CHAPTER 28

Causes and consequences of coati sociality

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Ring-tailed coatis (*Nasua nasua*) © B. Hirsch

Introduction

Over fifty years ago John Kaufmann conducted a two-year study on the white-nosed coati (*Nasua narica*) on Barro Colorado Island, Panama. The resulting monograph (Kaufmann 1962) is a solid examination of the natural history of the species, with an emphasis on understanding its social structure. Although many such studies now exist, Kaufmann's study bordered on revolutionary at the time because this was one of the first studies to gather detailed ethological data of wild vertebrates via habituation of free-living social animals. The idea of following animals from a distance of just a few metres, and observing the nuances of their behaviour, was relatively novel at the time. The results of Kaufmann's work, and similar studies on primates and other carnivores, have greatly enhanced our understanding of how and why animals live in groups. Such issues frame the core of the modern field of behavioural ecology.

Animals live in groups when the benefits (e.g. a greater ability to survive threats from predators and pathogens) are greater than the costs (e.g. increased competition for resources such as food or mates) (Krause and Ruxton 2002). Overlaying such cost–benefit ratios are the genetic relatedness of individuals and the willingness of animals to cooperate in a manner that increases the benefits and decreases the costs of sociality. Among the musteloid carnivores, studies of coatis have contributed more to our understanding of the causes and

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consequences of group-living in the sub-order than any other species, with the possible exception of the European badger (*Meles meles*). Indeed, among the smaller members of the order Carnivora, studies of coatis (along with those of badgers, da Silva et al. 1993; Woodroffe and Macdonald 1993; Johnson et al. 2001; dwarf mongooses [*Helogale parvula*], Creel and Creel 1991; Creel and Waser 1994; Cant et al. 2013; and meerkats [*Suricata suricatta*], Clutton-Brock et al. 1999, 2001, 2008) provide the core of our understanding of how and why individuals live in groups. Furthermore, because not all individual coatis are social, coatis are an ideal study system to study why an individual animal might choose a group-living or solitary lifestyle.

Against this backdrop of costs and benefits of group-living, we examine coati social structure based on insights gained from a series of multi-year studies conducted on *N. narica* and *N. nasua* (the ring-tailed coati). We draw principally from our work in Panama and Argentina, but also discuss insights gained from work conducted in the United States, Mexico, Guatemala, Costa Rica, and Brazil (Table 28.1).

Table 28.1 Multi-year studies of white-nosed (*Nasua narica*) and ring-tailed (*N. nasua*) coatis.

Species	Locale	Habitat	References
N. narica	Barro Colorado Island, Panama	Seasonal tropical forest	Gompper 1994, 1996; Gompper et al. 1997a, 1998
N. narica	Barro Colorado Island, Panama	Seasonal tropical forest	Russell 1979, 1981, 1982
N. narica	Barro Colorado Island, Panama	Seasonal tropical forest	Kaufmann 1962
N. narica	Jalisco, Mexico	Subtropical dry forest	Valenzuela 1998; Valenzuela and Macdonald 2002
N. narica	Arizona, USA	Dry forest	Hass 2002b; Hass and Roback 2000
N. narica	Tikal, Guatamala	Tropical forest	Binczik2006; Booth-Binczik2001
N. nasua	Iguazú, Argentina	Subtropical Atlantic forest	Hirsch 2007a, b, 2009, 2011a, b
N. nasua	Pantanal, Brazil	Seasonal floodplain	Olifiers 2010; Bianchi 2009; Bianchi et al. 2014

Distribution, phylogeny and conservation

To better understand the determinants of sociality in coati species, it is important to note that this group is composed of several species that differ in their ecology and behaviour. Coatis comprise two genera: *Nasua* and *Nasuella*. All species in both genera are believed to be highly social, although detailed field studies of social structure have only been conducted on white-nosed and ring-tailed coatis. *Nasua* species occupy diverse habitats from the south-western United States to Northern Argentina (see Macdonald et al., Chapter 1, this volume). The white-nosed coati is found in Central and North America, and at its northern extreme, the arid Chiricahua and Huachuca Mountains of Arizona and New Mexico in the United States. The species is found throughout mainland Mexico and Central America, except the Baja Peninsula. The southern geographic range limits of the white-nosed coati are unclear; the species occurs throughout Panama and may also occur in parts of Colombia and Ecuador. Whether the species is sympatric in these regions with the ring-tailed coati, and how the two species interact if sympatric, has yet to be examined. The ring-tailed coati is found throughout much of South America, reaching the southern limits of its range in northern Argentina and Uruguay (Gompper 1995; Gompper and Decker 1998).

A third species of *Nasua*, the dwarf coati, *N. nelsoni*, is endemic to low-lying Cozumel Island, Mexico. The dwarf coati is closely related to the white-nosed coati, but is morphologically distinct and has been isolated on Cozumel Island for several thousand years. The appropriate taxonomic status of the dwarf coati is unclear (Decker 1991; McFadden et al. 2008, 2010). Applying species-level recognition would lead to the dwarf coati being one of the rarest of small carnivore species, deserving immediate conservation attention (Cuarón et al. 2004). Alternatively, if the dwarf coati is merely attributed status as a subspecies of the white-nosed coati (that is, *N. narica nelsoni*), conservation concerns are lessened, as well as concerns about mainland white-nosed coatis released on Cozumel hybridizing with dwarf coatis.

