Chapter 12
Primatological Approaches to the Study of Group Coordination

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Abstract This chapter outlines why non-human primates provide some of the best comparative models for students of coordination in small human groups. It then summarises what and why non-human primates need to coordinate at the group level. From this review, group movements emerge as the major paradigm of primatologists in this study context. In this integrating chapter, the content of the contributions to Part III is placed within the broader context of this book on coordination in human and non-human primates.

12.1 Introduction

Many animals live in groups where a number of decisions need to be made at the group level on a regular basis. For example, many social insects collectively choose new nest sites, migrating birds agree on a common migration route, some carnivores and primates hunt cooperatively, and virtually all group-living species need to coordinate their daily activities and movements with each other (Conradt and Roper 2005; Kerth 2010). Human groups stand out from those of other animals in that human groups exhibit more diversity, complexity, and social dynamics than those of any other species, including those of non-human primates (i.e. the more than 400 species of lemurs, lorises, tarsiers, monkeys, and apes). Because human societies have their biological roots in the primate order (Chapais 2010), it is evident to evolutionary biologists that many aspects of human behaviour – especially those related to successful survival, reproduction, and parenting – have a more or less pronounced biological legacy (see, e.g. Kappeler et al. 2010). Comparative studies across different species can therefore help identify common principles in behavioural

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evolution, as well as unique, species-specific solutions. In the context of group decisions and coordination, recent broad comparisons across animal species have begun integrating relevant research on humans, revealing several fundamental insights regarding important variables that structure collective decision making (Conradt and List 2009).

At a more fine-grained level beyond our biological legacy, non-human primates are the obvious outgroup for obtaining comparative insights into fundamental mechanisms of group coordination that have also shaped human behaviour, specifically because humans and primates share many more features of their life history and socioecology than humans share with social insects or fish, for example. For instance, because human groups and those of other primates are on average much smaller than those of many other taxa, individuals recognise each other and they establish social relationships that last years or even decades (e.g. Jolly and Pride 1999; Silk et al. 2003). The main aims of this integrating chapter are to detail some of the reasons for the suitability of primates as a point of reference for students of human behaviour, to identify obvious limitations of this comparative approach, to explain the dominant research paradigm in primate group coordination studies, and to place the subsequent chapters on various aspects of primate group coordination within this overall framework.

Non-human primates not only exhibit great variation in social systems suitable for interesting comparative studies of adaptation across species, but they also share several traits that predestine them for comparisons with humans beyond the obvious close phylogenetic relationship. First, the majority of extant primates live in groups in which several males and females of different ages are permanently associated, a feature that distinguishes them from groups in the majority of other mammalian orders (van Schaik and Kappeler 1997). This type of social organisation creates conditions for a maximum of inter-individual conflicts of interest based on sex, age, rank, and reproductive status, leading to divergent interests regarding optimal behaviour that require coordination of activities. Second, non-human primate groups are also socially structured, with a variety of individualised competitive, affiliative, and mating relationships that can exacerbate conflicting interests. Third, non-human primates have some of the relatively largest brains among mammals, providing opportunities for more complex behavioural mechanisms and cognitive solutions of dyadic and group-level problems that resemble some of those observed among humans (Conradt and List 2009). Comparative studies among primates indeed support the hypothesis that large brain size has evolved to cope with the social problems created by increasingly large and complex groups (Dunbar and Shultz 2007; Shultz and Dunbar 2007). Fourth, non-human primates dispose of a great variety of communicative signals in different modalities (especially gestures and vocalisations), which are useful for the proximate regulation of group coordination. Finally, great apes (orangutans, gorillas, chimpanzees, and bonobos), uniquely among non-human primates, exhibit rudimentary forms of shared intentionality (Tomasello et al. 2005; see below), which underlies most cases of human group coordination. Thus, non-human primates share several key features of their social systems and life histories with humans that distinguish them from group-living insects, fish, or birds, which tend to rely on a limited set of mechanisms to achieve group coordination (Couzin et al. 2005).

