Parental Behavior in Carnivores

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Abstract The mammalian order *Carnivora* is generally defined as species that feed exclusively or to some degree by eating other animals. The *Carnivora* comprise around 280 species, divided into 16 families, 13 of which are terrestrial and 3 aquatic. Carnivores are spread across the entire planet, including the two polar regions and on land and sea. Consistent with such diverse ecologies, there is no typical pattern of parental care distinguishing carnivores from other mammals. Using examples from different taxonomic *families*, our aim is to illustrate the diversity of parental care in *Carnivora*. Major topics include parental care before and after birth of the young, paternal, and alloparental care and the process of weaning. Given the position of many carnivores at the apex of food chains, a greater understanding of their patterns of parental care as a vital part of reproductive biology is essential to conservation programs.

Keywords Maternal care · Paternal care · Helpers · Prenatal preparation · Parturition · Postnatal care · Weaning · Independence · Diversity

1 Introduction

The mammalian order *Carnivora* according to recent molecular phylogenetic studies is a monophyletic taxonomic group (Eizirik et al. 2010; Hassanin et al. 2021) made up of species generally characterized by a high proportion of vertebrates in their diet. The *Carnivora* comprise around 270–290 species (depending on sources), a number comparable to that of primates (256 species) but considerably less than

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the most numerous mammalian orders, *Chiroptera* (bats), with an estimated 977 species and *Rodentia* (rodents) with an estimated 2000 species. Nevertheless, the range in body mass of carnivores, from the 25 g least weasel *Mustela nivalis*[1] to a 4000–6000 kg male southern elephant seal *Mirounga leonina*, exceeds that of all other living mammalian orders (Mittermeier and Wilson 2009). *Carnivora* are commonly divided into 16 *families*, 13 of which are terrestrial and 3 aquatic (Table 1).

Members of this order typically have strong jaws and dentition characterized by large, daggerlike canine teeth adapted for catching and holding prey and the remaining teeth shaped for cutting, tearing at, and masticating meat. Other adaptations to the demands of a carnivore's hunting lifestyle typically include speed and agility, muscular strength, highly developed sensory acuity, and strongly convoluted brains indicative of the importance of learning and other cognitive abilities. Together, these characteristics are thought to account for the considerable charismatic appeal of many carnivores. Nevertheless, only the *Felidae*, *Phocidae,* and *Otariidae* (Table 1) are obligate carnivores, depending exclusively on a diet of fresh animal protein for their survival. All other carnivores are also scavengers or foragers to a greater or lesser degree, which include in their diet carrion, insects, and other invertebrates, fungi, and plant material such as berries, fruits, leaves, roots, and nuts. Exceptions among carnivores are the giant and the red panda *Ailuropoda melanoleuca* and *Ailurus fulgens*, respectively, which can be considered obligate herbivores feeding almost exclusively on bamboo, and the mainly frugivorous kinkajou *Potos flavus* and African palm civet *Nandinia binotata*. The bat-eared fox *Otocyon megalotis,* white-tailed mongoose *Ichneumia albicauda*, and aardwolf *Proteles cristata*, for example, are primarily insectivorous.

Hunting and/or scavenging is time-consuming. It can be dangerous, and success is often uncertain, obligating mothers, which in many carnivore species are the sole caretakers of the young, to leave them alone for extended periods. On the other hand, meat is calorie-rich, is easy to digest (as reflected by the relatively short and simple digestive tracts of carnivores compared to herbivores, for example), and can be brought to the mother and/or to the young. Some canid species transfer solid food to the mother and young by regurgitation, a canid innovation that allows mates or other caretakers to feed the mother at the den, whose ability to hunt may be compromised in late pregnancy and early lactation, and to introduce the young to solid food around the time of weaning (Macdonald and Sillero-Zubiri 2004).

A notable feature of carnivores is their worldwide distribution and the varied habitats they occupy. Carnivores can be found across the whole planet, including the two polar regions, aquatic environments, and the full range of terrestrial habitats: coastal areas, bushland, swampland, desert, forest, jungle, inland savannah and steppe, high-altitude mountains, urban environments, and at all latitudes. A further notable feature is their diversity of social and mating systems, ranging from species leading primarily solitary lives, such as most *Felidae* and *Viverridae*, to those forming pairs, family groups, or packs such as many *Canidae* or *Hyaenidae*, or even large complex societies such as members of the *Herpestidae* and *Mustelidae.*

[1] Latin names of species are given only at first mention, and they are listed in Table 1 according to the taxonomic *families* to which they are presently considered to belong.

