

Chapter 15

Coordination in Primate Mixed-Species Groups

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Abstract Groups formed by individuals from different species (mixed-species groups) are a widespread phenomenon amongst primates. Although the formation and maintenance of such mixed-species groups may incur costs to participating individuals, they render a net benefit, mainly through increased safety from predators and increased foraging efficiency. In contrast to the large number of studies that have examined the benefits and costs of primate mixed-species groups, there are still very few studies that have analysed the mechanisms of group coordination in mixed-species groups. Available evidence suggests that this coordination is mainly through vocal communication, but since the same vocalisations may be employed in intra-specific within-group and between-group communication as well as in inter-specific communication, it is difficult to analytically separate intra- and inter-specific coordination. The need for inter-specific coordination is likely to be highest when asymmetries in benefits from a mixed-species troop's formation are strong. Thus, "goal-dependent management of interdependencies" is necessary to maintain the integrity of mixed-species groups.

15.1 Introduction

Apart from forming groups with conspecifics, many vertebrates habitually associate with *heterospecifics*, that is, members of other species (fish: e.g. Krause et al. 2000; Parrish et al. 2002; birds: Powell 1985; Greenberg 2000; mammals: Stensland et al. 2003; Quérouil et al. 2008). In primates, such mixed-species groups, also known as *inter-specific* or *polyspecific associations*, are widespread amongst Neotropical and African rainforest monkeys but less common or absent in Malagasy lemurs and

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Asian monkeys (Struhsaker 1981; Waser 1987; Freed 2006; Haugaasen and Peres 2009). Such associations might occur randomly because groups from different species are simultaneously attracted to the same resources and endure for short times only (e.g. Whitesides 1989). However, there is strong evidence for non-randomness of many mixed-species groups (see Sect. 15.2), and many species spend considerable time, if not most of their activity period, in mutual association. Such mixed-species groups give rise to questions concerning their ultimate biological functions as well as the proximate mechanisms for the establishment and maintenance of association. This chapter first presents basic information on the occurrence of mixed-species groups amongst primates and then discusses their biological functions. It then addresses specific questions of coordination in mixed-species groups. Source references will be preferentially made to publications that have emerged since 2000, when the first review on this topic was published (Cords 2000).

15.2 Definition, Non-randomness, and Association Patterns

15.2.1 What Are Mixed-Species Groups?

In order to establish whether primates are found in a mixed-species group paradigm, primatologists usually define a criterion distance. Whenever members of different species are located at or within this criterion distance, the respective single-species groups are considered to be *inter-specific associated*. Criterion distances of 20, 25, and 50 m have been used in different primate studies. It is conceivable that a higher criterion distance results in finding primates more often in association.

15.2.2 Do Mixed-Species Groups Form Randomly?

To examine whether mixed-species groups occur by chance or not, *Waser's gas model* (Waser 1982) is usually employed. This model uses an analogy of primate group movements with the movements of a perfect gas and calculates expected rates of encounters between heterospecific groups with known mean travel speeds and mean group radii. From these variables, the mean duration of association and the expected proportion of time spent in association can be derived and compared to the observed time spent in association (Whitesides 1989; Holenweg et al. 1996).

While the application of Waser's gas model has been instrumental in testing for the randomness of associations, its weaknesses are also immediately apparent. Primate groups do not usually move randomly (as gas molecules do) through their home ranges. Movements can be goal-oriented, with food and water resources,

neighbouring groups, shelters, and sleeping sites constituting goals (Garber 2000; Janson 2000). If two species overlap at least partially in the temporal distribution of their activities, if they are attracted to the same goal, if there is a limited set of optimal travel routes between different goals, or if similar mental maps are used for navigation, then groups from different species could meet or associate more often than predicted by chance alone (DiFiore and Suarez 2007). A more conservative test for non-randomness of associations should thus include “attractors” and travel decisions derived from optimal foraging theory. It is likely that for those associations where species spend most or all of their time in association (see Sect. 15.2.3), and where active establishment of association takes place (see Sect. 15.4.1), even more conservative tests will demonstrate nonrandomness of association.

15.2.3 Association Patterns

Primate mixed-species groups are usually composed of members from two or three (rarely more) different species. Participating species may come from the same genus (congeneric mixed-species groups: e.g. *Cercopithecus ascanius* – *Cercopithecus mitis*, *Saguinus mystax* – *Saguinus fuscicollis*) or may stem from different genera (heterogeneric mixed-species groups: e.g. *Cercopithecus diana* – *Procolobus badius*, *Saimiri boliviensis* – *Cebus apella*). The differentiation between congeneric and heterogeneric mixed-species groups is relevant for the comparison of costs for the establishment and maintenance of mixed-species groups (see Sect. 15.3.2).