The mountain coatis, which comprise the genus *Nasuella*, occur in the cloud forests and alpine tundra (páramo) of the Andes of Venezuela, Colombia, Ecuador, and perhaps Peru (Balaguera-Reina et al. 2009; Helgen et al. 2009). The distributions of the mountain coati species are poorly known. Traditionally, a single *Nasuella* species was recognized: *N. olivacea*. Recently, however, detailed morphologic and molecular examinations of the genus by Helgen et al. (2009) have resulted in the recognition of two distinct taxa: the eastern mountain coati (*N. meridensis*), which is endemic to the Venezuelan Andes, and the western mountain coati (*N. olivacea*) endemic to the Andes of Colombia and Ecuador (see Macdonald et al., Chapter 1, this volume).

At higher taxonomic levels, molecular analyses indicate that coatis are most closely related to olingos (genus *Bassaricyon*), with the split between the two genera occurring in the Miocene (Koepfli et al. 2007). Understanding of intra-*Nasua* evolutionary relationships is more preliminary. While fossil *Nasua* are first recorded from Late Pleistocene South American deposits (Berta et al. 1978), molecular estimates of divergence times of white-nosed and ring-tailed coatis indicate a split at 7–8 mya, well before the Great American Interchange (GAI) that occurred with the rise of the Isthmus of Panama about 3.5 mya. The presence of North and South American sister taxa of *Nasua* may be a function of pre-land bridge waif dispersal to South America prior to the GAI, followed by isolation and differentiation prior to secondary contact after the rise of the Panamanian land bridge (Koepfli et al. 2007; Forasiepi et al. 2014). Helgen et al. (2009) included several white-nosed and ring-tailed coatis in their molecular phylogeny of mountain coatis and observed that *Nasuella* was the sister lineage to *N. narica*. This suggests that *Nasua,* as currently recognized, is not monophyletic, and *Nasuella* species should be reclassified as *Nasua* species, resulting in four or five species of *Nasua.* However, a better resolution of coati phylogenetics awaits more detailed studies that incorporate samples collected over the full range of the genera; several ongoing studies have found high levels of intraspecific sequence variability for *Nasua* and *Nasuella*, suggesting our current understanding of coati phylogenetics is rather rudimentary (Koepfli et al. unpublished data, and Tsuchiya et al. unpublished data; see also Koepfli et al., Chapter 2, this volume).

The two mainland species of *Nasua* are widely distributed and have been found at high population densities in some locations (e.g. >50 individuals per km^2, Wright et al. 1994). For the most part, conservation concerns focus on particular populations or discrete locales. While overhunting and habitat destruction have resulted in declining or extirpated coati populations in some areas, there is little evidence for large-scale declines in coati populations across Central and South America. In contrast, the dwarf coati is listed as a threatened species in Mexico (SEMARNAT 2002) and Cuarón et al. (2004) argue the taxon should be designated Critically Endangered by the IUCN based on small and rapidly declining population size, and small geographic range. The conservation status of the mountain coati species is also of concern. The combined impacts of habitat loss, hunting, and climate change are likely to have a negative influence on the local and regional persistence of these high-elevation species (Helgen et al. 2009), and Balaguera-Reina et al. (2009) propose that a Near Threatened IUCN status is justified.

Linking social structure, morphology and feeding ecology

Much of what is known about the biology and ecology of coatis is based on Kaufmann's initial study of white-nosed coatis on Barro Colorado Island, Panama. One of the behavioural patterns that Kaufmann documented on Barro Colorado was that adult males and females differed in their degree of sociality. In general, coati groups (or 'bands'), are composed of adult females and their offspring, while larger adult male coatis are usually solitary outside of the mating season. White-nosed coati groups generally range between 4 and 26 individuals (Table 28.2), although Booth-Binczik (2001) reported a group of more than 150 individuals in Tikal, Guatemala. The typical group size of ring-tailed coatis is similar to those of white-nosed coatis: 5 to 65 individuals (Table 28.2). At approximately two years of age, male coatis become reproductively mature and leave their group to live solitarily (Kaufmann 1962; Gompper and Krinsley 1992; McColgin 2006; Hirsch 2011a). Dispersing males may occasionally live with other

Table 28.2 White-nosed (*Nasua narica*) and ring-tailed (*N. nasua*) coati density, group size, and home range size for different populations. BCI = Barro Colorado Island; CCBR = Chamela–Cuixmala Biosphere Reserve; CBSP = Carlos Botelho State Park.

