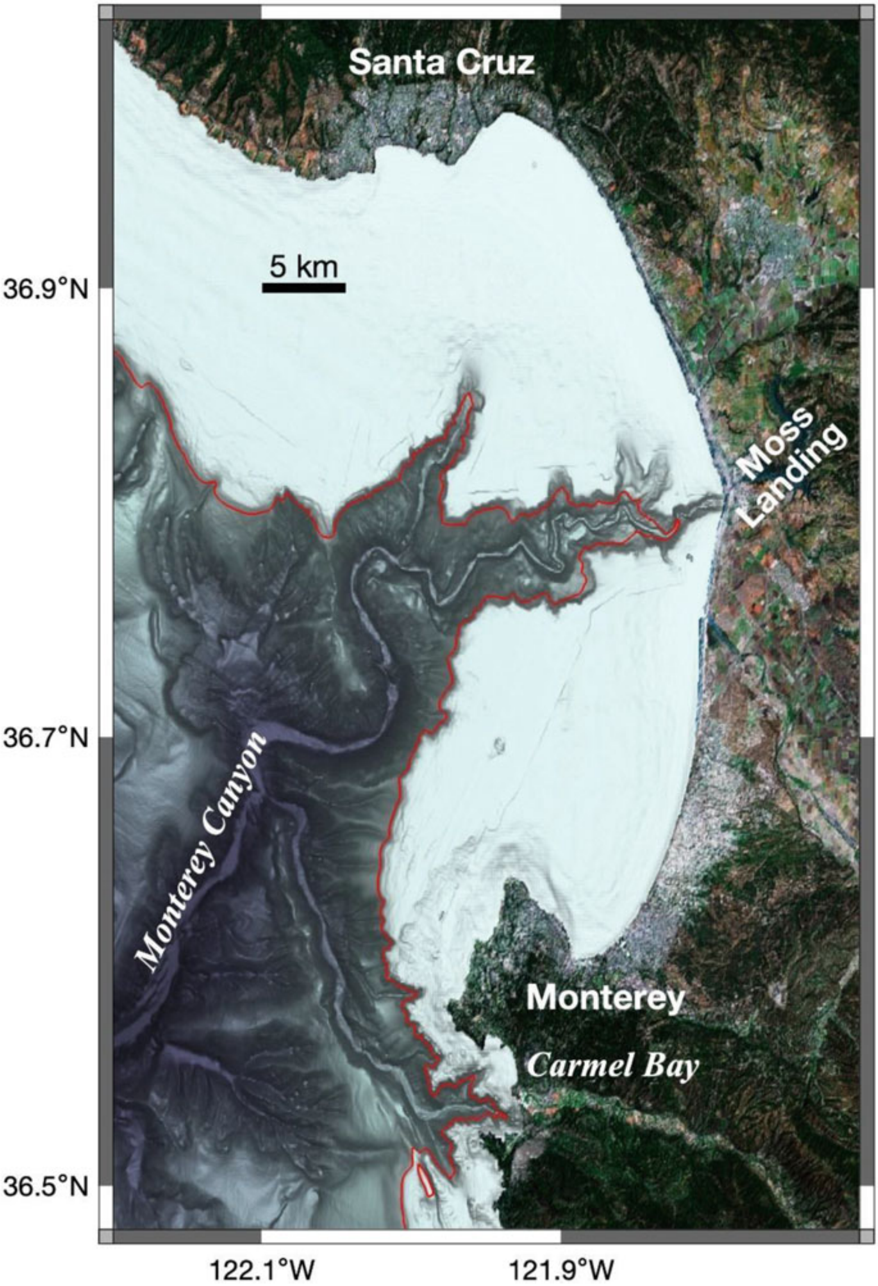

Fig. 8.8 Bathymetric features of the Monterey Bay submarine canyon. The 200 m line is in red. (NOAA, 2022, map credit: John Ryan/Monterey Bay Aquarium Research Institute)

8.5 Overview of Hunting Strategies, Group Sizes, and Hunting Success

Hunting strategies of Bigg's killer whales vary depending on prey type and are highly influenced by their foraging specializations. Hunting strategies have been extensively studied in land mammals (Palmer et al., 2023; Chakrabarti et al., 2023; Tallian et al., 2023; Smith & Holekamp, 2023; Jordan et al., 2023) and are dependent on the most efficient manner to successfully kill a variety of prey items of different sizes, injury risk levels, escape abilities, and predator avoidance strategies. A large percentage of killer whale predation events occur below the surface, so our knowledge is incomplete. Fortunately, because of the long span of our study and over 100 predation observations, we can methodically describe the primary hunting modes and techniques by prey type.

Bigg's killer whales in Monterey Bay prey on 12 different marine mammal species. California sea lions, followed by elephant seals and harbor seals, are the most frequently taken prey (Fig. 8.9). There is a bias toward recording more prominent predation events involving gray whales, as killer whales may spend several hours attacking prey and several days feeding on a gray whale even if predation events are limited to two months a year. Conversely, harbor seal captures may be under-reported, as they are caught silently and quickly and can be easily missed in prey identification (See Srinivasan, 2023, Chap. 7). Similarly, dolphin and porpoise captures may be underestimated as well, since these species are also caught

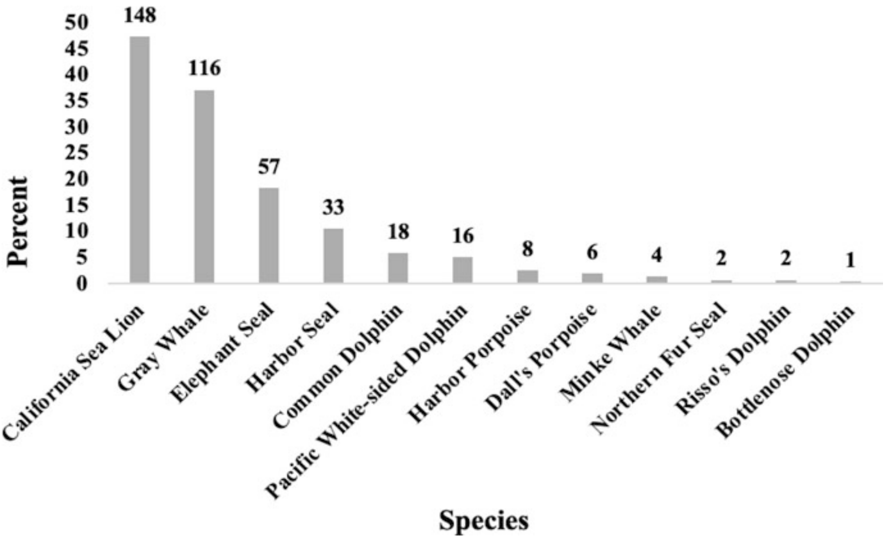

Fig. 8.9 The proportion of prey hunted by Bigg's killer whales in Monterey Bay, from 1991 through June of 2022

Table 8.1 Summary of predation behavior on cetaceans (excluding gray whale calves, see Sec. 8.5.4), including success rate

Species	Minke Whale	Pacific White-sided Dolphin	Common Dolphin	Risso's Dolphin	Bottlenose Dolphin	Harbor Porpoise	Dall's Porpoise
Predation events	4	16	18	2	1	8	6
Killer whale average group size & range	10.3, 6–14	5.1, 2–13	4.9, 2–10	7.5, 7–8	3	5.4, 2–13	6.3, 6–9
Duration of kill (mins)	30–45	7–112	15–54	20–35	38	1–30	5–15
Duration of feeding (mins)	<60	<30	<30	<30	<40	<30	<60
# Consumed	4	11	13	2	1	8	4
# Escapes	0	5	5	0	0	0	2
% Success	100%	68.7%	72.2%	100%	100%	100%	66.6%

Table 8.2 Summary of predation behavior on pinnipeds, including success rate

Species	Northern Elephant Seal	Harbor Seal	California Sea Lion	Northern Fur Seal
Total predation events	57	33	148	2
Killer whale average Group size & range	4.3, 1–20	3.4, 1–14	5.4, 1–16	9, 6–12
Duration of kill (min)	3–90	2–86	3–279	<10
Duration of feeding (min)	15–150	30–120	5–150	<5
# Consumed	52	29	128	2
# Escaped	5	4	22	0
% Success rate	91.2%	88.7%	86.4%	100%

quickly, and multiple dolphins may be hunted and consumed. Tables 8.1 and 8.2 summarize predation behavior on cetaceans and pinnipeds, including success rates.

8.5.1 *Hunting Strategies Pass from Matriarchs to Offspring:* Killer Whale Culture

It takes many years for young killer whales to master hunting strategies needed to capture and kill marine mammal prey. During gray whale attacks, actively involved mothers often pause to bring calves and juveniles close so they can witness hunting techniques used by older killer whales. CA51A (Aurora) brought her young son

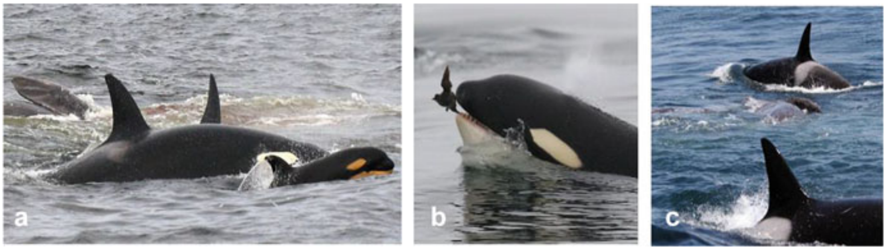

Fig. 8.10 Offspring learn hunting strategies from their mothers and practice those strategies. (**a**) Matriarch CA51A brings calf CA51A4 for a close look at a gray whale calf attack, (**b**) Juvenile female CA51A2 grabs a rhinoceros auklet after playing "hit the bird," (**c**) CA140 and her likely mother CA40 work together on a gray whale kill. *Photo Credit:* ***a*** *and* ***b****. Alisa Schulman-Janiger,* ***c****. Nancy Black*

CA51A4 (Eclipse) close to a gray whale calf under attack (Figs. 8.10a, 8.3 for matriline). Matriarchs encourage youngsters to practice hunting skills on small sea lions and birds, like the rhinoceros auklet (*Cerorhinca monocerata*) that CA51A2 (Andi) caught (Fig. 8.10b). On several occasions, CA51A (Aurora), her mother would hit a bird with her flukes (tail lobbing), as CA51A2 watched; then they practiced this move side-by-side, with CA51A2 exactly imitating her mother. These apparent practice moves can progress to tossing the bird into the air—a skill frequently used to debilitate pinnipeds or small cetaceans.

Using seabirds to hone hunting skills is probably an example of social learning through imitation, similar to killer whales intentional stranding on beaches to capture pinnipeds near Patagonia, Argentina (Lopez & Lopez, 1985, see also Srinivasan, 2023). CA140 (Emma) and her likely mother CA40 (Xena) have participated together in numerous gray whale attacks for three decades (Fig. 8.10c). CA140 now has three offspring and three grand-offspring. This presumed four-generation family are extremely proficient gray whale hunters, with expert knowledge of gray whale hunting techniques transmitted through three levels of adults to the next generation of killer whales. The matrilineal social structure facilitates cultural transmission of hunting behaviors through social learning (Rendell & Whitehead, 2001).

8.5.2 Pinniped Hunting Strategy

Pinnipeds are a primary prey source for Bigg's killer whales. Ford (2019) found that harbor seals are the most common prey for mammal hunting killer whales in the inland waters of the Pacific Northwest. Dahlheim and White (2010) observed more Dall's porpoise (*Phocoenoides dalli*), as prey in southeast Alaska (inland waters with steep drop-offs), whereas California sea lions are most targeted in the more pelagic open-ocean region of Monterey Bay. Similarly in the open waters of the Gulf of Alaska, Steller sea lions (*Eumetopias jubatus*), Dall's porpoises and harbor seals are the most common prey (Heise et al., 2003). Like Monterey Bay, gray whale calves and subadults are seasonally important prey in the eastern Aleutians (Barrett-Lennard et al., 2011). Elephant seals ranging from adult males to just-weaned pups are often prey in Monterey Bay.