Mixed-species groups can always be formed by same single-species groups, or a group from one species may associate with various groups of another species at different times. In the former case, for instance, in congeneric mixed-species groups of the genus *Saguinus*, home ranges (i.e. the area in which a group resides) of the participating groups are usually of the same size and overlap completely or almost so. In the latter case, for instance, in heterogeneric mixed-species groups of *S. boliviensis* and *C. apella*, *Callimico goeldii* and *Saguinus labiatus/S. fuscicollis*, or *Procolobus rufomitratu*s and *Cercopithecus ascanius*, home ranges are of different sizes. In this case, home ranges of groups of one of the participating species (*S. boliviensis*, *C. goeldii*, *P. rufomitratu*s) overlap with the home ranges of several groups of the other species (*C. apella*, *S. labiatus/S. fuscicollis*, *C. ascanius*) (Podolsky 1990; Porter 2001; Teelen 2007). This pattern also has implications for the costs and benefits of mixed-species groups (see Sect. 15.3).

The time spent in mixed-species groups varies considerably, not only between different species combinations but also between populations and different groups (see Table 15.1). In mixed-species groups formed by members of the genus *Saguinus*, the time spent in association may vary between almost 100% and as little as 19% (Heymann and Buchanan-Smith 2000). Similarly, different species of *Cercopithecus* may spend almost all their active time (i.e. between leaving and entering a sleeping site) in mixed-species groups or associate less frequently

Table 15.1 Examples for variation of time spent in mixed-species groups

Species combination	% of time spent in mixed-species groups	Source of variation	References
<i>Saguinus mystax</i> + <i>Saguinus fuscicollis</i>	89–93	Group	Smith et al. (2005)
<i>Saguinus labiatus</i> + <i>Saguinus fuscicollis</i>	43–57	Group	Pook and Pook (1982)
	50–70	Group	Porter (2001)
	0–63	Season	Rehg (2006)
<i>Saguinus imperator</i> + <i>Saguinus fuscicollis</i>	19		Windfelder (1997)
<i>Callimico goeldii</i> + <i>Saguinus fuscicollis</i> + <i>Saguinus labiatus</i>	13–89	Season	Porter (2001)
	24–100	Season	Rehg (2006)
<i>Callimico goeldii</i> + <i>Saguinus fuscicollis</i>	21–22	Group	Porter (2001)
	0–12	Season	Rehg (2006)
<i>Callimico goeldii</i> + <i>Saguinus labiatus</i>	0–7	Season	Rehg 2006
<i>Cercopithecus ascanius</i> + <i>Cercopithecus mitis</i>	18–74	Population	Cords (1990)
	0–30	Population	Chapman and Chapman (2000)
<i>Cercopithecus mitis</i> + <i>Cercopithecus ascanius</i>	11–49	Population	Cords 1990
	22–25	Population	Chapman and Chapman (2000)
<i>Cercopithecus ascanius</i> + <i>Procolobus tephrosceles</i>	3–50	Population	Chapman and Chapman (2000)
<i>Procolobus tephrosceles</i> + <i>Cercopithecus ascanius</i>	12–32	Population	Chapman and Chapman (2000)
<i>Procolobus tephrosceles</i> + <i>Cercopithecus mitis</i>	0–9	Population	Chapman and Chapman (2000)
<i>Cercopithecus diana</i> + <i>Cercopithecus campbelli</i>	56–87	Group	Wolters and Zuberbühler (2003)
<i>Cercopithecus diana</i> + <i>Procolobus badius</i>	31–72	Season	Wachter et al. (1997)

(Gautier-Hion et al. 1983). Differences in body size (as a proxy for ecological differences) and the degree of overlap in the plant portion of the diet seem to be determinants of the permanency of congeneric mixed-species groups. For example, *S. mystax* and *S. fuscicollis* differ strongly in body size and spend most of their time in association, whereas *Saguinus imperator* and *S. fuscicollis* differ much less in size and spend more time in single-species than in mixed-species groups (Heymann 1997). The time spent in mixed-species groups in different populations of *C. ascanius* and *C. mitis* and in different months of the year within the same population of these two species increases with the amount of overlap in the plant diet (Struhsaker 1981; Cords 1990). This is in contrast to heterogeneric mixed-species groups of *C. diana* and *P. badius*, where the time spent in association does not correlate with diet overlap (Wachter et al. 1997).