Locale	Species	Individuals per km^2	Group size	Group home range size (km^2)	References
Tikal, Guatamala	*N. narica*	13		5–8	Booth-Binczik 2001
BCI, Panama	*N. narica*	55.6	7.2		Wright et al. 1994
BCI, Panama	*N. narica*	19.7	7.3	0.34–0.45	Kaufmann 1962
BCI, Panama	*N. narica*	51.5	15.3	0.17–0.48	Gompper 1997
BCI, Panama	*N. narica*	54.8	9.5	0.76	Russell 1979
Manuel Antonio, Costa Rica	*N. narica*	70			Vaughan and McCoy 1984
Palo Verde, Costa Rica	*N. narica*		5.4		Burger and Gochfeld 1992
Los Tuxtlas, Mexico	*N. narica*	33	22.5	0.5–1.10	Coates-Estrada and Estrada 1986a
CCBR, Mexico	*N. narica*		10.2		Hass and Valenzuela 2002
CCBR, Mexico	*N. narica*	42.4	6.1		Valenzuela 1998
CCBR, Mexico	*N. narica*			3.81	Valenzuela and Ceballos 2000
Arizona, USA	*N. narica*	1.2–2		2–3	Lanning 1976
Arizona, USA	*N. narica*		17		Hass and Valenzuela 2002
Arizona, USA	*N. narica*	0.8	19	15.78–32.21	Hass 2002
Arizona, USA	*N. narica*	0.5		6.78	McColgin 2006
Pantanal, Brazil	*N. nasua*	9.1–16.7	6–7		Desbiez and Borges 2010
Iguazú, Argentina	*N. nasua*		31.5	~3.5–5	Hirsch 2007b
CBSP, Brazil	*N. nasua*		11–15	4.45	Beisiegel and Mantovani 2006
Mato Grosso do Sul, Brazil	*N. nasua*	33.7		0.14–0.15	Costa et al. 2009

young males for several months (Gompper and Krinsley 1992; Hirsch, personal observation), but interactions between adult males are typically antagonistic and are frequently characterized by either violent fighting or complete avoidance. Although adult male coatis of both species typically live alone, there are differences between the two species. Adult male white-nosed coatis have been observed occasionally associating with groups of adult females outside of the mating season (Gompper and Krinsley 1992; Booth-Binzcik 2001; Logan and Longino 2013), while ring-tailed coati groups typically have one adult male integrated into the group year round (Hirsch 2011a).

What drives coati sexual segregation? Two principal and non-exclusive hypotheses have been put forth: 1) resource competition and 2) predation threat. To understand resource competition among coatis, it is important to note the food resources for which coatis frequently compete. Coatis principally consume invertebrates and fruit, and only occasionally consume vertebrates (Table 28.3). Coatis consume fruits from a large number of plant species, which likely reflects the high levels of plant biodiversity in the Neotropics. Yet despite the broad dietary breadth of coatis, in some regions a small number of fruit species can comprise a disproportionately large proportion of their diet (Gompper 1996). For instance, in Iguazu, Argentina, 44% of time spent foraging for fruit was focused on Pindó palm fruits (*Syagrus romanzoffiana*, Hirsch 2009). Although there is intra-annual variation in the reliance on fruits, it is unclear whether seasonal fluctuations in coati diet are primarily driven by fluctuations in invertebrate or fruit availability. Alves-Costa et al. (2004) argued that changes in invertebrate abundance were largely responsible for these shifts, while Hirsch (2009) found that monthly fruit consumption patterns closely matched overall fruit availability, and thus concluded that fruit abundance drives seasonal fluctuations in diet. While Hirsch (2009) assumed that the high energy content and lower handling costs of fruit makes them a more valued food resource than invertebrates, coati movement patterns do not fully support this assumption. Even though coatis often exhibit directed straight-line travel between consecutive fruit trees more than 200m apart, Hirsch et al. (2013) found that coatis would also travel in circuitous patterns, which sometimes increased their tree-to-tree travel distances by more than 500% (Figure 28.1). Hirsch et al. (2013) concluded that this behavioural pattern may be partially due to 'dietary-switching' whereby coatis regularly switch from directed travel towards fruit trees, to non-directed invertebrate foraging. This pattern is consistent with the idea that coatis need both high-energy carbohydrates, as commonly found in ripe fruit, and proteins found in invertebrates. Coati travel patterns may be the result of switching back and forth between fruit foraging and invertebrate foraging during the day to achieve an optimal balance of these nutrients (Hirsch et al. 2013).

Table 28.3 Diet of white-nosed (*Nasua narica*) and ring-tailed (*N. nasua*) coatis from studies conducted across their geographic ranges. BCI = Barro Colorado Island; CCBR = Chamela–Cuixmala Biosphere Reserve; CBSP = Carlos Botelho State Park.