Frequently encountered killer whale groups are spotted patrolling the inner Bay (off Moss Landing Harbor), and west along the edge of the canyon, looking for marine mammal prey (Fig. 8.8). On one occasion, we observed a group of six killer whales in this area catch a weaned elephant seal, a sea lion, and a harbor seal within four hours. Killer whales will often carry their partly eaten carcass around with them as they travel for a few hours, sometimes passing it among individuals.

Killer whales are regularly sighted along the north edge of the canyon near its drop-off, or the 100–200 m depth contour running east to west. Some remain in the area for several days or even over a few weeks, taking advantage of the high numbers of pinnipeds traveling in and out of Monterey Bay from Moss Landing and Elkhorn Slough, ~ 11 km long tidal slough and estuary where sea lions haul out and harbor seals rest and feed (Fig. 8.11). Occasionally, these killer whales are observed near shore around the Carmel Bay area, south of Monterey—another good place to catch harbor seals and sea lions near their haul-out sites.

The techniques used to hunt California sea lions, harbor seals, and northern elephant seals differ in method and kill duration. Large male elephant seals are challenging to catch, as they spend much of their time diving and continue that dive pattern as they travel back and forth to their breeding areas, so killer whales may encounter them less often than weaned youngsters. There are two main breeding areas: north of Monterey (Año Nuevo), and one to the south (Piedras Blancas). Killer whales tend to cooperate to prevent the adult elephant seals from diving out of the killer whale's depth range or try to wait them out, but more effort is involved to catch them. Killer whales also ram elephant seals and try to drown them quicker than sea lions, as they are not as dangerous or as aggressive (Fig. 8.12a, b, d). They usually spend over 30 minutes to a few hours feeding on adult elephant seals, which have a large volume of bright red blood due to their deep diving physiology (Le Boeuf & Laws, 1994). Repeatedly, killer whales hit and throw young elephant seals several meters into the air on first contact to injure them quickly (Fig. 8.12b). Killer whales may target several small elephant seals over a few hours.

Harbor seals are taken quickly, often with one quick lunge near the surface. We may see one killer whale make a quick splash and grab the seal or capture it quickly below the surface without much activity (Fig. 8.12c). At other times, killer whales forcefully hit the seal with their flukes over eight meters into the air. Killer whales often share the prey; however, since these seals are small, they typically feed on one for only 5–10 minutes.

Large adult male California sea lions take the longest time to kill, as they might use their teeth to fight back. The killer whales may use smaller sea lions as practice/social learning opportunities by prolonging attacks to show their juveniles and calves how to hunt. Some of these extended attacks can last over one hour. Often after the matriarch hits the sea lion, her calf imitates the mother's moves. These

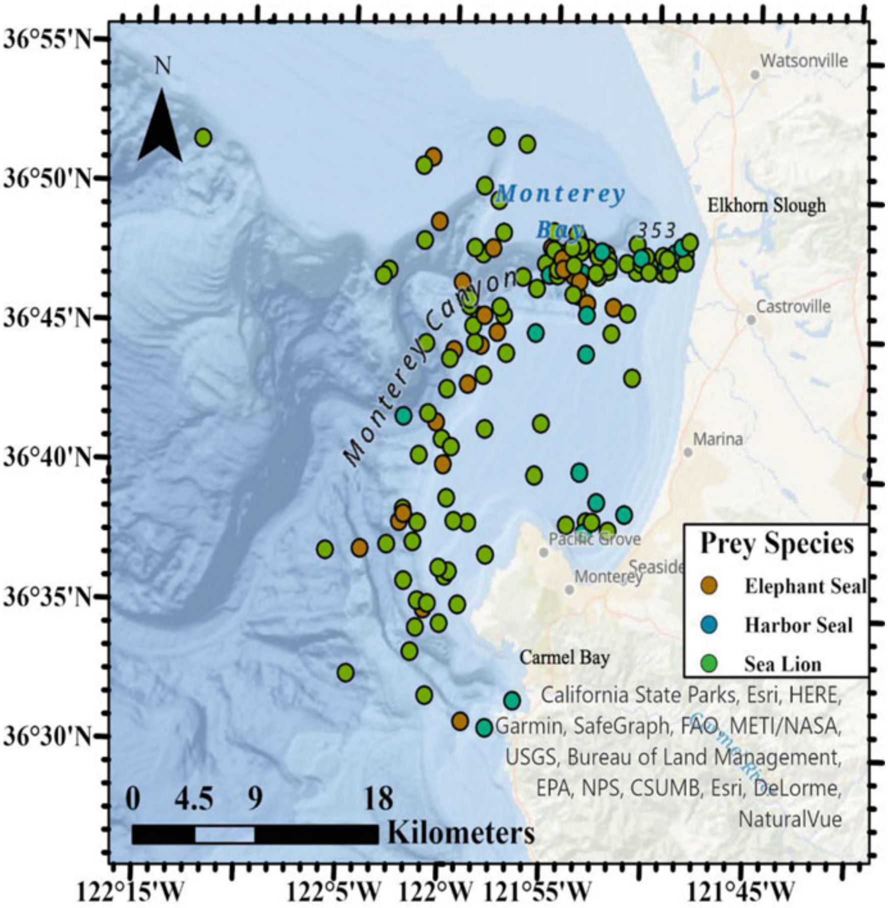

Fig. 8.11 Pinniped hunts observed 1991–2022 (many points are direct overlaps, map credit: Mason Donny)

practice runs are usually repeated multiple times. To subdue larger sea lions, killer whales often hit them out of the water with their heads, turn belly side up, and hit them with their powerful flukes, which provides a good angle to deliver a hard hit (Fig. 8.12e). They also can mix hits with fast rushes past the sea lions and slam them with their flukes as they rush by, and then ram them with body slams or dorsal fin slams.

The adult females do most of the work, often in pairs as they work together to surround sea lions, which do not have many defense tactics. After being hit repeatedly, sea lions often lie near the surface immobile, looking both above and below for the next hit. The killer whales eventually hold them underwater to drown them. They often skin the pinnipeds before feeding on them.

Fig. 8.12 Different pinniped hunting and feeding strategies. (**a**) Killer whales traveling with a captured northern elephant seal, (**b**) grabbing and throwing a northern elephant seal, (**c**) with a harbor seal in its mouth, (**d**) with an elephant seal carcass draped around its dorsal fin, and (**e**) whale belly up, hitting a California sea lion with its flukes. *Photo credit: **a**. Monterey Bay Whale Watch/ Mike Kauffmann, **b**. Jodi Frediani, **c** & **e**. Daniel Bianchetta, **d**. Nancy Black*

8.5.3 Dolphin and Porpoise Hunting Strategy

Killer whales in our study use a similar technique for hunting both dolphins and porpoises, even though porpoises occur in small groups of fewer than ten individuals and dolphins can occur in groups of hundreds or even thousands of individuals. Killer whales appear to prefer schools of common dolphins (*Delphinus delphis*) over other species. Common dolphins travel in large, tightly cohesive groups that may include several hundred to over one thousand individuals. They are typically not found in Monterey Bay year-round but are present during periods of warmer water such as during El Niño Southern-Oscillation events and in some fall and winter months when the sea surface temperature is warmer than usual in Monterey Bay. When schools of common dolphins (usually the long-beaked type *D. delphis bairdii,* but sometimes the short-beaked *D delphis delphis*) are present in the area, they usually travel in a circuit pattern throughout the Bay, often near the canyon edge and over shelf waters. Other dolphins, such as Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) and Risso's dolphins (*Grampus griseus*), typically spread out over several kilometers. The large and tightly grouped common dolphin pods are probably easily detected by roving killer whales and an attractive target.

If killer whales miss the chance to hit the dolphin and toss it out of the water with their head (Fig. 8.13b), they usually try to isolate a single animal and chase it—this tactic is often successful. Sometimes the killer whales continue to hit the dolphin

Fig. 8.13 Killer whales hunting dolphins and porpoises. When they violently throw a small mammal into the air by their forceful actions, presumably to stun it, we term this "punting." (**a**) Punting a Pacific white-sided dolphin, (**b**) Punting a common dolphin, and (**c**) Punting a Dall's porpoise. *Photo credit:* ***a****. Lori Mazzuca,* ***b****. Monterey Bay Whale Watch / Katlyn Taylor,* ***c****. Nancy Black*

with their flukes until it is severely injured, grab it and drown it underwater, then tear up the prey and share it with the group. Killer whale group size during dolphin hunts is typically small, with just one matriline.

During the autumn of 2015, we were working with a BBC crew to film killer whales hunting dolphins. Long-beaked common dolphins were abundant, and we located killer whales 11 times over four weeks. On one occasion, we watched as they were apparently cautiously and quietly approaching one group of approximately 1500 dolphins. The killer whales were tracking them from about 0.5 km. After they followed the dolphins for about 15 min, they slowly moved closer to about 200 m distance. One adult female killer whale burst out of the water and began porpoising at full speed toward the dolphins, then dove and came up out of the water tossing a dolphin into the air with her rostrum. The dolphin was stunned and probably injured. A few killer whales (including the female who had tossed the dolphin) quickly chased and grabbed it, and then held it underwater. They appeared to share the prey, finished feeding in about 10 minutes, and moved on—leaving behind an oily slick and a pair of floating lungs and a pile of intestines. During this period, we encountered killer whales hunting common dolphins on seven occasions, with six successful predations and one escape.

Killer whales utilize similar techniques to hunt common dolphins, Pacific white-sided dolphins, (Fig. 8.13a) Dall's porpoises, and harbor porpoises. Since killer whales preferentially travel along the canyon edge, they have higher chances of encountering and hunting Pacific white-sided dolphins and Dall's porpoises than harbor porpoises, which are found in shallow waters. Dall's porpoises are one of the fastest swimming cetaceans and could outpace killer whales. To successfully hunt Dall's porpoises, killer whales may have to catch and injure them at first contact (Fig. 8.13c).

Killer whales may infrequently travel over the shelf into shallower waters (60 m–100 m), possibly seeking harbor porpoises that occur in waters of <200 m. Harbor porpoises travel solo or in small groups over the shallow shelf, both north and south of the canyon (Forney, 1999; Byrd, 2001), making them good targets for killer whales. Because attacks and feeding bouts involving dolphins and porpoises are short, the actual number of kills is likely underestimated. Coastal common bottlenose dolphins (*Tursiops truncatus*) are typically found just outside the surf line throughout the inner Bay and are rare targets for killer whales in Monterey Bay. There's only one instance in August 2006 of a bottlenose dolphin predation event. While watching five humpbacks feeding close to shore near the mouth of the canyon by Moss Landing, we spotted three killer whales nearby (two females and a juvenile). They were surfacing erratically, 0.8 km off the mouth of Elkhorn Slough, one whale spyhopped right after we arrived, and we thought another whale was carrying something in her mouth. Two minutes later, the two females (CA138 and CA51A) popped up next to a surface oil slick, and there was a piece of blubber floating near it. Seven minutes later, we photographed 13-year-old CA51A surfacing near us with a bottlenose dolphin calf in her mouth. We did not see any dolphins swimming nearby; the attacks likely occurred shortly before we arrived.

Risso's dolphins occur throughout Monterey Bay and are the most frequently seen dolphin. Risso's dolphins frequent the canyon, often near the shelf break, and inside the Bay in shallow shelf water when market squid (*Doryteuthis opalescens*) are spawning. Bigg's killer whales in Monterey Bay do not typically predate Risso's dolphins. The reasons for excluding Risso's from their diet could be because Risso's dolphins are large (4 m in length) and occasionally display group aggressive and defensive behavior toward other baleen whales and dolphins.