Table 1 Carnivore *families* with some general characteristics and a list of species mentioned in the text. Group living propensity of the species refers mostly to their parental behaviors

Family	Extant species	Size range	Litter size	Species in the text	Latin name	Group living propensity
Mustelidae	57	20 g/45 kg	1–18	American mink	*Neogale vison*	Solitary
Weasels, otters, and badgers				Asian small-clawed otter	*Aonyx cinerea*	Group living
				Domestic ferret	*Mustela putorius furo*	
				European badger	*Meles meles*	Facultative groups
				Fisher	*Pekania pennanti*	Solitary
				Giant river otter	*Pteronura brasiliensis*	Group living
				Least weasel	*Mustela nivalis*	Solitary
				River otter	*Lontra canadensis*	Facultative groups
				Sea otter	*Enhydra lutris*	Facultative groups
				Tayra	*Eira barbara*	Solitary
				Wolverine	*Gulo gulo*	Solitary
Felidae	37	1–300 kg	1–10	Domestic cat	*Felis silvestris catus*	
Cats				African lion	*Panthera leo*	Group living
				Black-footed cat	*Felis nigripes*	Solitary
				Bobcat	*Lynx rufus*	Solitary
				Caracal	*Caracal caracal*	Solitary
				Cheetah	*Acinonyx jubatus*	Facultative groups
				Cougar	*Puma concolor*	Solitary
				Iberian lynx	*Lynx pardinus*	Solitary
				Leopard	*Panthera pardus*	Solitary
				Margay	*Leopardus wiedii*	Solitary
				Ocelot	*Leopardus pardalis*	Solitary
				Pallas's cat	*Otocolobus manul*	Solitary
				Tiger	*Panthera tigris*	Solitary

(continued)

Table 1 (continued)

Family	Extant species	Size range	Litter size	Species in the text	Latin name	Group living propensity
Canidae	35	1–50 kg	1–16	African wild dog	*Lycaon pictus*	Group living
Dogs				Arctic fox	*Vulpes lagopus*	Facultative groups
				Bat-eared fox	*Otocyon megalotis*	Group living
				Black-backed jackal	*Canis mesomelas*	Group living
				Domestic dog	*Canis lupus familiaris*	
				Maned wolf	*Chrysocyon brachyurus*	Pair living
				Raccoon dog	*Nyctereutes procyonoides*	Facultative groups
				Red fox	*Vulpes vulpes*	Pair living
				Gray wolf	*Canis lupus*	Group living
Viverridae	34	1–14 kg	1–6	Binturong	*Arctictis binturong*	Solitary
Civets, genets, and olyans						
Herpestidae	34	200 g/4.5 kg	1–7	Banded mongoose	*Mungos mungo*	Group living
Mongooses				Dwarf mongoose	*Helogale parvula*	Group living
				Meerkat	*Suricata suricatta*	Group living
				White-tailed mongoose	*Ichneumia albicauda*	Solitary
Mephitidae	12	200 g/4.5 kg	1–10	Eastern spotted skunk	*Spilogale putorius*	Solitary
Skunks and stink badgers						
Procyonidae	12	1–10 kg	1–7	Kinkajou	*Potos flavus*	Facultative groups
Raccoons						
Eupleridae	8	500 g/10 kg	1–6	Malagasy civet	*Fossa fossana*	Pair living
Malagasy mongooses and civets				Malagasy narrow-striped mongoose	*Mungotictis decemlineata*	Group living

(continued)

Table 1 (continued)

Family	Extant species	Size range	Litter size	Species in the text	Latin name	Group living propensity
Ursidae	8	25–700 kg	1–5	American black bear	*Ursus americanus*	Solitary
Bears				Brown bear	*Ursus arctos*	Solitary
				Giant panda	*Ailuropoda melanoleuca*	Solitary
				Polar bear	*Ursus maritimus*	Solitary
				Sloth bear	*Melursus ursinus*	Solitary
				Spectacled bear	*Tremarctos ornatus*	Solitary
				Sun bear	*Helarctos malayanus*	Solitary
Hyaenidae	4	8–70 kg	1–5	Aardwolf	*Proteles cristata*	Pair living
Hyenas				Brown hyena	*Hyena brunnea*	Group living
				Spotted hyena	*Crocuta crocuta*	Group living
Prionodontidae	2	400 g/1 kg	2–3			
Linsangs						
Nandiniidae	1	1–3 kg	1–4	African palm civet	*Nandinia binotata*	Solitary
African palm civet						
Ailuridae	1	3–6 kg	1–3	Red panda	*Ailurus fulgens*	Solitary
Red panda						
Phocidae	18	30–3000 kg	1	Southern elephant seal	*Mirounga leonina*	Solitary
Earless seals; true seals				Baikal seal	*Pusa sibirica*	Solitary
				Harbor seal	*Phoca vitulina*	Solitary
				Hooded seal	*Cystophora cristata*	Solitary
				Ringed seal	*Pusa hispida*	Solitary
				Weddell seal	*Leptonychotes weddellii*	Solitary
Otariidae	15	25–1000 kg	1	Antarctic fur seal	*Arctocephalus gazella*	Solitary
Eared seals, fur seals, and sea lions				Galápagos fur seal	*Arctocephalus galapagoensis*	Solitary
				New Zealand sea lion	*Phocarctos hookeri*	Solitary

(continued)

Table 1 (continued)

Family	Extant species	Size range	Litter size	Species in the text	Latin name	Group living propensity
				South American fur seal	*Arctocephalus australis*	Solitary
Odobenidae	1	400–1700 kg	1	Walrus	*Odobenus rosmarus*	Group living
Walrus						