Locale	Species	% fruit or plant parts	% invertebrates	% vertebrates	Unit of measure	References
Tikal, Guatamala	*N. narica*	20–40	50–80	<1	Items consumed	Booth-Binczik 2001
BCI, Panama	*N. narica*	14.3–74.4	25.6–85.7	<1.0	Foraging time	Gompper 1996
BCI, Panama	*N. narica*	12–45	54–89	<1	Foraging time	Russell 1982
CCBR, Mexico	*N. narica*	46.1	39.1	14.8	% food items in scat	Valenzuela 1998
Iguazú, Argentina	*N. nasua*	2–29	70–98	<0.01	Foraging time	Hirsch 2009
CBSP, Brazil	*N. nasua*	96.6	15	0	% occurrence in scat	dos Santos and Beisiegel 2006
Mato Grosso do Sul, Brazil	*N. nasua*	85.4	64.3–85.1	9.3	% occurrence in scat	Alves-Costa et al. 2004
Parana, Brazil	*N. nasua*	72.6	16.2	5.8	Total volume in stomach	Aguiar et al. 2011
Pantanal, Brazil	*N. nasua*	39	47	14	% food items in scat	Bianchi et al. 2014
Venezuela	*N. nasua*	41	58	2	Total volume in stomach	Bisbal 1986
Minas Gerais, Brazil	*N. nasua*	24.5	34.9	19.8	% food items in scat	Ferreira et al. 2013
Bolivia	*N. nasua*	65.9	30.5	40	% occurrence in stomachs	Redford and Stearman 1993

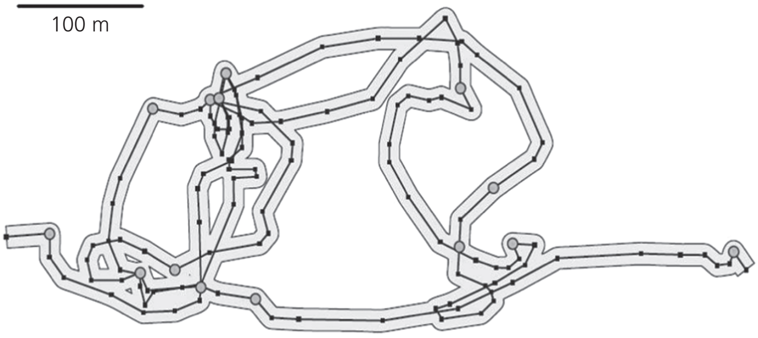

Figure 28.1 Daily travel path of one coati group in Iguazu, Argentina. Solid circles represent the location of fruit trees. From Hirsch et al. (2013).

Regardless of what intrinsic and environmental factors influence changes in fruit consumption, fruit is an important component of coati diet, and foraging group size (that is, the size of sub-groups that coati bands sometimes split into while foraging) correlates with the seasonality of fruit availability (Figure 28.2; Gompper 1997). This correlation suggests intra-group competition for a limited resource; which is supported by the finding that fruit ingestion rates decreased as the number of individuals within 3 m of the focal coati increased (Hirsch 2011b). Fruit trees visited by large coati groups are often quickly depleted, thus some individuals in large groups are likely to get few or no fruits when a group visits a tree. In such scenarios, social groups may split into smaller foraging groups, resulting in a greater proportion of fruit available for each individual (Gompper 1996; Hirsch 2009).

Overlaying the issue of how foraging strategies influence coati sociality are sexual dimorphism in body size and the timing of reproduction. While young males and females (aged 0–1.5 years) are similar in size and weight, adult females weigh only 62–73% of an average adult male (Gompper 1996; Olifiers 2010). Differences in body size and competitive ability can alter the costs and benefits of sociality for coatis of different sexes, and may help explain the question: Why do females live in groups and males leave their natal groups at two years of age? Most females in social groups are closely related to the maturing males and thus male dispersal before or during the mating season provides

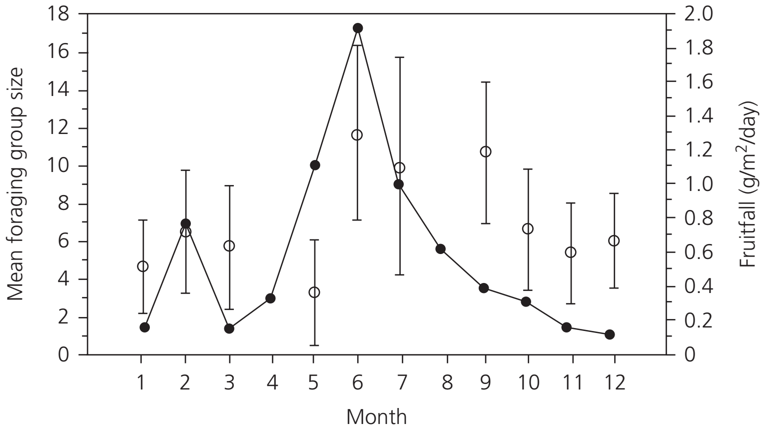

Figure 28.2 Mean coati foraging group size (open circles ± SD) and mean fruitfall (closed circles) from Barro Colorado Island, Panama. From Smythe (1970) and Gompper (1997).