We have only observed two Risso's dolphin predation events in Monterey Bay: in 2005 and 2021, by two different groups of killer whales not associated (to date) with our regularly seen Bigg's killer whale population or with Bigg's killer whales from the Pacific Northwest. Instead, these appear to be from a presumed offshore mammal specialist killer whale population not linked to the Bigg's killer whales in our study. Like the killer whales that hunted sperm whales 112 km off central California in 1997 (Pitman et al., 2001), some individuals exhibited cookie cutter shark bite scars—which are not seen on any of our local Bigg's killer whales (Dwyer & Visser, 2011; Olson, 2023). The lack of predation on Risso's dolphins by Bigg's killer whales in Monterey Bay could suggest that hunting Risso's dolphins is not a skill transmitted among the matrilines.

In 2000, we witnessed a remarkable mobbing encounter involving a group of 15 Risso's dolphins that chased seven Bigg's killer whales commonly seen in Monterey Bay. Both species were porpoising out of the water for about 30 minutes at 28 km/hr. as the killer whales fled from the Risso's dolphins until the Risso's dolphins caught up with the killer whales and surrounded them. The Risso's dolphins appeared to encircle the killer whales, halting them in their path. The killer whales grouped tightly in place, staying on the surface. After approximately seven minutes, the killer whales broke free. The Risso's dolphins chased them a second time, quickly caught up to them, and again prevented their movement for another five minutes until the killer whales eluded them and porpoised away; the Risso's dolphins did not pursue. This resembled "classic" mobbing behaviors as described in birds (Curio, 1978) and primates (Cheney & Seyfarth, 1987) where they approach, harass, and sometimes attack potential predators. On another occasion, we documented Risso's dolphins harassing two offshore killer whales (shark specialists not known to prey on marine mammals) in southern California (Dahlheim et al., 2008).

Long-finned pilot whales were reported as possibly mobbing killer whales off Norway and the Strait of Gibraltar (Stenersen & Similä, 2004; De Stephanis et al., 2015) and Curé et al. (2012) found pilot whales were acoustically attracted to killer whales in Norway. Pitman et al. (2017) reported on mobbing-like behavior seen in humpback whales in various locations worldwide where approaching humpback whales often harassed killer whales that were either attacking or feeding on various prey. Humpback whale mobbing-like behavior sometimes allowed the prey of killer whales to escape (discussed later in Sect. 8.5.6). Dolphins are also known to mob sharks (Essapian, 1953; Wood et al., 1970; Saayman & Tayler, 1979; Connor, 2000). Adult African elephants (*Loxodonta africana*) have mobbed lions (*Panthera leo*), which can prey on elephant calves (Joubert, 2006; McComb et al., 2011) and cheetahs (*Acinonyx jubatus*) abandon hunts after being detected and followed by Thomson's gazelles (*Gazella thomsoni*). Mobbing across species is widespread, it appears to occur primarily to alert predators that they have been detected, to alert others of the predators' presence, and to summon others to assist in the mobbing and driving off the predator (Carlson & Griesser, 2022).

The smaller dolphins regularly hunted by killer whales show a strong flight reaction in response to killer whale presence in the vicinity, or during a potential attack. Dolphins likely communicate the "threat" to the rest of the group, as all dolphins react at once and porpoise high out of the water, swimming rapidly away. Sometimes a school of several hundred dolphins split up, with each group heading in different directions. Killer whales usually do not chase these large groups of fleeing dolphins; instead, they try to catch them by surprise and isolate one individual. Deeper water pelagic species of dolphins that occur in Monterey Bay are often found in mixed-species groups of several hundred to several thousand individuals. The most frequent mixed-species groups include Risso's dolphins, Pacific white-sided dolphins, and northern right whale dolphins (*Lissodelphis borealis*). These mixed groups are large and participating in such associations could be an anti-predator strategy for Pacific white-sided dolphins that are susceptible to killer whale attacks in Monterey Bay. Besides deterring predation, these large mixed-species groups could provide additional foraging opportunities (Stensland et al., 2003; Kiszka et al., 2011;

Cords & Würsig, 2014; Bacon et al., 2017; Kanaji & Miyashita, 2021; Syme et al., 2021).

8.5.4 Gray Whale Hunting Strategy

Gray whale cow/calf pairs are the last gray whales to migrate north toward their feeding grounds in the Bering and Chukchi Seas, Alaska after spending several months in the warm water nursery lagoons of Baja California, Mexico (Swartz et al., 2006; Urbán et al., 2021). Some southbound calves are born near California, but most are born near Mexico. Gray whales take a coastal route when migrating and often travel in 100 m water depths (Braham, 1984). Gray whale cow/calf pairs typically travel closer to shore than the rest of the population and are frequently sighted along the edge of kelp beds or the surf line in shallow waters. The habitual behavior of traveling in shallow waters and along the coast is likely an anti-predator strategy against killer whales. The shallow waters allow gray whale mothers to better defend their calves with lateral tail throws, reduce the ability of killer whales to drown them, and expose killer whales to the risk of injury from impacting the substrate.

As gray whales reach Monterey Bay on their northern journey, most cross the Monterey submarine canyon, forcing the gray whales to cross deep water at some point. Gray whales without calves usually take a direct northwest path after they reach the Carmel Bay area (5 km south of Monterey Bay) toward Pt. Año Nuevo, which is 71 km north of Carmel Bay and juts out from shore. This takes them across the outer Monterey submarine canyon waters over 1000 m deep waters (Fig. 8.8). Once gray whales cross Monterey Bay, they are back in the shallow shelf waters again, which extend from 8 to 40 km from shore for a major part of their journey to Alaska. However, gray whale cow/calf pairs generally hug the coastline within 1 km from shore for most of their journey.

Hunting, killer whales have a distinct advantage when gray whale cow/calf pairs traverse the deep waters of the canyon system with fewer escape options. Killer whales are frequently found patrolling the edge of the canyon, back and forth over many hours. They can do this along either side of the Bay, but predominantly seem to prefer the latitude 36°47–48 N, along the north edge, (100–200 m water depths) often traveling east, near shore, and then west toward Soquel Canyon (see Figs. 8.1 and 8.8)—the northern offshoot from the main canyon. They often travel up this canyon, then head back down the north edge of the main canyon toward the east again.

Gray whales are often vocally silent over deep water possibly to avoid detection by killer whales and then may resume vocalizing upon reaching the 100 m depth contour. Their calls include low-frequency moans, knocks, and bong sounds. Attacks occur in areas where gray whales have been known to increase their sound production as they approach the shelf edge, after crossing deep water (Crane & Lashkari, 1996). Killer whales are presumably finding gray whale calves by

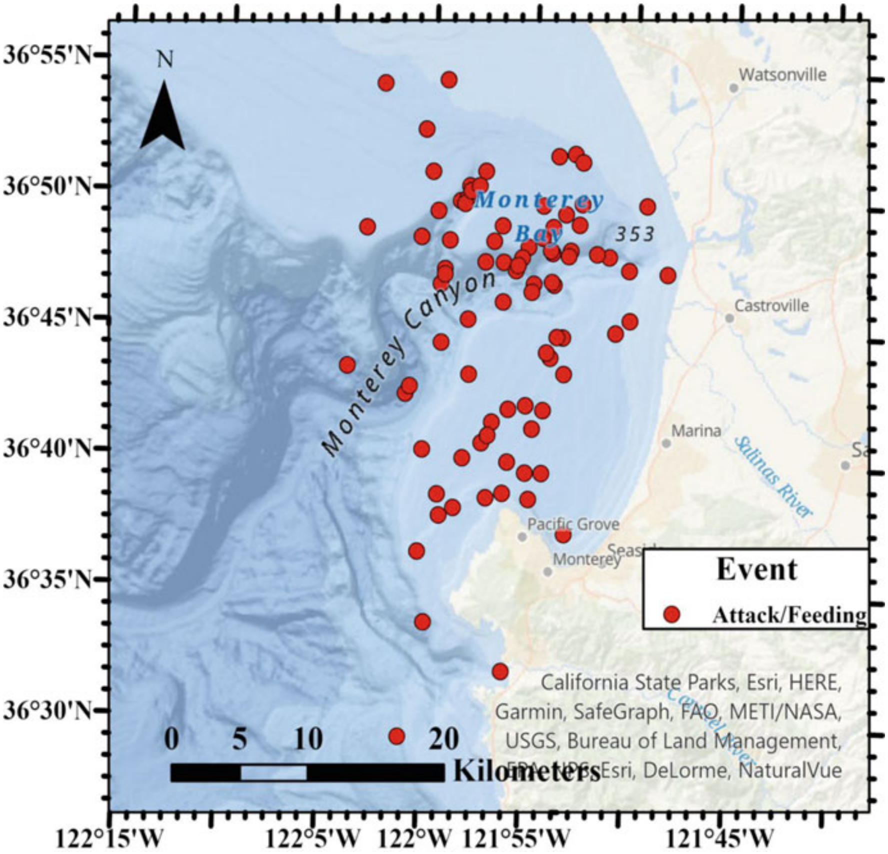

Fig. 8.14 Gray whale attacks and feeding events recorded from 1991 through 2021, showing the focus along the canyon edge and over the shelf just after cow/calf pairs leave the protection of shore to travel north through Monterey Bay (map credit: Mason Donny)

passive listening (Deecke et al., 2005). After the gray whale mothers and their calves leave the southern end of Monterey Bay and start their venture across the deep canyon waters for the next 24 km, they switch behaviors to become stealthy, quiet, and barely surface to blow—"snorkel behavior" (Ford & Reeves, 2008). They have little to no visible blow and usually show only blowholes and little body at the surface, in contrast to whales without calves, which typically show more body and stronger blows when surfacing.

Besides a preference for the canyon edge to hunt gray whale cow/calf pairs, killer whales also target shelf waters before the beginning of the canyon system (Fig. 8.14). In recent years (2019–2022), killer whales seem to have improved their hunting efficiency by capturing gray whale calves as the cow/calf pairs begin crossing Monterey Bay. The longest attack recorded lasted for six hours (in 1998) and included most of the six key matriarchs in the Monterey Bay population; since then, attacks last closer to 1–2 hours. We interviewed fishermen who fished on a regular basis during spring months from the 1950s to 1980s, who said they rarely saw killer whales attack gray whales; we noted <10 gray whale attack records in Monterey Bay during that same period. Gray whale calf attacks are now annual seasonal events. There was an overall increase in gray whale abundance from 2008-2016 (e.g., 27,000 in 2016, Stewart & Weller, 2021). Their populations were decimated during commercial whaling (~1500–1900 around the 1900s, Swartz et al., 2006). The Eastern Pacific gray whale population was reclassified as recovered (exceeding 21,000) in the early 1990s, and was taken off the US Endangered Species List in 1994. Killer whales most likely continued to hunt gray whale calves, but much less frequently during low calf production years. With time, killer whales appear to have improved hunting efficiency; for example, the shortest successful attack on a gray whale calf took only 15 minutes in 2017 (Tables 8.4 and 8.5, Event #3).