Mixed-species groups of birds (called “mixed flocks” by ornithologists) generally consist of many more species than primate mixed-species groups. In temperate

zones, 10–15 (and in the tropics, as many as 100) different bird species can constitute these mixed flocks (see Greenberg 2000 for review). Similar to primates, it is almost always only one group per species that participates in mixed-species bird groups. However, in contrast to primates, the number of individuals per species is generally much lower; usually, only a pair or a family associate with other species, and sometimes only solitary individuals join mixed flocks (Terborgh 1990). Some species may participate more consistently in mixed flocks and may be more attractive to other species (“nuclear species” or “core species”) while others join and follow less consistently (“attendant species”; Greenberg 2000). Home range or territory size seems to be the principal factor limiting participation in mixed flocks (Powell 1979; Pomara et al. 2007). Groups of species with smaller home ranges appear to attend mixed flocks only when groups of species with larger home ranges pass through the area. Noteworthy is that this pattern is similar to some mixed-species groups in primates.

15.3 Benefits and Costs for Primates in Mixed-Species Groups

15.3.1 Benefits

The benefits of mixed-species groups in primates can be grouped into two categories: benefits related to the reduction of the predation risk, and benefits related to an increase in foraging and feeding efficiency.

15.3.1.1 Reduction of Predation Risk

A reduction of the per capita predation risk mainly results from the increase in group size through associating with heterospecifics (see Table 15.2). Demonstrating the action of the “dilution effect” and the “confusion effect” (see Caro 2005 for examples of these effects in other animals) would require comparing predation rates between single-species and mixed-species groups. For several reasons, this is often difficult, if not impossible, however. First, successful predation events are rarely observed, hampering any meaningful statistical comparison. Second, species might tend to associate when the predation risk is high, and to live in single-species groups when the predation risk is low. This problem could only be overcome by estimating the hunting efforts of predators. In fact, Noë and Bshary (1997) have shown that *P. badius* associate more often with *C. diana* during seasons of the year when chimpanzees – a principal predator of *P. badius* but not of *C. diana* – are more likely to hunt.

A reduction in the predation risk can also be obtained through the “improved detection effect,” as large groups are more likely to detect an approaching

Table 15.2 Potential benefits of primate mixed-species group

Reduction of predation risk	<p>“Dilution effect”: Risk of being attacked and preyed upon decreases with increasing group size</p> <p>“Confusion effect”: Confusion of an attacking predator increases with increasing group size</p> <p>Vigilance-related effects: “Detection effect”: probability of detecting a predator increases with groups size due to increased vigilance (“more eyes see more”) Differential and complementary species-specific vigilance Eavesdropping on other species’ alarm calls Joint defence against predators (mobbing, attacks)</p>
Increased foraging and feeding efficiency	<p>Access to habitats and resources that are not available to single-species groups</p> <p>Increased encounter rates with resources: Probability of detection of resources increases with group size Exploitation of other species’ knowledge of resource distribution in habitat Scrounging resources detected by the other species Exploitation of feeding residuals of other species Exploitation of prey flushed by other species</p> <p>Increased rates of feeding and foraging (Avoiding visits to resources exhausted by other species (Increased resource defence)</p>
Reduced risk of parasitism	<p>Risk of being attacked by blood-sucking insects decreases with group size</p>

predator than small groups. This effect is the result of more individuals being vigilant at any point in time in a larger group (“more eyes and ears”) and a larger space being surveyed by a larger group. Benefits of improved detection can be asymmetric between species if individuals of one species show consistently higher levels of vigilance than individuals of the other species (Smith et al. 2004).

Vigilance-related effects can be more easily tested than the previously mentioned dilution and confusion effects by comparing rates of vigilance in and out of association, although this may become difficult in species that are almost permanently associated. Benefits of improved detection might also be confounded by species tending to associate in relation to the current predation risk (see above). Additionally, apart from protection against predators, vigilance may function against potential conspecific competitors. However, in this case individual rates of vigilance are expected to increase in mixed-species groups, as has in fact been observed in *C. ascanius* (Chapman and Chapman 1996).

The results of various studies have provided support for an antipredator function of associations. First, experiments that examined vigilance in and out of association in captive *S. labiatus* and *S. fuscicollis* revealed that when in association, more time was covered by at least one individual being vigilant compared to single-species

groups, and at the same time the per capita costs of vigilance (time spent vigilant) were reduced (Hardie and Buchanan-Smith 1997). Similarly, wild *C. diana* and *S. mystax*, respectively, increased the time spent being vigilant when not associated with *Cercopithecus campbelli* and *S. fuscicollis*, respectively (Wolters and Zuberbühler 2003; Stojan-Dolar and Heymann 2010). Second, ranging at different forest strata can provide an additional advantage of mixed-species group formation. It has been shown in associations of tamarins and of guenons that species ranging lower in the forest are more likely to detect terrestrial predators, whereas species ranging in higher strata are more likely to detect aerial predators (Gautier-Hion et al. 1983; Peres 1993). Third, individuals living in mixed-species groups can also benefit from eavesdropping on the alarm-calling behaviour of the other species. For example, *C. diana* respond to the alarm calls of associated *C. campbelli* (Zuberbühler 2000), and *S. mystax* and *S. fuscicollis* mutually understand and respond to each others' alarm calls (Kirchhof and Hammerschmidt 2006). Finally, forces can be combined in association to attack and dissuade predators such as through joint attacks or mobbing of adult males from the different associated species (Eckardt and Zuberbühler 2004).