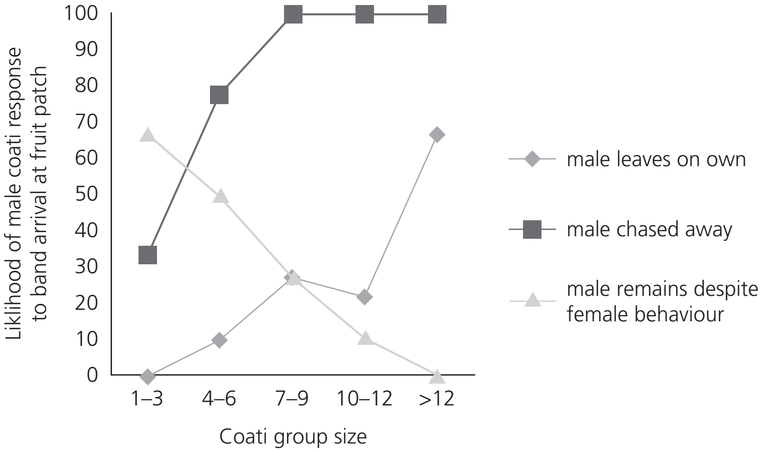

Figure 28.3 Adult male coati responses to the arrival of coati foraging groups of different sizes. Males are less likely to abandon a fruit patch on the arrival of a small group of females, but large groups of females are always successful in excluding males from a patch. Based on data collected from Barro Colorado Island, Panama, and presented in Gompper (1996).

an inbreeding-avoidance mechanism (Gompper et al. 1998; McColgin 2006). Furthermore, males that forage solitarily no longer need to compete for food at a fruit patch, and thus have a clear energetic benefit from living alone. So why don't females also forage solitarily? Gompper (1996) hypothesized that their smaller size makes it difficult for them to defend a fruit patch from a large male. To balance the power that males gain by being larger, females remain in groups. A single large male can exclude a smaller single female from a food patch, but a group of small females can exclude a larger male (Figure 28.3). These interactions are dependent on the size and distribution of resources, thus sexual dimorphism combined with the potential for coalitionary agonistic interactions at clumped fruit patches could have driven sexual differences in sociality (Gompper 1996).

Reproduction, survival, and demographics

A difficulty in focussing on how body size and resource availability affects coati social structure is that it fails to take into account that coatis are pulse breeders and that they inhabit a landscape in which they are susceptible to predators. Coati reproduction is highly seasonal, and in most populations, females come into oestrus once annually, after which they enter anoestrus (Mayor et al. 2013). Male reproductive traits such as testosterone concentration, testis volume, semen concentration, and sperm motility also show strong patterns of seasonality (da Paz et al. 2012). A typical mating season lasts 2 to 3 weeks and adult females in the same social group appear to exhibit more or less simultaneous oestrus (Russell 1982; Hirsch and Maldonado 2012). There can also be strong synchrony in the timing of mating and parturition across groups (Kaufmann 1962; Russell 1982; Booth-Binczik et al. 2004; Hirsch and Maldonado 2012). In some populations, all, or almost all, adult females can conceive between 1 and 7 offspring per year, thus there is potential for high reproductive output at both individual and group levels (Russell 1982; Hirsch and Maldonado 2011, Table 28.4). Highly seasonal reproduction in mammals is often associated with seasonal fluctuations in food abundance. For example, the timing of coati births on Barro Colorado Island coincides with the seasonal peak in fruit abundance, and it is posited that the timing of births is adaptive for enhancing female reproduction and juvenile survival (Russell 1982). The tight reproductive seasonality found in coatis also has important implications for male sociality and reproductive skew. In most populations, multiple adult males associate with female social groups during the mating season to gain access to receptive females. This competition over females should favour larger males with superior fighting abilities. Coati males have evolved atypically large canine teeth that they use during these fights, and severe injuries such as large deep wounds, severed tails, and facial disfigurement are often seen on adult male coatis, especially during and after the mating season (Hirsch and Gompper, personal observation).

Despite extreme male–male competition for access to females during the short mating period, there is also evidence that female choice is important. Females may mate with multiple males, and females have been observed leaving their social groups to mate with peripheral males (Hirsch and

Table 28.4 Annual reproductive output of white-nosed (*Nasua narica*) and ring-tailed (*N. nasua*) coatis for different study sites.

Locale	Species	No. offspring per female	% females giving birth	References
Tikal, Guatamala	*N. narica*		~100	Binczik 2006
BCI, Panama	*N. narica*	3.5		Russell 1982
CCBR, Mexico	*N. narica*	4		Valenzuela 1998
Arizona, USA	*N. narica*		~100	Hass and Valenzuela 2002
Iguazú, Argentina	*N. nasua*	4.6	~100	Hirsch 2007b
Amazon, Peru	*N. nasua*	4.2	64.7	Mayor et al. 2013

Maldonado 2011). This behaviour sometimes leads to multiple paternity litters, which reduces reproductive skew (Hirsch and Maldonado 2011). Nonetheless, for males, retaining access to groups of females is important. At Iguazú, adult male coatis that were consistently associated with social groups achieved higher reproductive success than solitary floater males (Hirsch and Maldonado 2011). This does not negate the active role of females. Hirsch and Maldonado (2011) hypothesized that females may be able to cooperate to drive away particular males from their group, while allowing other males to enter. This female choice influences male mating success, and thus sociality, in a similar way to Gompper's (1997) observation of females forming coalitions to defend food resources from adult males.