We have recorded 116 predation events on gray whale calves since 1992. Of the total predation events, 31 attacks and 80 cases of feeding events lasting one to four days were witnessed by the author(s), partially or fully. Many times, we encounter killer whales feeding on a carcass that they killed during the night or that we missed during the day. The number of annual gray whale calf attacks varied greatly, from zero to 12 (see Table 8.3, for a summary of gray whale calf predations and success rates), and relatively few (0–20) gray whale cow/calf pairs pass through Monterey Bay each day (Perryman et al. 2002). Additional attacks likely occur which cannot be confirmed, but there is a large sighting network, and most boaters know to report gray whale attacks by marine radio. We have found that when killer whales are in Monterey Bay during the gray whale calf migration, there are other killer whale groups spread over several kilometers in the vicinity. If one killer whale group finds a gray whale calf and initiates an attack, other killer whales in the area may rapidly approach the attack zone from various directions drawn perhaps by killer whale vocalizations during the attack. Distributed prey search patterns and cooperative hunting likely increase their chances to find elusive gray whale cow/calf pairs and if successful allow different killer whale groups to share and consume the carcass.

Once killer whales have located a gray whale cow/calf pair, they may pursue the mother and calf for a short distance as the grays try to swim (average speed ~11 knots), toward the shore. Invariably, killer whales catch up to the pair and begin to block their forward movement. The mother and her calf stay close together, with the calf constantly pushing tightly against her. The gray whale mother tries to use her pectoral flippers to block the killer whales and her flukes to lash out at them. Both mother and calf spend much of their time rolling. The mother tries to lift her calf up on her back or belly, often holding her breath longer so that much of her calf is out of the water, allowing the calf to breathe longer, rest, and be shielded from killer whale attacks. Eventually, the mother must raise her head to breathe, and killer whales often take advantage of the situation to strengthen their attacks (Fig. 8.15).

A singular objective of hunting killer whales is to separate the mother and her calf. Afterward, all their efforts focus on the calf. From the start, the killer whales take any opportunity to ram the calf from below or smash forcefully into its head while they try to bite the tongue. This assault often lasts over an hour, while the gray whale mother fights to stay with her calf. Once she is finally separated from her calf, the calf has little chance of survival. There is much white water throughout the attack as the killer whales repeatedly ram the calf, hitting its soft, vulnerable underside and head (often knocking its baleen out) with their heads, bodies, and sometimes flukes. They can ram the calf so hard that it may get shoved halfway out of the water (Tables 8.4, 8.5, and 8.6). The killer whales continue to ram the calf and sometimes breach and fall on the calf, bite its flippers to pull and hold it underwater, continually try to grab and bite its tongue (causing much blood loss), and push against or lie on top of the calf to eventually drown it (Fig. 8.15).

Group size during these attacks varies greatly. The 11 selected attacks displayed in Tables 8.4, 8.5, and 8.6 ranged from 4 to 45 whales, but typically only 3–7 killer whales actively attack the gray whale calf. Over the years, we have noticed that certain individual killer whales tend to dominate in certain specific hunting strategies (or attack roles). In many cases, much of the attack is accomplished (and perhaps coordinated) by reproductive females such as CA140 (Emma), her daughter, CA140B (Louise), CA51 (Star—see Fig. 8.2 for her matriline), and her daughter, CA51A (Aurora), and four other reproductive females and now their daughters.

For the three selected attack events displayed in Table 8.6, these matriarchs performed multiple active roles: trying to separate the gray whale pair, repeatedly ramming the gray whales (especially older and more experienced females CA140 and CA51), and repeatedly trying to drown the calf. During Event #7 (see Table 8.4 and 8.5, 2019), a five-year-old juvenile CA51A3 (Dipper) moved on top of the calf four times by mimicking the hunting strategy used at least 12 times during that attack by mother CA51A. CA140B bit the calf's flipper during two attacks. Males present in these three selected attacks played considerably smaller roles, with the notable exception of CA140C (Ben, Emma's son): he took advantage of his large size to repeatedly try to separate, ram, and drown calves. Even as a juvenile, CA140C displayed heightened interest in taking active roles during gray whale hunts—possibly influenced by his proficient mother.

During this onslaught, the mother gray whale and her calf attempt to break the gridlock. At times killer whales take short breaks apparently to rest, giving the mother and calf a chance to head to shallow waters. However, given that most attacks occur near the deep-water canyon edge, the gray whales have a long distance to transit to reach the safety of shallow waters. We have seen gray whales succeed in reaching the shallows (Tables 8.3, 8.4, and 8.5—Event #4), usually if the attack starts in shallow water beyond the canyon edge, or if the killer whale group is small (with inexperienced younger whales). In 2005, CA51 and her three offspring (an adult daughter and two young sons) attempted to kill a gray whale calf, but the gray whale cow/calf pair swam several kilometers to shore and escaped, this small group included whales too young and inexperienced to stop them. In 2019, this same matriline (now with a grown son, a nearly grown son, and a subadult daughter) was able to kill a gray calf by themselves in two hours (Tables 8.4 and 8.5, Event #8), during all previously documented kills, they had help from other families and adult females.

Killer whale attacks can last from 15 minutes to six hours, although they typically last for 1–2 hours (see Table 8.3 for mean and range). After the calf is dead, the

Table 8.3 Summary of predation behavior on gray whale calves, including success rate

Species	Gray Whale Calf
Total predation events	116
Killer whale mean group size & S.D. range during the attack	4.6, 2–7
Killer whale group size range present in attack area	2–49
Duration of kill (mean hours) and range (hours)	2, 0.25–6
Duration of feeding (hours)	12–75
# Consumed	102
# Escapes	14
% Success rate	87.9%

mother gray whale swims away and continues northward. On rare occasions, after a long defensive struggle, a gray whale mother leaves her calf to fend for itself, and the calf may have sustained grievous injuries (broken jaw, lost baleen, mangled tongue), with no chance of survival. This occurred during both attacks seen in 2019 (Tables 8.4 and 8.5—Events #7 and #8). One calf had to fend for itself for nearly 1.5 hours, and the other for 30 minutes. In both cases, killer whales were consuming the calf's tongue while it was still alive.

Some male killer whales, such as CA140C (Ben), regularly participate in gray whale attacks. Males are typically more involved when only one small matriline is present (Fig. 8.16). The juveniles and calves whose mothers are most involved remain close to the mothers during attacks and such close associations may enhance learning opportunities. We also witnessed two different male pairs in two attacks who worked together to take down a calf. Several males in our population travel alone or as pairs rather than in a matriline, either because the mother died, or they dispersed from their natal matrilines.

8.5.5 Gray Whale Feeding Event: Prey Consumption

Regardless of attack initiators in a gray whale attack, all killer whales share in the carcass afterward, usually taking turns to feed—which is different from top terrestrial predators (Tallian et al., 2023; Smith & Holekamp, 2023; Jordan et al., 2023; Chakrabarti et al., 2023). After the gray whale calf is killed, the carcass remains below the surface. Once the carcass comes to the surface after the killer whales let it go at depth, it floats until the killer whales grab it and pull it down again, where it possibly sinks to the bottom with pressure. Water depth is often <200 m–400 m (Table 8.4). Killer whales often remain in a localized area feeding for hours and up to a few days, so presumably, the carcass falls to the bottom once it passes a neutral buoyant point. This differs from observations that (Barrett-Leonard et al., 2011) made in False Pass, Alaska, another area where killer whales hunt gray whale calves. They report that the carcass sinks to the bottom, and killer whales return for several days after feeding on it, but they do not see the carcass floating on the surface as we do. From our observations, it takes about one hour after the kill before a distinct slick

Table 8.4 Summary of 11 selected (out of 31) gray whale predation events between 1992 and 2021, focusing on killer whale hunting strategies (roles), water depth, number of pods (matrilines), and attack duration

	Date	Hunting strategy (roles)	Water Depth start (m)	# of Pods	Attack Duration (Hours)	Comments
Event #1	April 7, 2009	Separate, ram, drown	380	3	0.33	Attack already underway
Event #2	May 3, 2012	Separate, bite, tail throw, ram, drown	1200	3	0.2	Attack already underway
Event #3	April 26, 2017	Slow follow from deep canyon to 100m canyon edge, then rapid attack	92	2	0.25	Entire attack seen, shortest recorded
Event #4	April 30, 2017	Separate, ram, push, drown	67	3	1.42	Attack already underway, *allowed grays to escape!*
Event #5	April 17, 2018	Separate, bite, ram, push, drown	338	1	1.42	Entire attack seen
Event #6	April 18, 2018	Push, ram, drown, paired attackers	590	3	0.27	Attack already underway
Event #7	April 27, 2019	Separate, ram, drown	365	1	4.25	Entire attack seen, *mom left after 2.83 hours, calf on its own for 1.42 hours
Event #8	May 1, 2019	Separate, bite, ram, drown	540	1	2.25	Mom left before attack was over, *mom left after 1.75 hours, calf on its own for 0.5 hours
Event #9	April 10, 2020	Ram, breach on grays	90	1	0.43	Attack already underway.
Event #10	April 13, 2020	Separate, ram, drown	120	11	2.08	Entire attack seen
Event #11	April 23, 2021	Separate, bite, hit, ram, drown	492	3	1.22	1.63 hrs attack (with other observers)

forms from the release of oil caused by killer whales feeding on the carcass. After hours of feeding, this slick can expand on the water's surface for over 1 km.

Killer whales begin feeding on the carcass through the gray whale calf's mouth, as that allows easy access to the huge soft tongue favored by the whales. After finishing the tongue, they begin to strip the blubber off the underside of the carcass (Fig. 8.17). Pieces of blubber often float on the surface, varying in size from strips about 30 cm to over 2.5 m long. After feeding for many hours, the carcass usually remains in one piece when it occasionally rises (or is brought) to the surface.

Table 8.5 Summary of 11 selected gray whale predation events between 1992 and 2021, including killer whale hunting strategies (roles), group sizes, number of active attackers, and sex and age-class breakdowns for each group

	Date	Hunting strategy (roles)	Group Size	# active attackers	# adult males	# adult females	# subadults	# juveniles	# calves
Event #1	April 7, 2009	Separate, ram, drown	10	7	1	4	1	3	1
Event #2	May 3, 2012	Separate, bite, tail throw, ram, drown	10	7	0	4	3	2	1
Event #3	April 26, 2017	Slow follow from deep canyon to 100m canyon edge, then rapid attack	9	NA (no IDs)	2	3	1	1	2
Event #4	April 30, 2017	Separate, ram, push, drown	13	7	2	5	2	2	2
Event #5	April 17, 2018	Separate, bite, push, ram drown	7	4	1	2	1	2	1
Event #6	April 18, 2018	Push, ram, drown, paired attackers	13	5	2	4	2	3	2
Event #7	April 27, 2019	Separate, ram, drown	5	4	1	2	0	2	0
Event #8	May 1, 2019	Separate, bite, ram, drown	4	4	1	1	1	1	0
Event #9	April 10, 2020	Ram, breach on grays	4	3	1	1	1	1	0
Event #10	April 13, 2020	Separate, ram, drown	45	7	4	16	8	10	7
Event #11	April 23, 2021	Separate, bite, hit, ram, drown	15	5	2	3	4	3	3

Fig. 8.15 Sequence of photos describing a gray whale attack. (**a**) Killer whales begin to chase after a gray whale cow/calf pair, (**b**) Several adult female killer whales reach the cow/calf pair and surround them to begin attack, (**c**) Killer whale rams the gray whale calf, which happens often throughout attacks, (**d**) Killer whale rams calf so hard from below that it is propelled out of water, and the baleen is knocked out, (**e**) Gray whale calf tries to get on top of mother as a killer whale (red line points to killer whale) tries to separate cow and calf by getting in between, (**f**) Killer whale trying to push calf underwater by getting on top of it, (**g**) Killer whale "nose to nose" with the calf, (**h**) Killer whale bites calf's flipper to pull it down (note teeth), (**i**) Final drowning of the gray whale calf, (**j**) Three matriarchs surround the calf near the end, to keep its mother away. *Photo credits:* ***a***. ***c***. ***d***. *&* ***h***. *Tory Kallman,* ***b***. *&* ***g***. *Blueplanetarchive/Peggy Stap,* ***e***. *&* ***f***. *Monterey Bay Whale Watch/ Mike Kauffmann,* ***i***. *&* ***j***. *Nancy Black*