15.3.1.2 Increased Foraging and Feeding Efficiency

The formation of mixed-species groups may also render benefits in terms of increased foraging and feeding efficiency. These benefits can result from access to habitats and resources that are not accessible while ranging in single-species groups, or from increased encounter rates with food resources (Table 15.1).

Several observations support these predictions. For example, *Callimico goeldii* expand their habitat use when in association with *S. fuscicollis* and *S. labiatus*, and as a consequence have higher rates of fruit feeding while in association (Porter and Garber 2007). The arboreal *P. badius* and *C. diana* descend to lower forest strata and the forest floor more often while associated with the terrestrial *Cercocebus atys*, which gives them access to termite mounds (McGraw and Bshary 2002). It is conceivable that these foraging benefits are an indirect consequence of anti-predator benefits: The presence of heterospecific individuals provides increased safety in habitats that are usually avoided or used very infrequently.

Increased encounter rates with food resources may simply result from increased group size, as the higher number of individuals in an association increases the likelihood of detecting a food resource that can also be exploited by heterospecific group members. However, this has not yet been demonstrated.

It is also conceivable that members of one species may also have a superior knowledge of the location and availability of food resources, which can then be exploited by the other species in the association. This is particularly likely when the associated species differ in the size of their home ranges. In this case, the species with the smaller home range is expected to have better local knowledge and can therefore be exploited as a “guide” by the other species. *Cercopithecus ascanius*

may use *C. mitis* as guides to food resources in cases where they have the larger home ranges, but the pattern is reversed in areas where *C. mitis* has the larger home ranges (Cords 1987). *Saimiri boliviensis* are led into large food patches by *C. apella* and *Cebus albifrons* (Podolsky 1990), these two species having much smaller home ranges than *S. boliviensis*. Similarly, *C. goeldii* – with large home ranges (150 ha) – probably exploit the knowledge about the location and abundance of food resources of *S. labiatus* and *S. fuscicollis*, who have much smaller home ranges (Porter 2001). In these cases, the net benefits of association are clearly asymmetrically distributed between species.

But even when home range size is similar or identical, as with *S. mystax* and *S. fuscicollis*, species may benefit from resource detection by others. *Saguinus mystax* initiate more feeding bouts than *S. fuscicollis*, which is obviously a benefit to the latter (Peres 1996). Conversely, *S. mystax* – travelling on average higher in the canopy than *S. fuscicollis* – scrounge on small resources in the lower forest strata detected by *S. fuscicollis*. In the extreme case, this scrounging may lead to the exclusion of the detecting species from the food resource (Peres 1996; Heymann, personal observations).

Associated species may also exploit dropped feeding residuals or prey flushed by the other species. *Saimiri boliviensis* gain access to the pulp of hard palm fruits that are opened, only partially eaten, and then dropped by *Cebus* (Terborgh 1983). *Saguinus fuscicollis* obtain a substantial proportion of their prey through capturing insects that escape from *S. mystax* (Peres 1992a; Heymann, personal observations).

Other potential benefits related to foraging and feeding have been seen with respect to avoided visits to exhausted food resources that might have otherwise occurred if travelling in single-species groups, as well as joint resource defence. The former is conceivable, but principally not testable and thus has no heuristic value. The latter is unlikely, since aggressive interactions during the defence of resources against other mixed-species groups usually take place within, not between, species.

15.3.1.3 Other Potential Benefits

Based on the correlation between temporal patterns of association and the activity of blood-sucking insects, Freeland (1977) suggested that mixed-species groups formed by mangabeys, *Cercocebus albigena*, with other primates in the Kibale Forest (Uganda) are a means of reducing the number of insect bites received by individual mangabeys. This suggestion has not received any further testing, however.

15.3.2 Costs of Mixed-Species Groups

The potential costs of mixed-species groups have received considerably less empirical attention than the benefits. This is not surprising, as it can be reasonably assumed that whenever species associate regularly with each other, the benefits

must exceed the costs or there would be counter-selection against mixed-species group formation. Nevertheless, it is likely that – as is true in other forms of sociality – mixed-species groups do incur some costs, including increased direct (e.g. interference) and indirect (e.g. scramble) feeding competition, increased conspicuousness to potential predators, and higher risks of parasite transmission (Danchin et al. 2008) (Table 15.3).