Diversity in mating systems ranges from the polygynous southern elephant seal that shows strong harem-based female defense to the female-dominated polyandrous mating system of the spotted hyena *Crocuta crocuta* to the varying degrees of monogamy in the *Canidae*. These varied geographical and social ecologies have resulted in a great diversity in patterns of parental care in which even members of the same taxonomic family and species of similar size can differ markedly (Bekoff et al. 1984). Nevertheless, some generalities can be noted. Apart from seals and walrus, carnivore young can be considered altricial although with the exception of the American mink *Neogale vison* and the giant panda, most have some fur at birth, perhaps because most carnivores do not build nests although most give birth within the shelter of dens or burrows and because the young of some species are left alone for extended periods when mothers or other caretakers must leave to hunt or forage.

Following convention, we define parental care as any behavior that directly contributes to the well-being and survival of the young. Thus, for the purpose of this chapter, we have excluded territorial behavior and mate guarding, typically by males, which, while possibly helping ensure mothers a resource-rich environment and limiting infanticide by roaming males, might principally serve other purposes such as males' access to mating opportunities.

As we argue in this chapter, knowledge of parental care in carnivores is rather limited. It is based on detailed knowledge of only a handful of species, and this is often gained under the artificial conditions of laboratories, zoos or animal parks, and farm or household conditions. This is understandable given the considerable difficulty in observing most carnivores, particularly in nature. The young are typically born into dens or burrows, which are often difficult to access and often defended by a dangerous, well-armed mother and sometimes together with the father and other members of the social group. Moreover, many carnivores are primarily nocturnal or crepuscular, increasing the difficulty of observing parent-young interactions. Despite such difficulties, it is our aim to illustrate the diversity of carnivore parental behavior by using some of the best-documented examples from different taxonomic *families* and to show how limited our knowledge of this fundamental aspect of carnivore behavioral biology still is.

For this purpose, we have arranged the chapter in three main parts corresponding to the three main phases of carnivore parental care: prepartum preparation for arrival of the young, parturition and behaviors directly associated with this, and postpartum care, including weaning of the young and subsequent care to their complete independence. We will not discuss physiological mechanisms underlying parental behavior as so little is known about these in carnivores. Available information mainly relates to the endocrine regulation of mating and fertility in a few domestic or semi-domestic and laboratory species (dog, cat, ferret, mink). Also, we will not present in detail and only partly discuss accompanying differences in social systems that may be strongly influenced by ecological factors.

According to present knowledge, in the great majority of carnivores, parental care is provided by the mother alone. But before discussing the three main phases of parental care, we briefly consider the role of fathers (and in section "Alloparental care" of other members of the social group) in helping raise the young.

Paternal Care

Male parental care is unusual in mammals, occurring in only 5–10% of species (Woodroffe and Vincent 1994), and in the majority of carnivore species, females care for the young alone. Male care of offspring would be expected only when the benefits of helping the female outweigh the costs (Clutton-Brock 1991; Gross 2005). Hence, even though fathers may increase the survival or quality of their offspring by helping care for them or their mother, this usually entails a trade-off between time invested in care of the family and time lost in obtaining additional mating opportunities.

Among carnivores, male parental care is most common in the *Canidae* where it is reportedly present to some degree in all species (Kleiman and Malcolm 1981). Forms of paternal care are usually classified as direct or indirect. Direct care refers to interactions between males and their offspring, which can be reasonably understood to increase offspring fitness. Common forms of direct care are grooming and/or cleaning the young, carrying or retrieving them, providing warmth by huddling with them, providing food, defense against predators, and playing or other forms of socializing. Indirect care involves those behaviors that could benefit offspring even if there is no direct interaction between the father and young. Examples include den construction, giving alarm calls, and providing food for the mother. Arguably, the most social canid is the African wild dog *Lycaon pictus* in which females produce up to 16 pups per litter, thus requiring support from the father and even other pack members (Malcolm and Marten 1982). Fathers of feral domestic dogs *Canis lupus familiaris* reportedly guard the nest site and regurgitate food for the pups (Pal 2005). Gray wolf fathers *Canis lupus* also reportedly participate in guarding the den (Ruprecht et al. 2012) and feed the nursing mother, and when the cubs leave the den around weaning, the breeding male as well as other adults regurgitate food for them (Packard 2010). Even the maned wolf *Chrysocyon brachyurus*, thought to be solitary, has been observed to spend time sleeping together with its mate, and after birth of the cubs, the male stays in the vicinity, reducing his home range and activity levels, suggesting that he may contribute to parental care.