Table 8.6 Summary of hunting strategies (roles) of individual identified killer whales by sex and age class (*F* Adult Female, *M* Adult Male, *J* juvenile), during three selected gray whale predation events

	EVENT #5				EVENT #10			EVENT #11			
DATE	April 17, 2018				April 13, 2020			April 23, 2021			
# killer whales	7				45			15			
Hunting strategy (roles)	*Separate*	*Bite*	*Ram/ push/ breach*	*Drown*	*Separate*	*Ram*	*Drown*	*Separate*	*Bite*	*Ram/hit*	*Drown*
CA140-F			4x/27%	9x/15%	1x/50%	9x/47%	2x/50%				
CA140B-F	1x/14%	1x/100%	3x/20%	24x/41%					1x/100%	3x/14%	2x/25%
CA140B1-J						2x/11%					
CA140C-M	6x/86%		8x/53%	26x/44%							
CA140D-J						1x/5%					
CA58-F					1x/50%	3x/16%	1x/25%				
CA58B-M						3x/16%					
CA51A-F								1x/25%		3x/14%	2x/25%
CA51A2-F										2x/10%	
CA50B-M								2x/50%			
CA51-F							1x/25%	1x/25%		13x/62%	4x/50%
CA27C-M						1x/6%					

Values indicate the number of times an individual killer whale displayed a specific attack strategy, and the percentage of that role in the overall attack

Fig. 8.16 Male, CA51C (Bumper), ramming the calf, with his small family of four assisting. *Photo credit: Monterey Bay Whale Watch/Mike Kauffmann*

Usually, the tongue is gone, the lower jaw is broken or missing, and large pieces of blubber are missing from the throat. Sometimes only the tongue and portions of blubber around the jaw, throat, and ventral region are gone (Fig. 8.17c, gray whale calf washed up on a beach in Monterey Bay the day after a nearby killer whale attack). Alternatively, they consume most of the carcass with nothing left besides the skeleton, intestines, lungs, and some internal organs; unlike blubber, these body parts are not high in fat content and are not consumed. When not feeding, killer whales usually mill within 0.5 km of the carcass and often socialize with other matrilines during that time.

Killer whales usually feed on the carcass from 12 to 48 hours, with many breaks in between feeding bouts, the longest feeding event we witnessed (Tables 8.3 and 8.4b—Event #11) lasted for 75 hours! Often, the initial groups that killed the calf spend the day feeding. The following day there may be a different group feeding, and the initial group may be gone. What is left of the carcass sinks or remains at the bottom to be fed upon by many other animals, commonly referred to as a whale fall. Dead whales create a biodiversity hotspot: over 400 species have been found associated with whale falls (Sumida et al. 2016).

Although several family groups of killer whales are present for the attack and subsequent feeding, not all are active in the attack. Many whales may stay in the area or closely inspect the action. The whales most involved are the adult reproductively active females, usually with 1–3 offspring present and sometimes grand-offspring. A

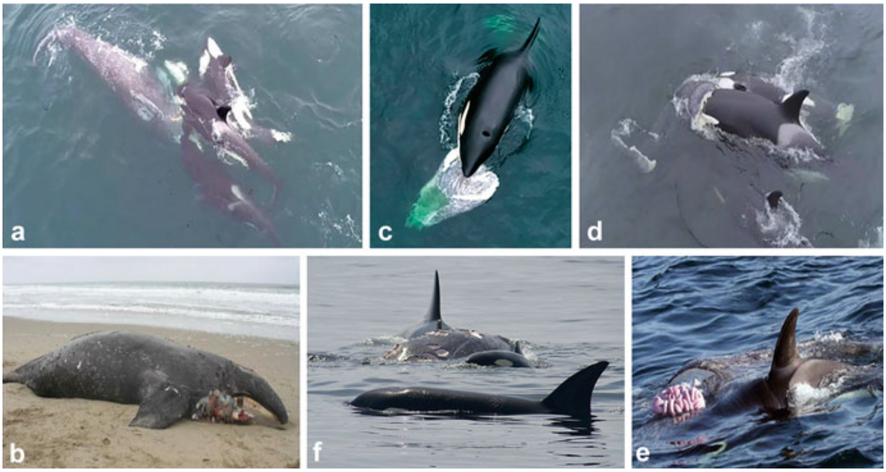

Fig. 8.17 Killer whales feeding on a gray whale carcass. (**a**) Group of five killer whales feeding on carcass, (**b**) Calf washed up on the beach after the attack, tongue and lower jaw blubber missing, (**c**) Killer whale carries large piece of blubber, (**d**) Killer whales dig into carcass with their bodies, and (**e**) Killer whale calf feeding with its mother on the carcass (**f**) Killer whales feeding on a gray whale carcass with many shark bites on it Photo credit: *(**a**) Monterey Bay Whale Watch/Mike Kauffmann, (**b**) Alisa Schulman-Janiger, (**c**) Monterey Bay Whale Watch/Jason Berring, (**d**) Monterey Bay Whale Watch/Mike Kauffmann, and (**e**) Nancy Black* (**f**) *Colleen Talty*

few females from different matrilines may work together and include relatives or close associates, which facilitates their successful attacks. In Monterey Bay, six matrilines are involved in most gray whale calf predation events. Usually, these matrilines occur in varying combinations of 1–6 present, with their second and third generation offspring (Fig. 8.18); four of these six key females are still alive. During attacks, these six matrilines may regularly cooperate with other less commonly observed matrilines. Many gray whale attacks include 11–15 killer whales (Fig. 8.19a) and three matrilines (Fig. 8.19b), this has varied from 2–49 whales, and up to 10 matrilines.

Female killer whale CA40 (Xena) is over 50 years old and is likely one of the eight oldest females in our Bigg's killer whale population. As a post-reproductive female, CA40 has been involved in numerous hunts involving young killer whales and perhaps has an important role in transmitting hunting techniques across multiple generations. The role of a grandmother in killer whale society has been reported to increase the success of families in Resident killer whales (Nattrass et al., 2019)—it is anticipated that post-reproductive and older females in mammal hunting killer whale groups have a similar key role in influencing hunting styles, preference, and success in Monterey Bay and elsewhere.

Our observations are similar to those in other gray whale predation reports (Baldridge, 1972; Goley & Straley, 1994; Melnikov & Zagrebin, 2005; Barrett-Lennard et al., 2011). There are a few differences between our study and observations reported by Barrett-Lennard et al. (2011) in Unimak Pass in Alaska. Group sizes during attacks were higher in Monterey, averaging 15 whales, compared to

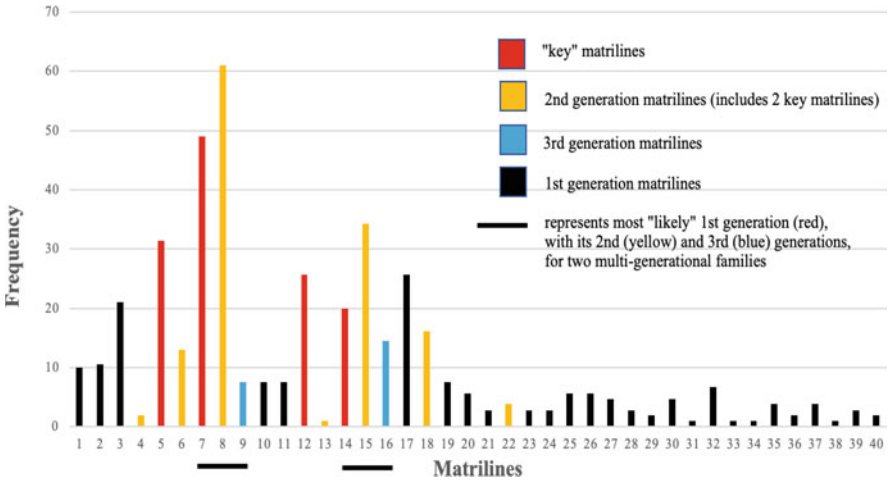

Fig. 8.18 Percent of attacks per matriline, 1992–2022. This graph shows 40 (of 53) matrilines that have been involved in gray whale predation events over the study period (including 9 now deceased). Note the key matrilines (likely related/close associates) (red, and orange with a line below) who have been involved in most of the gray whale attacks, followed by their second generation (orange). Note black line under 7, 8, 9 (CA40, CA140, CA140B), and 14, 15, 16 (CA50- dead), CA51, CA51A) shows likely 3 generations of related matrilines. Orange bar 8 (CA140) and orange bar 15 (CA51) are part of the six key matrilines. Black bars are other matrilines, some with second generations that have split off

10.3 whales in predations in Unimak Pass. In Monterey, we sometimes see large groups of 20–30 whales that aggregate around predation events, much larger groups than to the north. The number of whales that participated in the attacks was comparable in both areas, with Monterey averaging 4.6 and Unimak Pass averaging 3–4 whales. However, Barrett-Lennard et al. (2011) included four years of data, whereas our study includes 30 years.

In Alaska, killer whales may abandon hunts if the gray whale mother vigorously defends her calf—whereas, in Monterey Bay, killer whales are persistent despite any defensive maneuvers by the gray whale mother. The attacks on gray whale cow/calf pairs in Alaska usually occurred in shallow waters (15–75 m) and nearshore. In Monterey Bay, the mean depth ranges for the attacks were 100 m. In Alaska, killer whales targeted calves as well as some yearlings, whereas in Monterey Bay, attacks involved gray whale calves born December–February of the same season (young of the year) and no juveniles were targeted. Unlike Monterey Bay, in Alaska killer whales use a herding strategy to push calves into shallow waters. Moreover, the shallow water depths did not appear to deter the killer whales from continuing their attack. There is a difference in hunting success between the two areas, with 87.9% for Monterey Bay killer whales and a success rate of <30% in Alaska waters. But sample size effects cannot be ruled out since in Alaska only eight events were analyzed. Also, habitat differences, killer whale experience, presence of older