In mixed-species of tamarins, the smaller species (*S. fuscicollis*, *C. goeldii*) are occasionally supplanted from food resources by the larger species (*S. mystax*, *S. labiatus* or *S. imperator*), but the rate of such interactions appears to be very low (Terborgh 1983; Heymann 1990; Peres 1996; Porter 2001). In an experimental study of *S. fuscicollis* and *S. imperator*, Bicca-Marques and Garber (2003) offered food on feeding platforms, measured the time spent on the platform and the number of individuals per species on the platform, and compared visits in single- and mixed-species groups. While the time spent on the platform was decreased in mixed-species groups for both *S. fuscicollis* and *S. imperator*, the number of individuals visiting the platform decreased in mixed-species groups for *S. fuscicollis*, but not for *S. imperator*. This indicates that the foraging costs of mixed-species group formation are less severe for the latter species. *Cercopithecus diana* and *C. campbelli* increase their daily travel path length when associated, although this has been interpreted as an anti-predator benefit of their association rather than a foraging cost (Wolters and Zuberbühler 2003). *Cercopithecus nictitans* have a narrower breadth of the feeding niche when associated with *C. diana*, which may reflect both interference and scramble competition (Eckardt and Zuberbühler 2004).

As previously mentioned, mixed-species groups might also be more conspicuous to predators than single-species groups, but this cost is certainly exceeded by the

Table 15.3 Potential costs of primate mixed-species group

Increased feeding competition	Direct or contest or interference competition: Some individuals can exclude others from resources due to superior strength and dominance; per capita food intake decreases with group size for individuals of the smaller/subordinate species
	Indirect or scramble or exploitation competition: Individuals have reduced access to resources because these have already been exploited by others; per capita food intake decreases with group size, but in the same way for all group members
Increased risk of predation	Larger groups produce more movement and noise and thus become more conspicuous to potential predators Calling to establish or to maintain association makes callers more conspicuous to potential predators
Increased risk of parasite transmission	Risk of transmission of directly transmitted parasites increases with increasing group size
Increased energy expenditure	Feeding competition results in longer daily path length, because groups have to travel further to obtain a sufficient amount of food Maintaining the association requires additional travelling when foraging goals differ between species Energetic costs of call production to establish or to maintain association

benefits resulting from mechanisms that reduce the predation risk in association (see Sect. 15.3.1.1).

Costs may also result from the behavioural efforts of establishing and maintaining association. For instance, mixed-species group establishment is often realised through the emission and exchange of loud calls (see Sect. 15.4.1), which could be energetically costly and make callers more conspicuous to acoustically orienting predators. Maintaining the association may require travelling to resources exploited by only one of the associated species. This is particularly likely in heterogeneric associations, where species differ more strongly in their food requirements (e.g. associations between the frugivorous-insectivorous *C. diana* and the folivorous *P. badius*) than in congeneric associations.

15.3.3 Consequences of Symmetry and Asymmetry of Net Benefits

Evidently, the balance between the benefits and costs of living in mixed-species groups must be tipped towards the benefits. Nevertheless, the magnitude of the net benefit can obviously vary between species; in other words, there can be an asymmetry in the benefits, as shown by examples provided in Sects. 15.3.1 and 15.3.2. This has obvious implications for questions of coordination in mixed-species groups. Members of species with a higher net benefit can be predicted to be more highly motivated to establish association and to take a more active role in inter-specific coordination.

15.4 Coordination in Mixed-Species Groups

One of the basic problems of group living – the need for coordination between individuals from different age/sex classes with different social and reproductive interests and strategies, physiological and metabolic needs, and foraging strategies – is acuminated in mixed-species groups. Here, not only the interests and needs of different age-sex classes of one species have to be reconciled, but also those of individuals from two or more species.

In studies of coordination in single-species groups, usually individual contributions to coordination are examined. In contrast, studies on coordination in mixed-species groups have generally focussed on the contribution of species instead of individuals (Cords 2000). This is surprising since it can be reasonably assumed that the balance of benefits and costs of mixed-species groups varies between different age-sex classes despite the expected net benefit for all individuals.

There are two principal contexts in which there is a need for coordination between species (see also Cords 2000):

1. Establishing/re-establishing the association. Associated species usually spend the night in different sleeping sites that can be some distance apart, making it

necessary to establish or re-establish association the next morning (e.g. Porter 2001; Smith et al. 2007). Also, associated species may become separated after travelling in different directions or through disruptive events such as inter-group encounters or predator attacks.

2. Maintaining association. Animals have to decide in which direction to travel, which food resources to visit, and how long to stay in a patch. Also, they have to decide when and where to rest and to sleep. For congeneric associations (e.g. *S. mystax* – *S. fuscicollis*, *C. diana* – *C. campbelli*), similar ecological and physiological requirements may make coordination less costly than for heterocongeneric associations (e.g. *C. diana* – *P. badius*), where different dietary strategies (frugivory-insectivory vs. folivory) and different physiological processes (digestion of easily digestible fruit pulp vs. stodgy leaves) might actually dictate different optimal travel routes and activity budgets.