After mating, females remain in their social group for most of the gestation period (average 70–77 days, Kaufmann 1962). A few days before giving birth, individual females leave their group and construct a nest for their litter, typically in a tree or rock ledge or crevice (Gilbert 1973; Olifiers et al. 2009). This behaviour, whereby group-living females leave their group and live alone with their new offspring for 1 to 2 months, is unusual among group-living mammals, and may be a strategy to avoid detection by predators. In some areas, capuchin monkeys, and other predators, attack and kill up to 84% of coati juveniles while in their nests (Sáenz 1994). Predation rates in that study area were unusually high, likely due to a high density of capuchins and a lack of concealing foliage during the juvenile nesting season. Because capuchin monkeys are far more dexterous in the canopy, extra adult female coatis are unlikely to provide sufficient protection. Spreading out nests and attempting to avoid detection via crypsis appears to be a more successful strategy for protecting juvenile coatis in the nest.

The combination of multiple reproductive females and large litter sizes facilitates the potential for rapid increases in coati populations. During a three-year study of ring-tailed coatis in Iguazú National Park (NP), Argentina, all four observed social groups increased in size almost every year (a group fission resulted in a reduced group size during one year, Hirsch 2007a, Figure 28.4). This increase was related to high juvenile survival (survival rate to 12 months ranged from 57% to 80%) and access to food from introduced fruit tree species. Former agricultural areas within Iguazú NP contained dense stands of non-native Oriental raisin trees (*Hovenia dulcis*) that produced large quantities of swollen, sugar-filled peduncles during the winter season when native fruit abundance was lowest. This led to more consistent food supplies over the course of the year than would be encountered by coatis in natural habitats, and, in turn, higher survivorship in the population (Hirsch 2009). Similarly, on Barro Colorado Island, one group comprised of 21

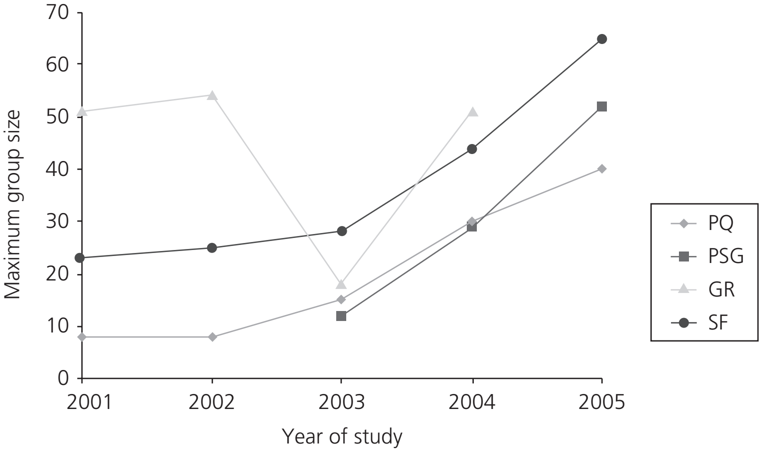

Figure 28.4 Maximum group size of four coati groups in Iguazu, Argentina from 2001 to 2005. During 2003, the GR split into two groups: GR & PSG, causing a drop in the GR group size between 2002 and 2003.

animals grew and underwent several fission events, such that four years later 43 animals comprised three groups. This doubling in numbers occurred while neighbouring social groups remained relatively stable in size (Gompper et al. 1997a).

Nonetheless, mortality of both juveniles and adults due to predation can be high in some populations, and social groups commonly go extinct or disband, especially when fruit shortages cause mortality or low reproductive success, or when social groups are so small that chance demographic fluctuations drive group dynamics (Gompper et al. 1997b). In Arizona and Mexican dry forests, over 75% of adult coati mortality (which varies from 0 to 54% per year for adult females) is caused by predation from jaguars (*Panthera onca*), pumas (*Puma concolor*), and ocelots (*Leopardus pardalis*, Hass and Valenzuela 2002). In other settings (such as Costa Rican dry forests) nest predation by primates can drive local dynamics. While cryptic strategies are used to conceal nests of neonates from predators, once juvenile coatis are mobile it would be difficult for a foraging group to move quietly enough to evade detection by predators. Conversely, groups are better able to detect, and thus ultimately avoid, predators (Hass and Valenzuela 2002; DiBlanco and Hirsch 2006). Adult males generally cannot benefit from within-group predator detection and dilution effects, and thus use a cyptic anti-predatory strategy similar to solitary adult females during the nesting season. Mortality of adult females was 6.5 to 13 times higher during the nesting season, which is consistent with the hypothesis that single animals, especially the smaller females, are more vulnerable to predation (Hass and Valenzuela 2002; Hirsch 2007a). Outside of the nesting period, members of a group can cooperate by attempting to drive off a small-bodied potential predator (Figure 28.5). Body size dimorphism may have led to these two distinct anti-predator strategies (Janson and Goldsmith 1995). For adult males, the need to cooperate against predators may be less of a concern as males are likely a formidable prey for small predators, while females depend on grouping

Figure 28.5 A sub-adult coati being killed by a *Boa constrictor* in Guanacaste Province, Costa Rica. Photograph is by Janzen (1970) who describes the attack and the response of the adults of the social group. The adult coatis attacked the approximately 3.4 metre snake extensively and repeatedly in a cooperative anti-predator effort.

for defence. For larger predators (e.g. large felids or crocodiles), however, the larger size of male coatis is likely of little consequence. In Jalisco, Mexico and Arizona, USA, where puma and jaguar accounted for over half of the deaths of adult coatis, predation rates were more than twice as high on solitary males than on adult females living in groups. Predation rates were also higher on adults living in smaller groups than on those living in larger groups (Hass and Valenzuela 2002).