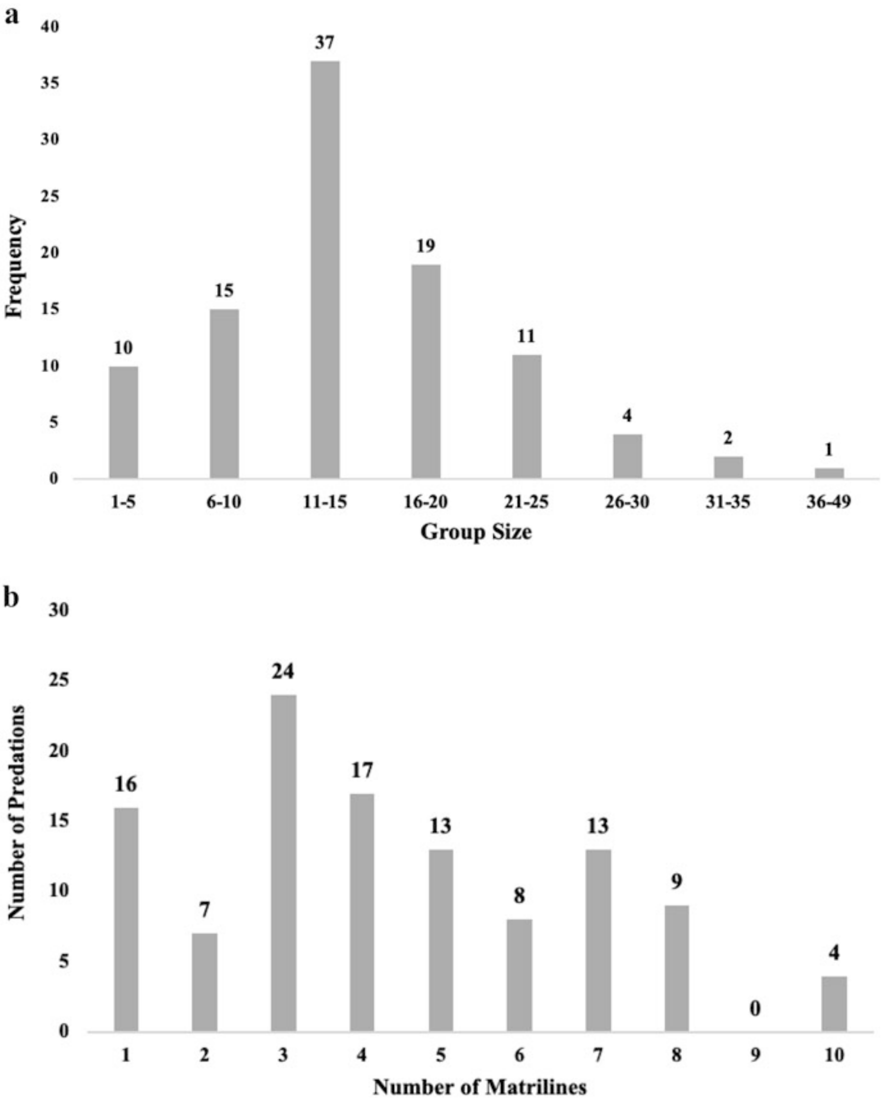

Fig. 8.19 (**a**) Frequency of group size categories for killer whales during gray whale predation events, 1998–2021. (**b**) The number of matrilines involved in gray whale predation events, 1998–2021

females, and attack modes could alter hunting success, and this needs further study. In terms of commonalities, killer whales interspersed periods of feeding with rest and social behavior and killer whales as far away as at least 10 km can arrive at a slick (kill) site.

Killer whales may selectively feed on seals, sea lions, dolphins, and porpoises when gray whale calf abundance is low. The number of gray whale calves born each

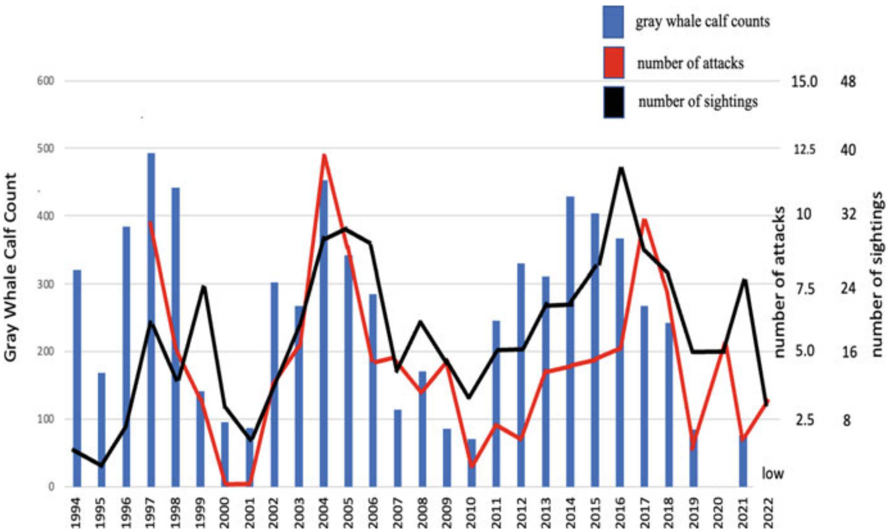

Fig. 8.20 The northbound gray whale actual calf count/year (not estimated number born), from Piedras Blancas (from Marine Mammal and Turtle Division, Southwest Fisheries Science Center/ Dave Weller, personal communication) overlaid with the number of gray whale attacks/year (red line) in our study, and the number of killer whale sightings (black line) during the northbound gray whale migration (April and May) 1994 to 2022

year can greatly vary (Fig. 8.20, actual calf count) with low calf production years in 2009 and 2010 and higher numbers in 2014, for example (Stewart & Weller, 2021). An increase in killer whale attacks and sightings appears to coincide with high calf production years (Fig. 8.20). In 2004, when calf numbers were high (estimated 1635), several families of killer whales remained in Monterey Bay nearly daily for five weeks. They successfully killed 12 gray whale calves and three calves escaped. In contrast, during years when killer whale presence varied (1999–2022, except 2004), we estimate an average of 3.7 ± 2.3 calves killed in spring. In most years, killer whale presence in Monterey Bay fluctuates with animals staying for a day or more and then moving out of the area and returning for another few days.

In 2017, killer whales killed six calves, and three calves escaped or were not pursued. In addition to the relatively high number of kills, the CA140s (Emma's family) were involved in all the attacks and escapes except for one kill. The matriarch, CA140 (Emma) was most involved in the attacks along with her adult daughter, CA140B, and her presumed mother CA40, who usually travels with Emma's presumed two male siblings but stayed with Emma throughout the season. Occasionally, her family was joined by several other killer whale families that participated in attacks or shared prey. CA140 and her familial associates are among the most successful and proficient predator units, having killed one calf in 15 minutes. This same group of nine whales also killed and fed on six calves in 12 days, often with one or more other families with group sizes ranging from just

Fig. 8.21 Killer whales socializing, playing, and rubbing against each other. Photo credit: (**a**) Monterey Bay Whale Watch/Mike Kauffmann, (**b**) Colleen Talty, (**c**) Jodi Frediani

those nine on two occasions to 13 whales on four days, and 17, 25, and 34 whales present on other kills. Three generations of whales working together could have contributed to successful outcomes.

Soon after killer whales finish feeding and leave the carcass, they often rest for hours, while others may continue traveling and leave the area. During this period, they often become socially active, interacting with other matrilines that gather for these feeding events—sometimes for days (Fig. 8.21). These predation events likely offer mating opportunities among whales that are not closely related and may occupy more distant home ranges yet visit Monterey Bay primarily to hunt gray whale calves in the spring. Calves from different families often play together and exhibit heightened social activity. The juveniles and older whales often rub and roll over each other (Fig. 8.21b). Our drone observations have captured whales playfully pushing down others by getting on top of them near the surface (Fig. 8.21a and YouTube video[2]). Adult males often interact with juvenile males and occasionally adult females, and may touch each other during penis displays. Some whales may frequently spyhop and breach (Fig. 8.21c); these "celebratory" behaviors are often displayed by killer whales who have gathered to feed on gray whales during spring months.

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[2] https://www.youtube.com/watch?v=80rH7ytG6Vc

8.5.6 Humpback Whale Interference

Since 2005, we have witnessed humpback whales interfering many times during predation events, attempting to prevent killer whales from attacking their prey or feeding on the carcass (Frediani et al., 2020). Humpbacks have been documented to interfere in killer whale predation events on other species or conspecifics since the 1980s; one of the first was in 1989 (D'Vincent et al., 1989), when a humpback whale interfered when killer whales were hunting another humpback whale's calf. These interactions may be partly due to humpback whales exhibiting anti-predator behavior in response to killer whale attacks, even on different species (Pitman et al., 2017). When humpbacks interfere with a gray whale calf attack, they often trumpet blow (Watkins, 1967), tail lob, raise their pectoral flippers, roll, spyhop, and slash their flukes near the killer whales. Humpbacks also rapidly dive, circle the attack area, and sometimes charge at the killer whales. Sometimes the humpbacks place themselves between killer whales and the gray whale calf, attempting to block the attackers. Occasionally, killer whales try to force humpbacks to leave the area by grabbing their flukes or flippers. On 3 May 2012, we documented the longest known interaction of humpback whales interfering with a gray whale attack/feeding event (off the edge of Monterey Canyon, near Point Pinos), which also involved the highest number of humpbacks: over 7 hours long, and 16 humpbacks (Pitman et al., 2017, Tables 8.4 and 8.5—Event #2). This was one of 115 worldwide encounters of humpbacks interacting with killer whales reviewed in that paper, 48 of these 115 interactions (42%) occurred in Monterey Bay. Several of those humpbacks were observed feeding hours earlier, as far away as 7.6 km. The gray whale attack was underway when first seen, 10 Bigg's killer whales were present, with seven actively involved (Table 8.5). Two humpbacks interfered during the attack, one dove where the gray whale mother was diving, right after her calf disappeared. The humpbacks mostly approached the killer whales (rather than vice versa) and closely followed/chased/charged them: trumpet blowing, flipper waving, and spyhopping. Tail-slashing seemed primarily directed toward the actively feeding juvenile female killer whale CA216B (Jagged)—as if trying to prevent her from feeding—or toward the larger male CA45B. The humpbacks did just one feeding lunge over the seven hours, focusing instead on the killer whales. The seven humpbacks usually stayed in a tight subgroup, others moved in and out during the observation period and remained agitated when we left due to failing light. Both females and males participated, from juveniles to adults; several displayed killer whale tooth rakes on their flukes from previous killer whale encounters. The cost and benefits of humpback whale interference/mobbing behaviors are unclear, and remain an area for future research (see Pitman et al., 2017).

8.6 Threats to the Population and Contaminant Levels in Bigg's Killer Whales

8.6.1 Climate Change

There have been some short-term changes that could be used to understand how temporary warming of seas can affect killer whale mammalian prey off California. One example is the marine heat wave known as "The Blob," which caused the warming of coastal waters from 2013 through 2016; those temperatures have since returned to previous levels (Peterson et al., 2015; Leising et al., 2015; Cavole et al., 2016). Warming oceans can have both positive and negative effects, depending on the species involved. For example, between 2013 and 2016 there were extremely high concentrations of anchovies inside Monterey Bay (Nancy Black, personal observation). Anchovies were most concentrated over the canyon and the shelf. We noted that these aggregated food patches attracted over 300 humpback whales and several thousand sea lions. In addition, over 1000 common dolphins were present at times during the year. These common dolphins are normally found in warmer waters to the south, but they occur in Monterey Bay during periods of increased sea temperature. In this case, the warmer water may have benefited these marine mammals—expanding their foraging range. Killer whales also benefited due to increased access to diverse and abundant prey, including sea lions and common dolphins.

Climate change in the Arctic could have deleterious effects on killer whale prey species, especially gray whales. For example, if gray whale feeding grounds in the Bering and Beaufort Seas warm significantly, there could be fewer benthic amphipods available for gray whales (Perryman et al., 2021; Stewart & Weller, 2021). Primary prey choice could then shift from benthic amphipods to pelagic krill. If pregnant female gray whales are unable to meet their energetic demands and leave the Arctic with a compromised body condition, their calves will not survive (Perryman et al., 2021). Gray Whale Unusual Mortality Events (UMEs) are another example of what a short-term change could represent, caused partially by habitat changes, prey shifts, and gray whale foraging area changes due to the temporary warming of seas (https://www.fisheries.noaa.gov/national/marine-life-distress/2019-2022-gray-whale-unusual-mortality-event-along-west-coast-and. Accessed June 2022).