What and why non-human primates need to coordinate at the group level can be explained primarily with respect to ecological factors. This may constitute a major difference to post-modern humans, where most coordinated group action has a social goal and function (see Chap. 7). Ecological factors that make group coordination in primates (as well as in other animals) advantageous can be related to the fundamental advantages of group living per se. Most primatologists agree that groups evolved from solitary or pair-living ancestors along with an evolutionary transition to diurnality, because living in groups confers several fundamental benefits that reduce per-capita predation risk (van Schaik 1983). Primates that became diurnal were faced with a new suite of predators, notably visually hunting raptors and large carnivores. Under these circumstances, aggregating into permanent groups (preferably with relatives to minimise the concomitant costs of sociality such as increased feeding competition) reduces the individual risk of being taken by a predator because of the dilution effect (Hamilton 1971): A single individual has a probability of one of being attacked by a predator it encounters; in a group of ten, this risk is reduced to 1/10. Animals in groups are also better at detecting an approaching predator and at confusing an attacking predator, and they can share vigilance, resulting in an overall increase in vigilance levels for the group while at the same time reducing the frequency of this costly behaviour for the individuals (Bertram 1978). Presumably secondary benefits of grouping include improved territorial defence against neighbours and new opportunities for cooperation, especially with kin. Only some primates, including our closest-living relatives (chimpanzees and bonobos), adopt a less cohesive, so-called fission-fusion lifestyle in response to relaxed predation risks and/or other selective pressures related to their feeding ecology (Aureli et al. 2008). Thus, the primary selfish aim of individuals in virtually all group-living primates is to maximise and maintain tight group cohesion.

The preservation imperative of group cohesion explains why non-human primates need to coordinate themselves at the group level. Inter-individual conflicts of interest, which are ultimately related to various costs of group living, exert a centrifugal force on group cohesion. These conflicts need to be reconciled at the group level to maintain cohesion. Selfish interests are therefore constrained by the trade-off that individuals face with respect to group cohesion. Because the potential costs of abandoning the safe harbour of a group will always outweigh the costs of foregoing a particular individual interest, group coordination is expected to be widespread (Conradt and Roper 2005; Conradt and List 2009).

Because non-human primates are relatively active, medium-sized mammals with relatively large energy-demanding brains, they need to spend most of their time searching and processing food. The size of a group's home range increases with group size and depends on their primary type of food, but all primate groups move several hundred metres in search of food, water, and suitable resting sites every day (Clutton-Brock and Harvey 1977). Because different classes of individuals within the group are thought to have diverging nutritional needs – compare, for example, a lactating female with a recently weaned juvenile – group movements provide the ecologically most salient context in which group coordination is required. Given that there are alternative, largely incompatible options for the subsequent activity (feeding, drinking, resting, socialising), and that for each subsequent activity there are alternative sites available (water hole a or b, feeding tree x or y), a consensus about the next destination must be reached. In addition, there may be conflicts about how much time to spend in each patch, such as when to move on, as some individuals need to drink or eat less or more than others. The overwhelming ecological significance of these decisions, along with their quantitative dominance, explains why primatologists have studied group coordination phenomena predominantly in the context of group movements (Petit and Bon 2010; see also Chap. 3).

In Chap. 13, Julia Fischer and Dietmar Zinner discuss communicative and cognitive aspects of group coordination within a single species. Also focusing on collective group movements, they briefly review different processes giving rise to collective activities in non-human primates and other animal groups. Their review outlines variations across species along several axes. Similar outcomes in different species can be characterised, for example, according to the level of self-organisation vs. explicit decision making, the level of the group (local vs. global) at which a decision is taken, whether individual interests overlap or diverge, or whether decisions are shared or unshared (see also Conradt and List 2009). Moving on to information transmission, they point out that both signals and cues can be important in bringing about a collective decision. They illustrate these different processes and mechanisms by reviewing recent studies of group movements in baboons. Because these animals live and move in an open, primarily two-dimensional habitat, group movements are comparatively easy to study, rendering a correspondingly large amount of detail for this taxon. Their chapter closes with a discussion of the cognitive underpinnings of collective decisions, and emphasises the lack of theory of mind and intentionality in non-human primates, which, in turn, compromise comparisons with many examples of human group coordination.