15.4.1 Coordination Through Inter-specific Vocal Communication

When associated species are ecologically similar and have a large overlap in their diet, coordinated travelling may simply be a by product of the convergence of optimal travel routes imposed by the local distribution of food resources. In this case, no communication would be expected to take place between species. However, most studies on primate mixed-species groups have noted that communication actually takes place between members of different species, further supporting the contention that many mixed-species groups do not simply represent the result of random encounters. Specifically, loud calls are used as a means of establishing/re-establishing association (see Cords 2000 for review).

Loud calls are often given in the early morning before or shortly after leaving a sleeping site (e.g. Gautier and Gautier-Hion 1983; Heymann 1990; see Cords 2000 for additional references). These calls can be exchanged before the association is established. In some mixed-species groups of *Cercopithecus*, adult males seem to initiate the association through inter-specific loud calling (Gautier and Gautier-Hion 1983). This can be understood from the special role of adult males in these primates in the defence against predators. Through association with other species, additional males can be recruited for joint defence against predators without increasing reproductive competition. Nothing is known about individual or at least sex-specific contributions to loud calling in other associations.

In associations between *Cercopithecus pogonias* and *Cercopithecus neglectus*, loud calling is more often initiated by males of the former species (Gautier and Gautier-Hion 1983). The authors did not link this to any obvious asymmetries in the benefits obtained from mixed-species group formation. However, it could be predicted that the tendency to take an active role, such as by initiating loud calling or calling more frequently, in establishing an association should be more strongly developed in members of those species for which the net benefit of associating is higher. In line with this prediction, *C. goeldii* initiates association with *S. labiatus*

and *S. fuscicollis* in the morning through loud calling in two thirds of records (Porter 2001). When a group of *C. goeldii* – which has much larger home ranges than *S. labiatus* and *S. fuscicollis* – abandons its association with one *Saguinus* group, it gives loud calls during travelling until it encounters another *Saguinus* group (Porter 2001). In associations between *S. fuscicollis* and *S. mystax*, the former species probably obtains a higher net benefit (Peres 1992a, b). Nevertheless, no clear support for a more active role of one species in establishing association through loud calling has been found (Heymann 1990), although Koch (2005) reported a trend towards *S. mystax* more often initiating calling, contradicting the net benefit prediction. Strong asymmetries in loud calling have been reported for mixed-species groups of *Cercopithecus* (Gautier-Hion 1988), but have not been linked to differential net benefits of association.

Through observational studies alone, it is difficult to tease apart whether apparently mutual loud calling is motivated by the interest in establishing association with another species or by an interest to communicate with neighbouring groups of the same species. Even if there is coincidental counter-calling between associates, this could potentially result from simultaneous but independent responses to loud calls from members of neighbouring groups of the respective species. However, support for a role of loud calling in establishing association has been provided through an experimental study of *S. fuscicollis* and *S. imperator*. Both species loud-called in response to playbacks of loud calls from the other species and approached the speaker following playbacks (Windfelder 2001). While *S. fuscicollis* responded slightly stronger to playbacks, *S. imperator* showed a higher tendency to approach the speaker (Windfelder 2001).

The distance by which two species are separated may influence the need for coordination and thus the tendency for loud calling. In mixed-species groups of *S. fuscicollis* and *S. mystax*, no loud calls are given on mornings when the single-species groups had used sleeping sites that were less than 20 m apart (Heymann 1990). When the species are close together, visual information or low-pitched vocalisations may suffice for rapidly establishing an association. When the species are further apart, loud calling will be necessary for establishing association. In line with this assumption, the two species took significantly longer to establish association than when no loud calling occurred (Heymann 1990). Obviously, the need for coordination is stronger when the two species are separated by greater distances.

Based on this finding, Koch (2005) examined the possibility that rather than different strengths of motivation for initiating calling, differential information on the whereabouts of the other species could be responsible for which species initiates loud calling. In mixed-species groups of *S. fuscicollis* and *S. mystax*, the single-species groups separate at variable times before they enter into their respective sleeping sites. Depending on how long before retiring the groups separate, or whether one species is present while the other species retires, information on the location of the sleeping site of the other species should vary. The species with less information should be more motivated to initiate loud calling. Three different conditions could be distinguished (1) *S. mystax* has information about the location of the sleeping site of *S. fuscicollis*, but not vice versa; (2) *S. fuscicollis* has information about the location of the sleeping site of *S. mystax*, but not vice

versa; (3) neither species has information about the location of the sleeping site of the other species. In condition (1), *S. fuscicollis* should initiate loud calling more often; in condition (2), *S. mystax* should initiate loud calling more often; and in condition (3), both species should initiate calling equally often. However, these predictions were not supported by the data (Koch 2005). This may indicate either that the assumptions underlying this hypothesis were wrong or that the observer's rating of what the species may know about the whereabouts of the other species does not accurately reflect the actual situation.