The overall gray whale population is estimated to have declined from about 21,000 in 1997–1998 to 16,000 in 2000–2001, following the 1999–2000 Gray Whale UME. Strandings increased and calf production dropped to less than one-third that of previous years (Punt & Wade, 2010). The gray whale population rebounded to about 27,000 in winter 2015–2016, but dropped to about 20,500 in winter 2019–2020 (Stewart & Weller, 2021) it dropped even further to approximately 16,650 in the winter of 2021–2022 (Eguchi et al., 2022), resulting from the 2019–2023 Gray Whale UME. Gray whales in Baja California's Laguna San Ignacio and Bahía Magdalena experienced a fourth consecutive gray whale breeding season (2019–2022) characterized by extremely low numbers of calves, increased adult

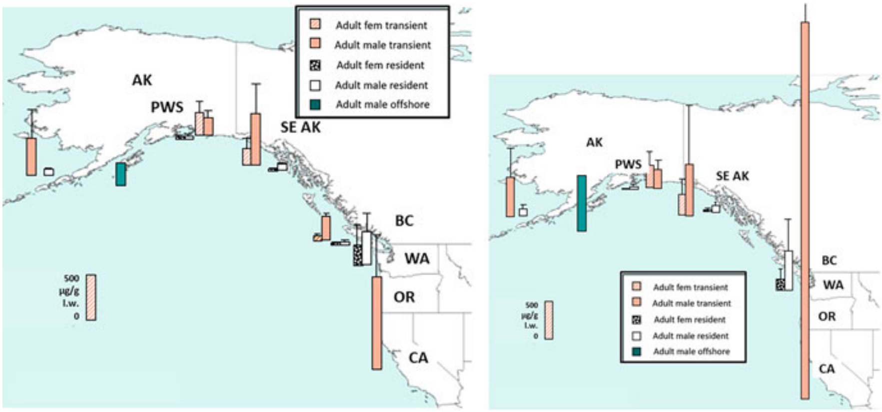

Fig. 8.22 Comparison of ∑PCB and ∑DDT concentrations in different populations of Eastern North Pacific killer whales. *BC data from Ross et al.* 2000. *PWS data courtesy of Ylitalo* et al. 2001, *Society of Marine Mammalogy Conference*

mortality, and an increase in the percent of "skinny, poor condition" adult whales (Laguna San Ignacio Ecosystem Science Program, 2022).

Despite lower annual gray whale calf estimates in 2019–2022, gray whale calf predation events continued. However, with decreased gray whale calf production (tied to decreased gray whale prey), killer whales could shift their foraging behavior, at least seasonally. Currently, other mammal prey are abundant, but there are already significant declines in most pinniped species in Alaska, which could expand down the coast. However, this is a complex system — and the full ecosystem consequences will not be immediately understood.

8.6.2 Contaminants

Killer whales near California have some of the highest levels of persistent organic pollutants (POPs), mostly dichlorodiphenyltrichloroethane (∑DDTs), polychlorinated biphenyls (∑PCBs), and flame retardants, compared to other killer whale populations in the Pacific—and are comparable to extreme levels recorded in other places in the world (Krahn et al., 2007, see Fig. 8.22). These relatively higher levels of PCBs and DDTs in California killer whales produced a distinctive "California signature" in biopsy analyses (Krahn et al., 2007). The high level of DDTs largely came from heavy agricultural use of DDT before its ban in the 1970s and from the Montrose Chemical Corporation (Torrance, CA)—once the world's largest producer of DDT, it operated from 1947–1982, and produced an estimated 800,000 tons of DDT (Kehoe & Jacobson, 2003). PCBs also come from runoff and dumping as it was used heavily in industry (Calambokidis & Barlow, 1991; Jarman et al., 1996; Krahn et al., 2007; Mongillo et al., 2016).

Desforges et al. (2018) predicted that greater than 50% of the world's killer whale populations will not survive in the long term. He categorizes as high risk the Northeast Pacific Bigg's killer whales (including the Monterey Bay, California population of Bigg's whales), due to the accumulation of high levels of PCBs via their mammalian prey. Severe and prolonged contaminant loads could negatively affect their reproductive, endocrine (adrenal and thyroid), and immune systems, resulting in lower calf survival and increased susceptibility to illnesses (Ross et al., 2000; Jepson et al., 2016; Desforges et al., 2018).

These chemicals do not biodegrade, they persist in the marine environment indefinitely and continue to cycle through the food chain (Kelly et al., 2007). We collected biopsy samples on several Bigg's killer whales between 1998 and 2004 in Monterey Bay and found that this population had extremely high contaminants in their blubber (Krahn et al., 2007). PCBs are fat-soluble: adult females transfer these chemicals from their blubber stores into the fetus and pass them at high levels to their first calves (and to a lesser extent to second calves)—which often may not survive. Adult male killer whales constantly accumulate POPs all their life, because they are larger and need to consume more prey, and physiologically cannot remove these contaminants as they cannot shunt them to newborns. Thus, male killer whales may have higher levels of organo-pollutants and be more susceptible to negative reproductive effects (Ylitalo et al., 2001). Killer whales have a 40% mortality rate for calves (Olesiuk et al., 1990). Multiple female killer whales in our study have lost their first calves. The Monterey Bay population has also lost several young adult males since our first catalog was published in 1997. We only have eight males >40 years old, compared to 24 females >40 years old, though male killer whales have a lower projected life span compared to females (Nielson et al., 2021). For Bigg's killer whales, the average estimated lifespan for females is 43 years old, and for males is 29 years old, the maximum (90%) lifespan for females is 59 years old, and for males is 44 years old (Nielson et al., 2021); some estimate that females can live to 65 plus years old (Olesiuk et al., 1990; Ford et al., 1996).

8.7 Future Research and Conclusion

The results presented here require additional analysis to fully characterize the foraging ecology of the mammal hunting killer whales in Monterey Bay. Some areas for further study include assessing social networks and group size dynamics in determining hunting success, understanding bioenergetic and trophic implications for killer whales consuming gray whale calves vs. other mammalian prey, evaluating predation risk effects in gray whales and other mammalian prey, and exploring the possibility of dominance structures during mating or feeding. Besides traditional vessel-based surveys, the use of drones may improve observations of predation and social behavior and help assess body condition (health and reproductive state, e.g., pregnancy) and nutritional state.

Monterey Bay is one of the best areas to study predation events in detail, due to the canyon providing proximity of deep water to the coastline. Besides enabling a thorough analysis of predation events from predator perspectives, our work reveals the value of longitudinal studies to better describe social learning and culture in killer whales as evidenced by their habitat and prey-specific predation strategies. Also, by following multigenerational matrilines, we can characterize the role of matriarchs, older and post-reproductive females, and males in killer whale societies, and their potential influence in dictating hunting effectiveness through knowledge transmission. Foundational data can be critical to assess the impacts of climate change (directly or indirectly) as well as other anthropogenic pressures on Bigg's whale populations in Monterey Bay and beyond. Ultimately, through sustained research, we may enhance our understanding of killer whale roles and top-down control in structuring marine ecosystems (Baum & Worm, 2009).

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Chapter 9
Sociality and its Relevance in Group Hunting Mammalian Predators

Mridula Srinivasan and Bernd Würsig

Abstract What sets apart social predators from other predators is their ability to hunt together and successfully attack prey larger than themselves, defend territories and offspring, and transmit information to successive generations. Group hunting may not be the norm and ecological pressures as well as the need to survive and reproduce require them to be nimble and switch to solitary hunts while maintaining diverse social groupings. Participation and allegiance to specific social groups may provide these social predators to evolve specialized group hunting techniques, protect young, and satisfy foraging and reproductive demands. Additionally, social membership may bestow group members with the capacity to adapt and be resilient to environmental disturbance through social learning. In this chapter, we summarize key findings and present commonalities and differences in the social dynamics and hunting strategies of spotted hyena, African & Asiatic lions, gray wolves, killer whales, and African wild dogs. For most terrestrial species, group hunting may at least in part be an artifact of gregariousness due to reproductive strategies—which are probably best established for African lions among our focal species, whereas for mammal-hunting killer whales, we speculate the opposite, wherein sociality is a by-product of a cooperative hunting lifestyle. Above all as scientists in the field, we must be persistent in conducting or contributing data toward comparative studies of social predators across marine and terrestrial environments.

Keywords Social predators · Resilience · Social evolution · Gregariousness · Reproductive strategies · Mammalian predators

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Artistic Rendering by Britney Danials. Original Photo Credit: Meredith Palmer, African lion (center); Stotra Chakrabarti, Asiatic Lion; Bobby-Jo Vial, African Wild Dog (Center right); Daniel Biachetta, Killer Whales (background); Illustrations—Britney Danials, Gray Wolf, Spotted Hyena, Killer Whale (foreground)

9.1 Introduction

Predators are rare for a reason—through intimidation and lethal impact, they can significantly alter prey population dynamics (Sih, 1987; Lima & Dill, 1990; Lima, 1998; Creel & Christianson, 2008). Therefore, predators usually represent a fraction of prey biomass, and their density (with exceptions) can often be closely aligned with prey size and biomass (Carbone & Gittleman, 2002). Predators can either be solitary, like polar bears (*Ursus maritimus*) and tigers (*Panthera tigris*), or live in groups and hunt cooperatively, like dolphins or chimpanzees (*Pan troglodytes)*. Even traditionally social predators, however, can move along a continuum from group living to solitary depending on their activities and external ecological forces at play. Among social predators, the decision to be solitary or participate in group membership is not a zero-sum game. Instead, group engagement should only occur when fitness benefits accrued by an individual in a group surpass the detrimental cost of sharing resources with other members (Alexander, 1974; Packer & Ruttan, 1988).

In this book, we learned about cooperatively hunting mammalian predators that exhibit similarities and differences in their social lives that are inescapably aligned with resource, habitat, and reproductive constraints. Here are some noteworthy perspectives gleaned from our different case studies. The views presented are not thorough but an introduction to areas worth further study, analysis, and synthesis.

9.1.1 Social Dynamics

- Except for African wild dogs—*Lycaon pictus*, all other species (*Panthera leo—African and Asiatic lions, Canis lupus—gray wolves, Crocuta crocuta—spotted hyena, and Orcinus orca—mammal-hunting killer whales*) exhibit fission-fusion societies, where social unit composition can change with activity and over time. Yet for all species, some strong and permanent associations are possible among related individuals (e.g., lion prides or killer whale groups) or unrelated individuals (e.g., male coalitions in lions, unrelated dominant breeding pairs in African wild dogs and gray wolves). As an extreme case, only death and dispersal can lead to pack composition changes in wild dogs (Creel & Creel, 2002).
- Social hierarchies vary across species, particularly in terms of feeding order. African lions and mammal-hunting killer whales are the most egalitarian during feeding. In killer whales (Srinivasan, 2023; Black et al., 2023), there is even tolerance toward unrelated individuals from other groups. This raises the possibility that killer whale groups exist in networked meta-communities, equivalent to spotted hyena clans that could be dispersed during hunting but aggregate to feed. While there are no feeding hierarchies in African lions (Palmer et al., 2023), Asiatic lion male coalitions (Chakrabarti et al., 2023) are not egalitarian, and the dominant male can exercise disproportionate rights when it comes to food sharing and mating access, highlighting the role of habitat and foraging ecology as

influential factors. In African wild dogs (Jordan et al., 2023), uniquely among the species considered here, the youngest feed first, whereas in gray wolves (Tallian et al., 2023), the dominant pair may feed first. Similarly, matriarchal social rank dictates feeding rights for spotted hyenas (Smith & Holekamp, 2023). The bone-crushing abilities and intense feeding competition of spotted hyenas are unique features distinguishing them from other social carnivores.