In Chap. 14, Juliane Kaminski highlights an experimental paradigm in great ape research that touches upon a critical difference between human and non-human primate group coordination: shared intentionality and its communication. Apart from language, humans also dispose of the ability to understand other individuals' mental states (theory of mind), both of which may facilitate group decisions and coordination on an explicit as well as implicit level (see Chap. 4 for a thorough treatment of this subject). The combination of the group members' individual brains in constructing shared goals is an aspect that uniquely characterises and facilitates human group coordination. The psychological mechanism underlying this effect, in combination with a prosocial disposition, defines shared intentionality (Tomasello et al. 2005). Kaminski discusses how the proximate behavioural mechanisms facilitating shared intentionality include gaze following, pointing, and other triadic gestural interactions. The existence of these behavioural building blocks of human uniqueness has been studied in several primate species, especially in great apes. Kaminski reviews these studies (and similar ones conducted with small children and dogs) in her chapter, emphasising the cognitive gap that separates *Homo sapiens* from other primates in this context. Differences at this level may explain the many unique functions and mechanisms of human group coordination discussed at length in the other contributions to this volume.

In the final chapter of Part III, Eckhard Heymann focuses on groups of non-human primates formed by members of two or more species within the broader context of safety and foraging. Such mixed-species groups are rare among primates, but they provide an interesting opportunity to study the mechanisms of group coordination because communication among different species is required. For humans, communication and coordination with members of other species may be relevant in the contexts of hunting, domestication, and animal training, but certainly to a less significant degree than among animals. Chapter 15 provides a summary of all known cases of regular heterospecific associations between non-human primates. His analysis of the potential costs and benefits confirms insights from similar studies in other taxa (e.g. Fitzgibbon 1990): By associating with a group of another species, a given group of primates can effectively double the anti-predator benefits without a pari passu increase to their ecological costs, because the cooperative species, by definition, exploit different feeding niches. Given these net benefits, Heymann goes on to explore with which behavioural mechanisms inter-specific coordination is achieved. It turns out that the exchange of loud calls appears to provide the main mechanism used by members of different species to establish and maintain spatial proximity and cohesion. Upon closer inspection, beyond the loose semblance of loud call exchange between inter-specific non-human primates and verbal communication among humans, more differences than similarities with human group coordination become apparent. These differences have to do primarily with the fact that the formation of shared mental states among non-human primates is unlikely.

The study of collective decision making and group coordination in non-human primates is still in a phase where inductive approaches predominate. Despite some early pioneering studies (e.g. Kummer 1968), this topic entered mainstream primatology only after stimulation provided by the publication of *On the Move* (Boinski and Garber 2000), an eye-opener to a fundamental problem in the behavioural ecology of all group-living animals, including non-human primates. The last decade has seen a diversification of study species and a sophistication of methods (see the summary provided in Chap. 3), but a predictive theoretical framework is still lacking. As exemplified by the non-human primate-oriented contributions to this volume, the communicative and cognitive mechanisms underlying group coordination have since been recognised as interesting topics. It is in these areas where comparative studies of non-human primates in particular can inform and inspire corresponding studies of humans. At the moment, the functional contexts of group coordination that are being studied differ too widely between humans and non-human primates for meaningful integration, although analytical models are being developed to do just that (see, for instance, Chaps. 2 and 4). One interesting approach towards bridging this gap could be the study of traditional human forager societies, who live in mobile camps with a median population of 26 individuals and migrate about seven times per year (Marlowe 2005). Thus, both collective group movements as well as all other communal decisions in the social domain could be profitably studied with a broad comparative perspective.

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