Male investment in some form has also been reported, at least occasionally, in three of the four species of *Hyaenidae* although it is apparently not found in the spotted hyena (Richardson 1987; Mills 1990; East et al. 2003). So-called raccoon dogs *Nyctereutes procyonoides* show long-term pair bonding, and males participate in rearing the young. In fact, they reportedly spend more time alone with the pups than females, guarding the litter at the den or in its close vicinity while females forage to satisfy their increased energy needs due to the high cost of lactation (Kauhala et al. 1998). Direct male care also occurs in the tropical otters: the giant river otter *Pteronura brasiliensis* and the Asian small-clawed otter *Aonyx cinerea* (Schmelz et al. 2017) and in families of the banded mongoose *Mungos mungo* (Rood 1974). Although male care in the form of playing with young and allowing them to take food items has been recorded in a number of felids in captivity (Kleiman and Malcolm 1981), it is difficult to know if this is an artifact of confined conditions as there are presently no reports of such activity in the wild. Direct paternal care has not been reported in any of the aquatic carnivores, and in fact, in species with large sexual dimorphism in body mass such as the southern elephant seal, males may severely injure or crush young pups to death – presumably sometimes even their own offspring – during battles with competing males for access to females for mating.

For any one topic, the examples given below represent only a fraction of the diversity of parental care in carnivores. Investigating in more detail any one aspect will surely reveal a richness and diversity beyond the bounds of this chapter.

2 Prepartum Behavior: Preparation for Arrival of the Young

For many mammals, parental care begins before birth of the young. Since altricial offspring require a particularly secure environment for early rearing (Case 1978), in many carnivores one of the most important prepartum behaviors is seeking out or actively constructing a nursery burrow or den. Such structures are vital to protect the young from harsh weather, and from aerial and land predators, which may include infanticidal males or other conspecifics (Ruggiero et al. 1998; Ross et al. 2010; Libal et al. 2011; Jackson et al. 2014; White et al. 2015). Den sites are critical resources that influence the survival of the young and ultimately the population dynamics of several species. The use of subterranean natal dens that can be readily defended is characteristic of almost all species in several families of carnivores (*Canidae, Hyaenidae, Mephitidae*) and prevalent in others (*Herpestidae, Mustelidae, Ursidae*) (Noonan et al. 2015). Many carnivores that use dens or burrows do not actively excavate them but occupy already existing structures such as hollow or fallen trees, rock crevices, or other naturally formed cavities or occupy burrows and tunnels constructed by other species. In contrast, mongooses, otters, hyenas, badgers, wolverines, and several canid species such as foxes, dingoes, coyotes, or wolves dig their own natal dens, a behavior not seen in any felids.

Only few species of carnivores have been reported to build nests of plant or other material within such nursery dens or cavities. Examples include the European badger *Meles meles* (Roper 1992), the American mink (Malmkvist and Palme 2008), and the red panda (Roka et al. 2015).

Properties of dens contributing to protection, including avoiding human disturbance, are reportedly more important for breeding females than habitat features such as prey density or structure of vegetation as reported for the Iberian lynx (Fernández and Palomares 2000), African wild dog (Jackson et al. 2014), gray wolf (Sazatornil et al. 2016), spotted hyena (Périquet et al. 2016), and the fisher *Pekania pennanti* (Matthews et al. 2019). Such shelters can also be important in helping to maintain a stable and adequate thermal environment for the altricial young (Reichman and Smith 1990). Dens of several species of the family *Felidae* such as Pallas's cat *Otocolobus manul*, Iberian lynx *Lynx pardinus*, and ocelot *Leopardus pardalis* contribute importantly to thermoregulation, as well as providing a refuge from other carnivores, including predatory conspecifics, and from humans (Fernández and Palomares 2000; Laack et al. 2005; Ross et al. 2010). Thermoregulatory factors in den selection were also found to be important in wolverines *Gulo gulo* (Magoun and Copeland 1998), and the Arctic fox *Vulpes lagopus* constructs and uses dens with southward-facing entrances to improve microclimate conditions (Smits et al. 1988). For most bear species, which have very altricial young, dens also provide a safe and sheltered environment for giving birth, nursing, and early cub growth in some species during winter hibernation (Oli et al. 1997; Seryodkin et al. 2003; Manchi and Swenson 2005; Zhang et al. 2007; Derocher et al. 2011; Faure et al. 2020).

Pinnipeds depend on and seek out solid substrates to give birth and, with the partial exception on the walrus *Odobenus rosmarus* (see section *Nursing*), for nursing the young. They utilize a wide variety of habitats, including pack ice, fast ice, and land. Phocid seal species give birth mostly on ice, whereas all 15 species of otariids give birth on land. The only surviving member of the *Odobenidae,* the walrus, is also an ice-breeding species (Bowen 1991). In several pinniped species, these sites are part of long-established breeding grounds with high individual philopatry, on beaches, rocky shores, or ice sheets; for example, the Galápagos fur seal *Arctocephalus galapagoensis*, southern elephant seal (Hindell and Little 1988), Antarctic fur seal *Arctocephalus gazella* (Hoffman and Forcada 2012), Weddell seal *Leptonychotes weddellii* (Cameron et al. 2007), and New Zealand sea lion *Phocarctos hookeri* (Chilvers and Wilkinson 2008). Because young seals are born without a substantial layer of subcutaneous fat and accumulate most of their lipid reserves after birth (Donohue et al. 2000), thermoregulatory factors are important in pupping site selection. However, the majority of seal pups are born into an environment that gives little protection against weather or predators, and predation is a significant source of pup mortality including in several species of ice-breeding pinnipeds (Bowen 1991). In this regard, the ringed seal *Pusa hispida* and the Baikal seal *Pusa sibirica* are exceptions as females of these species construct dens from snow under ice ridges or over breathing holes (Smith and Stirling 1975; Miyazaki 2009). Such dens have a main chamber and smaller tunnels off the central cavity and provide thermal protection and concealment from predators such as Arctic foxes and polar bears *Ursus maritimus*.