After prolonged resting periods, both *S. fuscicollis* and *S. mystax* usually utter low-pitched vocalisations ("contact calls") before starting to move; this happens whether or not the species are associated (personal observations). While these vocalisations probably serve a function in intraspecific coordination, it is currently not known whether they also function in the coordination of movements of the mixed-species group.

During travelling, associated species may have to decide upon the direction of travel. Loud calling and countercalling during travel, even when in spatial proximity, may reflect coordination and decision making, but the possibility that loud calling is stimulated independently in the associated species through listening to loud calls from neighbouring groups not perceived by observers is difficult to exclude. Male *C. pogonias*, giving more loud calls than males from the associated species, may have a prominent role in the coordination of travel (Gautier and Gautier-Hion 1983). The difficulty of separating intra- and interspecific functions has hindered further analyses of the role of vocalisations in interspecific coordination during travel so far. Experimental approaches such as playback experiments are unlikely to render solutions. When travelling together, species do have information on the other species. Thus, playbacks create a situation in which existing information and information simulated by the playback can be contradictory, may create confusion, and therefore elicit inappropriate responses.

It is noteworthy that in some mixed-species groups no evidence has been found (or reported) for a role of loud calls in coordination, which might be related to the stability, permanency, and composition of the mixed-species groups concerned (see Cords 2000 for review). Loud calling should be used in more stable and permanent mixed-species groups, or where particular groups are always associated with each other, but Cords (2000) also pointed to the fact that this does not fit all mixed-species groups. Specifically, mixed-species groups of *C. goeldii* with *Saguinus* are not very permanent and stable, and a single group of *C. goeldii* may associate with several groups of *S. fuscicollis*/*S. labiatus* at different times, but nevertheless loud calling is employed for establishing association (see above). This seems to indicate that the relationship among association patterns (stability, permanency, and composition of the mixed-species groups), the net benefits, and the coordination/communication effort are quite complex. When the degree of association is low, this may mean for one species that the net benefit is low and thus little effort (loud calling) is spent establishing and maintaining association (this could be the case for *Cercopithecus cephus*; Gautier and Gautier-Hion 1983). However, it may also mean that the establishment and maintenance of mixed-species groups are

constrained such as through the temporal use of very specific habitats (as, in the case of *C. goeldii*, bamboo forests that are not entered by potential association partners), but that whenever the opportunity for establishing a mixed-species group arises, corresponding efforts are made.

The diversity of findings with regard to whether or not loud calls are used for interspecific coordination may reflect different stages in the evolution of interspecific communication, as suggested by Kostan (2002). These stages range from “unidirectional assessment” to “symmetric communication”; which stage is reached actually depends on the benefits and costs of the interspecific interaction (Kostan 2002). It is also feasible that our less than clear understanding of the findings can be due to communication motives that have yet to be identified.

15.4.2 Is There Really Interspecific Coordination?

Loud calling and countercalling as described in the previous section clearly indicate that there is a strong attraction between species or at least of one species to another. But if coordination is defined as “the goal-dependent management of interdependencies by means of hierarchically and sequentially regulated action in order to achieve a common goal” (Chap. 1), is there any evidence for coordination in mixed-species groups? At an abstract deductive level, common goals can be defined in mixed-species groups as the results of those activities that lead to benefits to individuals from participating species (e.g. predator avoidance, increased foraging efficiency). On a more concrete level, common goals can be resources to be visited or routes to be taken. It is, however, more difficult to identify whether there are actions that are hierarchically and sequentially regulated. Calling and countercalling may be seen as sequential actions, but as has been pointed out, they are not necessarily hierarchical.

It is conceivable that despite the benefits that can be achieved through the formation of mixed-species groups, the needs for coordination and the rules for coordination are much simpler than in single-species groups. Individuals of gregarious species usually depend on living with conspecifics for survival and reproduction, making sociality obligatory. The formation of mixed-species groups can bring substantial benefits that may directly enhance survival and indirectly also enhance reproduction. However, mixed-species groups are unlikely to be a condition for survival, and they are definitely not a condition for reproduction. Thus, mixed-species groups can be a facultative form of sociality, and selection pressures on effective interspecific coordination are likely to be much weaker than on intraspecific coordination.