Connecting disease and social structure

Because of the large variance in group size and sexual differences in sociality, coatis provide an excellent model system for examining how social structure mediates the interactions of diverse parasitic species with their hosts. In contrast to our understanding of how resource competition and predation avoidance influence coati social structure (and indeed, the social structure of vertebrates in general), our understanding of how the social–asocial dichotomy influences the likelihood of contracting or transmitting parasites, and how these parasites influence social structure, is under-developed. Pathogens can have dramatic impacts on the health of individual coatis. Ring-tailed coatis infected by *Trypanosoma cruzi* and *T. evansi* (the causative agents of Chagas disease in humans and Mal de Cadeiras disease in horses) exhibit altered haematological measures and decreased body condition indices, characteristic of chronic disease (Herrera et al. 2001; Olifiers 2010; Olifiers et al. 2015; see also Newman and Byrne, Chapter 9, this volume). Given the high prevalence rates of some pathogens in coati populations (e.g. >48% for *T. cruzi* in the Brazilian Pantanal, Alves et al. 2011; Rocha et al. 2013) and the high (effectively 100%) contact rates among group members, these health effects are likely important drivers of group size dynamics with respect to certain directly transmitted diseases (e.g. canine distemper virus). However, there have been relatively few studies of disease-associated declines in coatis at either the social group or population scale (but see Valenzuela et al.'s [2000] examination of a notoedric mange *Notoedres cati* epizootic in Jalisco, Mexico).

Gompper (2004) documented how two ectoparasite taxa (*Amblyomma* ticks and *Eutrombicula* chiggers) differentially infected (solitary) male and (group-living) female white-nosed coatis. During the rainy season, 48% of adult males were parasitized by ticks compared to 26% of female group members. The opposite pattern was seen for chiggers: 39% of adult males were parasitized compared to 90% of female group members. Although neither of these parasitic taxa are transmitted directly among hosts, the difference in the observed likelihood of infection was attributed, in part, to the extent of sociality. Lower prevalence and intensities of ticks in group members was likely due to mutual-grooming. A similar pattern and conclusion was reported by Olifiers (2010) for coati–tick interactions in the Brazilian Pantanal. Chigger prevalence fluctuated greatly within groups and independently between groups (Gompper 2004), and during any given period prevalence within a group was either all or nothing. Females who briefly became solitary to give birth lost their chigger infestations, while males had increased prevalence of chiggers during the mating season when they associated with groups. These data indicate dilution effects (an individual living in a group differs in the likelihood of being targeted by a mobile parasitic taxon), detection effects by the host (the ability to detect and avoid or remove some species of vectors and ectoparasites), and detection effects by the ectoparasite (e.g. an increased likelihood of detecting cues such as CO_2 plumes produced by group-living hosts that allow a parasite to seek out a host).

Contrasting coati social behaviour: Barro Colorado Island and Iguazú

Because coatis have a wide geographic range and live in many different habitats, it may be possible to link intraspecific variation in social behaviour to local ecological variables and test socio-ecological models. Many of these models were developed and tested with primate species (Wrangham 1980; van Schaik 1989; Clutton-Brock and Janson 2012), and thus coatis provide a phylogenetically independent test. Unfortunately, to date, necessarily detailed information is only available for two well-studied populations: Barro Colorado Island, Panama (white-nosed coati) and Iguazú NP, Argentina (ring-tailed coati). While comparing these two sites and species does not permit a full test of the influence of ecology on social structure, differences between the two do allow for some conclusions to be drawn about the ultimate forces shaping the social structure of this clade.

On Barro Colorado Island, Gompper et al. (1997a) found that within groups, closely related adult females would frequently direct aggression towards unrelated members of their group (Figure 28.6), defending concentrated resources used by their offspring and close kin (see also Figure 28.3). While it was uncertain if these unrelated females were immigrants into the group, or were simply not close relatives of the dominant females, kin selection underpins cooperative behaviour within these coati groups. However, cooperation during dominance interactions was occasionally noted between non-kin, indicating that genetic relatedness alone is not always the sole determinant of cooperation among group members. These patterns closely resemble patterns of kin selection, reciprocity, and social behaviour found in other mammal species (primates, Chapais et al. 2001; Silk et al. 2004; hyaenas, Engh et al. 2000; dolphins, Krutzen et al. 2003; reviewed in J. Smith et al. 2010).