In addition, pregnant females may adjust their hunting range as parturition approaches. This is particularly the case for solitary carnivores such as pinnipeds, mustelids, and most felids where the mother raises the young alone. This change might be due to anatomical constraints of the pregnant mother, change in prey type or a focus on nest defense. Even after the young start to accompany their mother on hunting or foraging trips, their still limited motor abilities and endurance may also influence her behavior. For example, female North American cougars *Puma concolor* reduce their home range around and following parturition (Seidensticker et al. 1973; Maehr et al. 1989), as do leopards *Panthera pardus* (Seidensticker 1976), tigers *Panthera tigris* (Sunquist 1981), bobcats *Lynx rufus* (Nielsen and Woolf 2001), and the mustelid tayras *Eira barbara* (Presley 2000). Harbor seals *Phoca vitulina* restrict their foraging range during lactation (Thompson et al. 1994) while several large-bodied phocid seals fast throughout lactation completely (Schulz and Bowen 2005).

Thus, from the above, we may conclude that carnivore species show a wide range of prepartum behaviors relevant to the successful raising of their young. And furthermore, that the availability of suitable breeding sites such as dens, burrows, or ice flows and associated productive hunting grounds are vital for the conservation of many carnivore species (Squires et al. 2008).

3 Parturition

This is a critical phase in the reproductive cycle of all mammals in which females give birth to live young in various stages of maturation, and as noted above, including for carnivores, all the young of which are altricial or semi-altricial. Parturition involves varying degrees of physical, physiological, and external hazard, both for mothers and their young. While giving birth, mothers and young, particularly in solitary species, may be vulnerable to attack by predators as at this time, mothers are largely unable to defend themselves or their offspring.

Carnivore mothers typically give birth alone, and even in monogamous pairs, the female often does not allow the male to enter the breeding den (Naaktgeboren 1968). All pinniped species (Boness and Bowen 1996), the sea otter *Enhydra lutris* (Estes 1980), the feline margay *Leopardus wiedii* (Moreira 2001), and some members of the *Eupleridae* such as the Malagasy narrow-striped mongoose *Mungotictis decemlineata* and the Malagasy civet *Fossa fossana* give birth to only one offspring (Nowak 2005; Schneider and Kappeler 2016). In other *families,* the litter size can differ markedly, for example, in *Ursidae* between one and two young in the sun bear *Helarctos malayanus*, sloth bear *Melursus ursinus*, spectacled bear *Tremarctos ornatus*, and giant panda, to as many as five in the American black bear *Ursus americanus* and brown bear *Ursus arctos* (Garshelis 2004). In *families* such as the *Mustelidae*, *Felidae, Viverridae,* and *Hyaenidae,* between two and six young is most common, but up to 14 has been reported in the least weasel (Sundell 2003) and up to 18 in the domestic ferret *Mustela putorius furo* (Lindeberg 2008). In some *Canidae* such as the domestic dog, the Arctic fox, and the African wild dog, there may be up to 16 pups (McNutt and Silk 2008; Table 1).

Duration of birth including the expulsion of each young and the interval between each expulsion can vary considerably. Large individual differences have been observed lasting from 8 to 225 min for mothers giving birth to singletons, as in the South American fur seal *Arctocephalus australis* (Franco-Trecu et al. 2016), and even in polytocous species, the rhythm can be very different, for example, in foxes 30–120 min between young (Naaktgeboren 1968), gray wolf 9–90 min, domestic dog 6–212 min (Klarenbeek et al. 2007), and the tayra 17–30 min (Poglayen-Neuwall 1974). In the domestic cat *Felis silvestris catus,* the rhythm can also vary but is usually approximately 20 min (Hudson et al. 2009). Mainly in cats, but sometimes also in dogs, delivery between young may be interrupted for as much as 24–36 h (Lopate 2012, own observations).

With the arrival of each offspring, mothers usually bite through the umbilical cord, eat the placenta, and vigorously lick the young and surrounding area clean of birth fluids (Naaktgeboren 1968; Poglayen-Neuwall 1974). When delivery is complete, mothers typically lie on their side or back, exposing their nipples to the offspring although in the case of the domestic cat, early-born kittens may already have attached to nipples and started suckling while parturition is still in progress (Hudson et al. 2009). In general, the young, stimulated by the mother's vigorous licking, attach to a nipple within minutes and start to ingest colostrum and milk (Naaktgeboren 1968).