- Killer whales, lion prides, African wild dogs, and spotted hyenas tend toward female-centric societies, i.e., matrilineal. In individual chapters, we cover the role of young and older females in orchestrating elaborate and successful hunts, facilitating social learning, defending offspring, rearing and caring for young, and determining mating access. Similarly, we also explore role of male social units, role of males in cooperative and solitary hunts, defense of pride and territories, and reproductive strategies. Associations within and between males and females offer further glimpses into the complexity of cooperative hunting social carnivore societies dictated by prey type and availability, home ranges, parental care, cub defense, and abundance of males and females in the area.
- Reproductive strategies vary widely among the species. In female-dominated spotted hyena clans, females and their offspring dominate adult immigrant males, which are smaller and weaker than female hyenas. Male and low-ranked females often initiate hunts more frequently than higher-ranked dominant females. For spotted hyenas, higher-ranked females enjoy higher reproductive success and body size is not a determinant of social rank. Also, offspring of higher-ranked mothers are exposed to higher levels of androgen in utero than lower-ranked mothers. Higher concentrations of androgen also appear to correlate with higher levels of aggression regardless of offspring sex (Holekamp et al., 2013). A single male and female African wild dog pair can monopolize breeding in their pack. Wild dogs are obligate cooperative breeders and large pack sizes are associated with large litters and higher pup survival. Moreover, older females in large packs raise more pups (Jordan et al., 2023). In wolves, dominant male and female usually share leadership roles. However, evidence from Yellowstone National Park, USA, suggests that dominant females may assume the highest leadership position (Stahler et al., 2020). Although considered monogamous breeders, gray wolves can exhibit cooperative breeding and flexible mating systems (Kleiman, 2011), and the larger male wolves (relative to females) may engage in aggressive encounters with conspecifics to access females or engage in mate defense (Cassidy et al., 2017). Male African lions have access to estrous females on a first come first served basis. In contrast, only dominant males in Asiatic lion societies have mating priority due to fewer females in the region. Mating competition is thought to exist among dominant adult males in mammal-hunting killer whales, although this is presently unproven.
- Compared to other social carnivores considered here, social learning and culturally transmitted hunting behaviors are prominent in mammal-hunting killer whales and reinforce the importance of multigenerational social units in long-lived mammals. Presence of older adults and matriarchs may have a favorable role in the maintenance and transmission of knowledge related to hunting

behaviors, territorial defense, and improved reproductive success. Moreover, the long-term beneficial presence of post-reproductive females in killer whale societies adds further credence to preserving the integrity of social units. Lions undergo menopause and have non-reproductive females within social units, but “grandmothers” do not increase kin reproductive success (Palmer et al., 2023). Social learning and culturally mediated behaviors require further study in African and Asiatic lions, gray wolves, and African wild dogs.

9.1.2 Hunting Strategies and Group Sizes

- Social predators employ a variety of prey and habitat-specific techniques to search, attack, subdue, and consume prey—constantly modulating and responding to the anti-predator behaviors of prey and changes in habitat features. The plasticity to modify hunting sequences and group dynamics, perform or regulate cooperative behaviors, and variation in participation (e.g., assuming specific roles and subsequent access to the spoils) provide witness to the adaptability of these predators under erratic ecological conditions.
- An understanding of the relationship between behavioral state-dependent group sizes and cooperative behaviors is an enduring conundrum in social carnivore ecology (Macdonald & Johnson, 2015; Peña & Nöldeke, 2018; Mbizah et al., 2019; Suter & Houston, 2021). Larger group sizes do not automatically correspond to spatiotemporal prey distribution and size. Rather, other factors, such as prey vulnerability, fission-fusion dynamics, reproductive costs, kinship, territoriality, offspring or resource defense, interspecific competition, seasonal environmental fluctuations, and landscape features can all influence group sizes (Macdonald, 1983; Packer et al., 1990; Creel, 1997; Kotze et al., 2018). For instance, in gray wolves, larger pack sizes in areas of high wolf density are associated with better reproductive success and increased capability to defend territories (Tallian et al., 2023). In spotted hyenas, individuals can often be alone despite being part of a large clan or high prey abundance. Thus, group living may be a by-product of needing to protect carcasses from lions and conspecifics and not attributable to the benefits of cooperative hunting (see Srinivasan & Würsig, 2023; Smith & Holekamp, 2023).
- While hunting group sizes can be proportional to prey type—i.e., larger group sizes to hunt larger or challenging prey and smaller group sizes for easily catchable small prey—this is not generalizable across and sometimes within species given the current state of knowledge. Cooperative hunts may produce higher hunting success when large prey is targeted than when hunting alone—but the net energy gain per capita may be compromised with increasing group sizes for killer whales, as is also the case for spotted hyenas and African lions. In African lions, however, smaller prides tend to form as large a group as possible despite reduced foraging efficiency, whereas larger prides, in the absence of a creche, can have variable group sizes (Packer et al., 1990). In contrast, African

wild dogs maximize per capita net energy gain when hunting in the larger groups, up to a point.

- An important avenue of research is the development of models and the testing of optimal group size dynamics in relation to foraging energetics throughout the hunt, ecological changes, and social dynamics. Such resultant models may also generate more ubiquitous rules of most efficient cooperative hunting among social mammalian predators (Baird, 2000; Cresswell & Quinn, 2010; Gogarten et al., 2015; Suter & Houston, 2021).

9.1.3 Territoriality

- Territoriality is a significant characteristic of social terrestrial carnivores but not for mammal-hunting killer whales. Some nuances emerge in this synthesis.
- African wild dogs are strongly territorial, and inter-pack encounters can be fatal. Despite this, packs have high degrees of home range overlap, with related packs overlapping to a greater degree than unrelated packs (Jordan et al., 2023). Similarly, female prides of Asiatic lions are extremely territorial with minimum overlap between neighboring prides. However, male coalitions with overlapping home ranges are more accommodating. Initial hostilities during territory acquisitions are replaced with tacit avoidance or lack of direct confrontation with time. The tolerance stems from the existence of small pride sizes and reduced mating opportunities and thick vegetation that allow female prides to elude prospective males (Chakrabarti et al., 2023). Among African lion prides, sociality can be considered necessary for survival in heterogeneous savanna landscapes, manifested through the defense of territories. Good quality territories that are resource-rich and provide access to water can also increase the chances of reproductive success (Palmer et al., 2023).
- In spotted hyenas, unlike many gregarious canids, philopatric females can exhibit extensive territoriality (Henschel & Skinner, 2010). Territorial behavior can include border patrol, aggression toward intruders, scent marking, and clan wars. The nature of territorial defense can be proportional to hyena abundance, resource availability, and intruder threat severity (Boydston et al., 2001). Gray wolves are strongly territorial. A new pack can typically form when a breeding pair establishes territory. The dominant female invests in breeding and pup rearing, dominant males engage in food provisioning, while subordinates assist in alloparental care, hunts, and territorial defense (Cassidy et al., 2017). In contrast, hunting killer whales display no territoriality, potentially attributable to vast home ranges, prey abundance, and no non-human predation risk (Srinivasan, 2023; Black et al., 2023). Mammal-hunting killer whales also uniquely display no overt inter-group aggression when occupying sympatric habitats and may reflect some degree of kin structuring, mutualism, or generalized reciprocity that needs further study (Clutton-Brock, 2002). But niche partitioning

can occur with different killer whale groups specializing in different prey in areas of spatial overlap.

9.1.4 Adapting to Human Dominated Landscapes

- Social mammalian predators display resilience, cooperative problem-solving, and ingenuity to adapt to human-disturbed environments. But there is a threshold beyond which their resilience can be outpaced by anthropogenic pressures.
- Contaminant loads in mammal-hunting killer whales are a large concern (Lawson et al., 2020; Remili et al., 2021). Marine mammal prey depletion or redistribution due to climate change and human impacts can further threaten killer whale populations. Additionally, the specialized consumption of marine mammal prey leading to severe bioaccumulation of toxins and contaminants could push mammal-hunting killer whales toward extinction by affecting reproductive success. Also, any instability in social structure caused by natural and unnatural perturbations may affect culturally transmitted behaviors that may be integral to their hunting prowess and adaptability (Srinivasan, 2023; Black et al., 2023).
- In the terrestrial environment, African wild dogs may arguably benefit in some ways from anthropogenic features, for example by utilizing roads for efficient movement; but overall, anthropogenic impacts threaten the survival of this wide-ranging species, through habitat loss, human-wildlife conflict, disease, and climate impacts on breeding phenology and recruitment (Abrahms et al., 2022; Jordan et al., 2023).
- Asiatic lions residing outside protected areas thrive on feral livestock that provides ample energy subsidies in the form of scavenging events and easily catchable prey. However, such habituation to anthropogenic food sources comes with a cost of changes in typical lion socio-biology, faster reproductive rates, loss of predatory behavior and fear of humans, increase in human-lion conflict, and disease spillovers (Chakrabarti et al., 2023).
- In African lions, solitary or small groups form outside protected areas. Perhaps as an adaptation to human pressures or due to factors such as low population densities, less competition, and prey scarcity. Understanding the impact on group dynamics in areas of human impact is an area for further study. Trophy hunting—intentional capture of lions for sport or recreation—is prevalent in many African countries and can lead to a reduction in male lions and disruption of social units, and higher infanticide due to loss of resident males in prides. Other forms of human-wildlife conflicts that may result in poaching and poisoning can indiscriminately destroy stable social units. Additional lifestyle impacts can occur within small and large protected areas if animal social units are interfered with, for example, when cubs are separated from their natal pride and translocated to other areas (Palmer et al., 2023).
- Wolves are also exposed to intense human impacts that involve culling of individuals with no understanding of potential ramifications on social dynamics.

  Given the level of cooperative hunting, territorial defense, and pup rearing, constant disruption of pack units through direct or indirect human effects could have impacts on culturally mediated behavioral traits. However, it is a challenging area of study due to the gradient of human pressures that wolves are globally exposed to, altering our perception and understanding of what constitutes baseline wolf social structure (Tallian et al., 2023).
- Spotted hyenas appear to withstand human stressors better than other social terrestrial carnivores. Due to their physiological and morphological endowments, hyenas thrive in a variety of habitats, feed on diverse prey, live in areas of high human densities, and can cope with disease better than other large carnivores. But given their preference for kin-based associations rather than non-kin, they are not immune to human impacts outside protected areas, and fractures in social bonds could impede their resilience to human stressors, which at this point we cannot adequately comprehend (Smith & Holekamp, 2023).
- As we enhance our understanding of human impacts on the social systems of mammal-hunting mammalian predators, their social flexibility and responses may largely determine their resilience and persistence on a rapidly changing anthropogenic planet. Thus, threat-mitigation and preservation of appropriate social units within and outside protected areas are equally pertinent for social mammalian carnivores and require integration into management decision-making (see also Durant et al., 2017).

9.2 Concluding Thoughts

For most terrestrial species, cooperative hunting may at least in part be an artifact of gregariousness due to reproductive strategies—which are probably best established for African lions among our focal species, whereas for mammal-hunting killer whales, we speculate the opposite, wherein sociality is a by-product of a cooperative hunting lifestyle. Above all as scientists in the field, we must be persistent in conducting or contributing data toward comparative studies of social predators across marine and terrestrial environments. If carried out at appropriate scales of species, population, societal culture (i.e., shared information or behaviors within a community), subgroup “family” units, and individuals, we have a chance to improve our overall understanding of mammalian social evolution, and thus better recognize species’ and populations’ adaptive responses and resilience to changing environmental conditions and human interventions.

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Correction to: Social Strategies of Carnivorous Mammalian Predators

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Correction to:
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The original version of the book was inadvertently published without incorporating the following corrections for Chapters: 2, 5, 6, 7.

Chapter 2: The source line of the artistic illustration in Chapter 2 has been updated as "Artistic rendering by Britney Danials. Original photo credit: Stotra Chakrabarti".

Chapter 5: Images of Figure 5. 17 and Figure 5.18 have been swapped without the figure legends.

Chapter 6: On page #184, the line of text "While African wild dogs are commonly referred to as the most successful hunters." has been changed to "African wild dogs are commonly referred to as the most successful hunters." and on page #217, "Packs are now giving birth up to 0 days later than three decades ago" has been changed to "Packs are now giving birth up to 20 days later than three decades ago".

Chapter 7: The caption of Figure 7.7. has been modified as follows:

-Fig. 7.7 A typical sequence of events during which killer whales successfully dislodge a seal from an ice floe through cooperation and coordination. See text for details. Illustrations by Hannah Rappaport

These chapters have now been corrected and approved by the authors.

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Index

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