Finally, the definition of coordination itself might be conceptually less appropriate for mixed-species groups because different levels of goals are present, which may more easily come into conflict compared to single-species groups. On an abstract level, members of species participating in mixed-species groups can be said to have a general common goal, namely, to obtain the benefits of mixed-species groups. This common goal might vary in response to environmental fluctuations (e.g. predator

density or attack rates; seasonal variation in food abundance) but should always be present – otherwise, there would be no motivation for forming mixed-species groups. On a more concrete level, specific goals, such as visiting specific resources or taking specific travel routes, may coincide between species in a mixed-species group if, for instance, a limited number of optimal travel routes synchronise and synlocalise the species (so-called pseudo-coordination). If the participating species do not converge on concrete goals, conflict may arise – a situation where the need for coordination would be the strongest.

15.4.3 Inter-specific Coordination in Mixed-Species Groups of Birds

The formation of mixed-species groups is a widespread phenomenon, but detailed behavioural studies that may cast some light on the patterns and mechanisms of coordination are very rare (Stensland et al. 2003). As with primates, vocalisations seem to play a key role in bird mixed-species groups (for a review, see Greenberg 2000). This is suggested by the observation that mixed-species groups of birds begin to assemble during the dawn chorus (Munn and Terborgh 1979). Furthermore, particular bird species give loud calls in the morning that may attract other species (Munn 1985). High vocalisation rates of the “nuclear species” (see Sect. 15.2.3) could promote the cohesion of mixed-species groups during travel (Greenberg 2000). But as with primates, it might be difficult to disentangle intra-specific from inter-specific functions of loud calls and other vocalisations. Since bird mixed-species groups generally include many more species than primate mixed-species groups (sometimes 30 or more; see Sect. 15.2.3), any attempt to disentangle these functions is practically impossible.

It has also been suggested that conspicuous visual displays of some bird species may attract others into mixed species and may also facilitate maintenance of association (Moynihan 1962), but this hypothesis has received little support (Greenberg 2000).

An interesting case of “coordination” has been reported by Goodale and Kotagama (2006) for drongos, *Dicrurus paradiseus*. These birds mimic the songs and contact calls of other birds that are participating in mixed-species groups. The vocal mimicry attracts other birds into the association more strongly than drongo calls alone. Researchers consider this to be “behavioural management” of other species by drongos in an overall mutualistic relationship (Goodale and Kotagama 2006).

15.5 General Conclusions

Although mixed-species groups of primates are amongst the best-studied mixed-species groups (Stensland et al. 2003), it is still very difficult to paint a general picture of inter-specific coordination. It is established that coordination is principally

through vocalisations, specifically loud calling. While there might be some observational bias (vocalisations are more easily observed and recorded than facial expressions or olfactory signals), it is plausible to assume that under the conditions of reduced visibility in tropical rainforests – the places where practically all mixed-species groups of primates exist – vocalisations are better suited for coordination than other modes of communication. In this respect, coordination between species does not obviously differ from communication within species. Furthermore, the same vocalisations (mainly loud calls) are employed for coordination within and between species. Interestingly, within-species loud calls are used in both within-group and between-group communication. Whereas this observation indicates that interspecific communication in the context of mixed-species group coordination can build upon available mechanisms, it makes the analysis of this coordination even more complicated. In many instances it can be difficult or impossible to determine whether the intended receivers of loud calling are members of the same group, members of another group of the same species, or members of another species. This added complication may be one of the reasons why detailed studies on coordination in primate mixed-species groups are still very rare.

We can be rather certain that coordination efforts in primate mixed-species groups are done in an effort to obtain the benefits of such groups, be it reduced predation risk, increased foraging and feeding efficiency, or reduced insect bites. These motivators fit the coordination definition of “goal-dependent management of interdependencies” (see Chap. 1), but, as has been discussed, it is more questionable whether they are “hierarchically and sequentially regulated actions in order to achieve a common goal.” Observed imbalances or asymmetries in benefits may mean that the goals achieved can be less than common. It is exactly this point where the study of coordination in mixed-species groups might contribute to the understanding of coordination in humans.

Appendix: Index of Scientific and Common Names of Primates Mentioned in the Text

Scientific name	Common name
<i>Callimico goeldii</i>	Goeldi's monkey
<i>Cebus albifrons</i>	White-fronted capuchin
<i>Cebus apella</i>	Brown capuchin
<i>Cercopithecus ascanius</i>	Red-tailed guenon
<i>Cercopithecus campbelli</i>	Campbell's monkey
<i>Cercopithecus diana</i>	Diana monkey
<i>Cercopithecus nictitans</i>	Putty-nosed monkey
<i>Cercopithecus pogonias</i>	Crowned guenon
<i>Procolobus badius</i>	Red colobus
<i>Saguinus fuscicollis</i>	Saddleback tamarin

(continued)

Scientific name	Common name
<i>Saguinus imperator</i>	Emperor tamarin
<i>Saguinus labiatus</i>	Red-bellied tamarin
<i>Saguinus mystax</i>	Moustached tamarin
<i>Saimiri boliviensis</i>	Bolivian squirrel monkey

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