Orientation to the mammary region and attachment to nipples may be aided by emission of chemical cues from the mother's ventrum, a so-called nipple-search pheromone (cf. European rabbit *Oryctolagus cuniculus*: Hudson et al. 1990; domestic cat: Raihani et al. 2009), the emission of which appears to be associated with the female's reproductive cycle and under hormonal control (domestic cat: Raihani et al. 2009). In some litter-bearing species, the young rapidly develop a nipple order, with each offspring using only one or two particular nipples. This seems to be generally the case in felids (Pfeifer 1980; Hudson et al. 2009) although apparently not necessarily in canids (Hudson et al. 2016). Establishment of an order in nipple use has also been reported in black bears (Rogers et al. 2020) and the binturong *Arctictis binturong* (Schoknecht 1984).

Presumably to protect the young, immediately after parturition, mothers are reportedly more aggressive, especially around the den site. This has been seen in dogs (Pal et al. 1998) and hyenas (Kruuk 1973) but is possibly more general.

4 Postpartum Care and Transition to Independence

Nursing

In mammals, maternal care entails a large energetic cost. Lactation in particular can nearly triple a mother's caloric requirements (Gittleman and Thompson 1988; Oftedal and Gittleman 1989) while exposing her to greater risk of debilitation, injury, or even death, thereby reducing her fitness and future fecundity (König et al.

1988; Clutton-Brock et al. 1989; Koivula et al. 2003). Given the low-fat reserves in some taxa such as felids and some mustelids (Mustonen and Nieminen 2012), mothers of some species must soon leave their young to hunt, scavenge, or forage. The opposite is typical for bears and aquatic species, which often have extensive fat reserves. Bears remain in dens with their newborn cubs for weeks to months without eating or drinking, something some of them do, for example, polar bears, since they give birth during hibernation (Garshelis 2004). Some seal species draw on their fat reserves to remain with their pups for extensive periods of up to 50 days until being compelled to return to sea to hunt (Boness and Bowen 1996).

Among pinnipeds, this fasting strategy mostly occurs in the *Phocidae*, with a nursing-foraging cycle more typical for the *Otariidae*. Mothers of the latter family usually accumulate only a small amount of subcutaneous fat before they arrive to their breeding sites; thus, they fast for only 5–11 days after giving birth and then alternate foraging trips to sea with visits to land to nurse their pups, sometimes leaving them for 2–13 days. An extreme case, however, is presented by the hooded seal *Cystophora cristata*, which gives birth on an ice flow, an unstable environment, and nurses her pup almost continuously for 4 days, during which time the pup gains around 7 kg per 24 h and doubles its birth weight, after which the mother leaves it permanently and returns to sea (Bowen 1991). The walrus is the only carnivore with an aquatic nursing strategy. The young remain with their mother wherever she goes and are nursed at sea as well as on land (Bowen 1991).

Apart from providing milk, mothers of many species such as the domestic cat regularly lick the anogenital area of newborn young to stimulate urination and defecation, usually ingesting the excreta, thereby contributing to nest hygiene (see section *Den hygiene and safety*; Turner and Bateson 2014, own observations). Because of the bactericidal effect of saliva, periparturient licking by females of their mammary and anogenital areas is particularly adaptive since these are the body areas of the mother that could be contaminated by fecal-borne bacteria and which the newborns' mouths come into close contact during birth and suckling (Hart and Powell 1990). Newborn mammals, which are born with a sterile gut, do not have the intestinal bacterial flora that protect against opportunistic pathogens (Greene 1984).

Den Hygiene and Safety

Although dens and nests provide major benefits by protecting offspring from predators and harsh weather, they can also have costs in terms of hygiene due to a buildup of ectoparasites and by attracting predators, including infanticidal conspecifics, due to the accumulation of odors, worn trails, or repeated visits by caretakers. One strategy some species are thought to use to counteract such dangers is to move the nursery site from time to time although this might also be done to accommodate the changing needs of rapidly growing young. Thus, female ocelots are reported to use two to four den sites for each litter and to move kittens one to five times between them (Laack et al. 2005). Domestic cats and bobcats also frequently move their litters, especially if the mother is disturbed by unfamiliar males or humans (Feldman 1993, Nielsen and Woolf 2001, Turner and Bateson 2014, own observations). Giant panda mothers also regularly change dens although the reason is unknown as this is the only species of *Ursidae* that has been observed to do so (Garshelis 2004). Frequent den changes have also been reported in spotted and brown hyenas *Hyena brunnea*. The most likely reasons are thought to be human disturbance and a buildup of fleas at the den (Mills 1990). Limiting parasite infestations may also help explain moving the young in other carnivores although information on this is presently lacking.

Transport of the young is facilitated by the particular posture the offspring of some species adopt, notably felids such as the domestic cat and canids, which when carried in the mother's mouth by the nape of the neck reflexively curl up in a fetal-like posture, remaining motionless and completely silent (Turner and Bateson 2014; own observations).

Mother-Young Recognition

Since maternal care comes at a large energetic cost, evolutionary theory predicts that to maximize their fitness, mothers should preferentially care for their own young (Hamilton 1964) and thus should be able to distinguish them from alien offspring. If a mother indiscriminately cares for both her own and unrelated offspring, this could increase even further her energetic requirements and be detrimental to the development of her own young (Fleming and Rauscher 1978; Horrell and Bennett 1981; König et al. 1988; Mappes et al. 1995; Andersen et al. 2011).

This can be true in the opposite direction also. In many mammals, it is important for the early survival of the young that they quickly learn to recognize their own mother and to distinguish her from other conspecifics. The attempt to suckle from an alien mother, for example, may result not only in rejection but also in serious injury or even death (Le Boeuf et al. 1972; Wolski et al. 1980; Trillmich 1981; Harcourt 1992). Even for the young of solitary species that remain hidden in nests or dens, it can be vital that they remain quiet at the approach of predators or potentially infanticidal conspecifics and only respond positively to the approach of their mother (Sieber 1986, cf. Vaňková et al. 1997, Torriani et al. 2006 in ungulates).

Olfactory and vocal cues have been found to play a particularly important role in mother-offspring recognition. This is clearly the case and has been best studied in herd and colony-living species such as various pinnipeds (review in Insley et al. 2003; see also Charrier et al. 2010, Pitcher et al. 2010, Trimble and Insley 2010, Sauvé et al. 2015) where for mothers, identifying their own young among the throng of the colony is a daily task. Playback experiments in spotted hyenas have confirmed mutual vocal recognition between cubs and mothers/caretakers (Holekamp et al. 1999), and Hepper (1994) found mutual olfactory recognition in the domestic dog between mothers and young, which may last as long as 2 years after permanent separation.

However, less information is available on other taxonomic groups. This may be because the need for individual recognition between mothers and their offspring is less obvious for solitary than for social species. An exception is the domestic cat in which due to mothers readily permitting the handling and experimental manipulation of their newborn young by familiar caretakers, mutual olfactory recognition between mothers and young has also been found and that the young retain a memory of their mother's scent for more than a year after permanent separation (Bánszegi et al. 2017b; Jacinto et al. 2019; Szenczi et al. 2022). Mothers may also emit specific vocalizations to greet or call their young to follow and which the young rapidly learn to distinguish from similar calls from other mothers (Szenczi et al. 2016).

Alloparental Care

Care of the young may not only be by the mother or the breeding pair. Other, even unrelated members of a social group may also contribute to raising the young by helping guard, groom, carry, play with, nurse, or otherwise feed the offspring of others. The extent of cooperative care of young varies widely among carnivore species, ranging from joint breeding site defense to nursing and provisioning unrelated offspring (Clutton-Brock 2016). Both juveniles and adults may participate in alloparental behavior, while allolactators are frequently females who have lost their own young (Kleiman and Malcolm 1981; MacLeod et al. 2013).

Social carnivores in particular frequently show alloparental care, often accompanied by some degree of reproductive suppression in helpers (Montgomery et al. 2018). These include members of the canid, felid, herpestid, hyaenid, mustelid, and procyonid *families* (Rood 1978; Lukas and Clutton-Brock 2012; Federico et al. 2020). Among communal breeders, such as the African lion *Panthera leo*, the spotted and the brown hyenas, and the banded mongoose, most females breed during each reproductive cycle and participate in some degree of alloparental care although temporarily nonbreeding females and males may also contribute to the care of young born in the group (Mills 1990; Lewis and Pusey 1997). In facultative cooperative breeders such as the black-backed jackal *Canis mesomelas* and Arctic fox, the parents and nonbreeding helpers alike care for the young (Johnsingh 1982) although the number of helpers is small, and parents can successfully raise their young without helper assistance (Clutton-Brock 2006). Obligate cooperative breeders, such as the African wild dog and the meerkat *Suricata suricatta*, require assistance from nonbreeding helpers to successfully raise their offspring. In these species, nonbreeding helpers may even provide the majority of care, and their number typically exceeds the number of breeders (Lukas and Clutton-Brock 2012).

Weaning

The transition from a diet exclusively of milk to starting to obtain and ingest solid food is a crucial stage in the development of all mammalian young as it involves major changes in the behavior and physiology both of mothers and their offspring. An influential theory first proposed by Trivers (1974) essentially sees the weaning process as one of conflict between parents and young. It states that the optimal amount of parental investment in offspring is unequal for the two parties, such that offspring can be expected to try to obtain a greater amount of resources than their parents are willing to provide. However, the empirical evidence gathered since has refined this statement, leading to suggestions that the existence of such conflict might be overstated (Mock and Forbes 1992; Bateson 1994, 2014) and that the relationship between mother and offspring at weaning is more one of synchronization and cooperation than it is of conflict (Kölliker et al. 2005; Hinde et al. 2010; Cox and Hager 2016; Royle et al. 2016; Bánszegi et al. 2017a).

The young usually achieve considerable independence well before being completely weaned. They are able to digest solid food and to eliminate without maternal stimulation and can maintain an adequate body temperature without being brooded (Olmstead et al. 1979; Bateson 2014). Their locomotor abilities have also developed markedly (Peters 1983), increasing their ability to feed, hide, return to the nest, or defend themselves (Baerends-van Roon and Baerends 1979), probably boosting their confidence and leading them to increasingly explore unfamiliar environments (Romand and Ehret 1984). Hormonal changes of the mother during the lactational period may lead to a decline in her motivation to return to her young and in a reduction in her willingness to nurse, for example, by blocking access of the young to the nipples (Martin 1986; Bateson 2014), and to a reduction in responsiveness to their separation calls (Bánszegi et al. 2017a).

As weaning approaches, the content of the milk may change, generally increasing in fat and protein and decreasing in lactose as has been reported for several species, including humans (Neville et al. 1991; Verd et al. 2018). Information on this, however, is limited for *Carnivora*, with only a few studies of some seal species, probably stimulated by their sometimes extremely short nursing period. The change in milk composition during the weaning period is generally consistent with findings in other mammals although some decline in fat content has been found just before weaning (Bryden 1968; Riedman and Ortiz 1979; Carlini et al. 1994).

Postweaning Care

We continue the main theme of this chapter emphasizing the diversity of parental care among carnivores with a consideration of postweaning patterns leading to eventual independence of the young. In the pinnipeds, where information is available, the young rapidly achieve complete independence once they start a life at sea (Boness and Bowen 1996). However, in several other obligate carnivore taxa, most notably the *Felidae*, where the survival of the young will depend on their ability to hunt, learning the necessary skills may require the young to remain with their mother or other members of the group for a longer period. The degree of "teaching" such skills varies in carnivores. In pack-hunting species that often pursue large prey, the young can gain experience by merely joining the hunt, so the degree of teaching is relatively low. In contrast, young solitary hunters such as most *Felidae* have few opportunities to interact with live prey unless provided by adults, usually the mother; hence, the degree of teaching is high (Thornton and Raihani 2008).

Thus, among felids, behavior suggestive of teaching has been reported in tigers (Schaller 1967), cheetahs *Acinonyx jubatus* (Kruuk and Turner 1967), caracals *Caracal caracal* (Ewer 1969), black-footed cats *Felis nigripes,* and domestic cats (Leyhausen 1979; Caro 1980). Juvenile lions, tigers, and leopards begin to make hunting excursions with their mother at 12–15 months of age (Bekoff et al. 1984). Lionesses are reported to distinguish between serious hunts, with only adults participating, and training hunts, with juveniles following and watching adults in pursuit of prey (Schenkel 1966). Leyhausen (1979) has described in detail how female cats first only bring the prey and consume it in the presence of the young, then later allow them to interact with the already dead prey, and finally bring them live prey that is freed in their presence. The mother does not assist or interfere with the efforts of the young to kill the prey but brings it back if it escapes. Further suggestive evidence of teaching by bringing live prey to the young has also been reported in meerkats (Thornton and McAuliffe 2006), river otters *Lontra canadensis* (Liers 1951), the eastern spotted skunk *Spilogale putorius* (Thorne and Waggy 2017), and the dwarf mongoose *Helogale parvula* (Rood 1978), all of which hunt individually.

In contrast, there are no records of adult pack-hunting canids modifying their behavior in such a way as to promote learning when young are present at a hunt. The only anecdotal examples of teaching in canids are in bat-eared foxes and the red fox *Vulpes vulpes*, which forage individually for invertebrate and small vertebrate prey (Macdonald 1980; Nel 1999).

The importance of learning also depends on whether specialized techniques need to be used either because the prey is difficult to catch or might pose a danger to the hunter. Felids are known to often kill prey by precise bites to the nape, throat, or the snout (Kitchener et al. 2010), and meerkats kill potentially dangerous scorpions using a complex sequence of moves to avoid being stung (Thornton and Raihani 2008). In contrast, canids have less specialized canine teeth and bite the prey with more or less accuracy. As young canids can practice this relatively imprecise technique by joining the hunting pack, adults do not need to teach them and can feed them with regurgitated meat rather than by releasing live prey.

5 Conclusion

Given the diversity of carnivore lifestyles as illustrated by the various examples in this chapter, it is clear there is no typical pattern of carnivore parental care, not even within taxonomic *families*. From the view of general biology, notable in this respect is the lack of a clear correspondence between taxonomic groups and patterns of parental care, with the exception that while the *Canidae* have biparental care, often with other social support, in the *Felidae* – with the exception of the lion –, the three pinniped *families*, the *Ursidae,* and the *Mustelidae*, parental care is provided by the mother alone. Considering this diversity, caution must be taken not to inappropriately overgeneralize patterns of parental care from one particular species or taxonomic group, or from laboratory and highly domesticated or semidomesticated species, to other carnivores, or indeed to other mammals more broadly (see Macrì and Richter 2015 for a related warning regarding the use of a limited number of mammalian species and experimental paradigms in biomedical research). More studies are needed across a greater range of species and taxonomic groups and where possible in the natural conditions, or at least approximations of these, under which each species has evolved. The need for such studies is underlined by the important role of carnivores as apex predators in the food chain in many ecosystems and thus their key role in ecosystem management and conservation.

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