While much less is known about the social behaviour of the ring-tailed coati, in Iguazú, Hirsch (2007a) did not find strong evidence for kin selection driving coalitionary aggressive behaviour. Hirsch (2007b) instead found that much of the aggression observed in two coati groups was juveniles fighting between themselves, or juveniles directing aggression at older, larger group members. While juvenile dominance has been found in some primate species (Datta 1988, 1991; Chapais 2004), these examples all involved juveniles that obtained a high dominance rank because they were related to high ranking group members that provided support during agonistic interactions. In the case of the Iguazú coatis, almost all juveniles were higher ranking than almost all adult females (as determined by dyadic agnostic interactions), which precludes the possibility of rank inheritance (Hirsch 2007b). Hirsch (2007b) posited that the high rank achieved by juvenile coatis was the result of coalitionary support by adult females. In contrast to the situation in hyaenas and some primate species, where mothers and other close relatives support their younger offspring (Cheney 1977; Hausfater et al. 1982; Chapais 1992; Holekamp et al. 1996; Engh et al. 2000; Chapais et al. 2001), adult female coatis supported all juvenile coatis regardless of the degree of relatedness between the adult female and the juvenile (Hirsch 2007b; Hirsch et al. 2012). This apparent lack of kin selection in coalitionary aggressive behaviour is unusual in social mammals, and it is uncertain why adult female coatis in Iguazú failed to preferentially

Figure 28.6 Three adult female white-nosed coatis form a coalition and aggressively attempt to exclude a larger adult male from an *Attalea* palm seed shadow on Barro Colorado Island, Panama. © M. Gompper.

support their offspring. Furthermore, genetic analyses did not support that these patterns arose due to high degrees of relatedness among all group members (Hirsch et al. 2012). These patterns of juvenile dominance and adult female support during agonistic encounters were similar in two social groups despite substantially different degrees of relatedness among group members (Hirsch et al. 2012). Although there is some tolerance for juvenile aggression towards older individuals in white-nosed coatis (Gompper, personal observation), the degree to which juveniles obtain preferential access to food, combined with the apparent lack of strong kin selection in ring-tailed coatis may eventually turn out to be a significant difference in behaviour between these two species.

Deference to juvenile ring-tailed coatis is also manifested through group geometry and coati social networks. Juvenile ring-tailed coatis generally maintain closer spatial proximity to each other than with older group members, and this clumped grouping of juveniles typically travels at the leading edge of the group, which ensures priority feeding access when arriving at fruit trees (Hirsch 2011b, c). Russell (1979) also reported that juvenile white-nosed coatis clump together, but in the centre of the group. Russell (1979) hypothesized that adult females preferentially located themselves at the edges of the group to protect the more vulnerable juveniles from predators. If true, this would collectively aid both unrelated and related offspring. In contrast, juvenile ring-tailed coatis in Iguazú position themselves at the most dangerous portion of the group in relation to predation risk (DiBlanco and Hirsch 2006; Hirsch 2007c, 2011b, c). Hirsch (2011b, c) proposed that the lower predation risk in Iguazú shifted the costs and benefits of spatial position choice to the point that the benefits of priority access at fruit trees outweigh the increased risk of predation.

As noted earlier, the other major difference in social patterns between these two coati species is the extent of sociality exhibited by adult males. While most adult males are solitary in both coati species, ring-tailed coati groups in Iguazú NP often include one adult male all year (Hirsch 2011a; Hirsch et al. 2012). For example, Hirsch (2011a) observed one adult male associated with a group for over 22 consecutive months. While white-nosed coatis on Barro Colorado Island sometimes have adult males briefly associated with social groups outside the mating season (Gompper and Krinsley 1992), the degree of adult male sociality differs substantially between the two coati study sites. One factor that could underpin this difference is that if predation risk is higher in Iguazú this could drive adult males to join groups for protection. However, this hypothesis is not supported, because the population density of ocelots, the primary predator at both sites, is far higher on Barro Colorado Island than in Iguazú (Moreno et al. 2006; Di Bitetti et al. 2006, 2008; Rodgers et al. 2014). Furthermore, the same patterns of minimal male sociality observed on Barro Colorado have also been observed in other white-nosed coati populations with even higher predation rates (Hass and Valenzuela 2002). Indeed, all published studies on white-nosed coatis have reported solitary adult males and little adult male sociality outside the mating season. In contrast, there are multiple reports of adult males present in social groups of ring-tailed coatis in Brazil: Mangabeiras Park, Minas Gerais; Tiete Ecological Park, São Paulo; Nhumirim Ranch, Pantanal; Parque Estadual do Prosa, Mato Grosso do Sul, and Campeche Island, Santa Catarina (Alves-Costa et al. 2004; Resende et al. 2004; Costa et al. 2009; Olifiers et al. 2009, J. Bonatti personal communication). It appears that these are species-level differences in the extent and plasticity of adult male coati sociality.

One concern with comparisons of coatis from Iguazú and Barro Colorado Island is the limited insight into whether observed differences in behaviour and sociality are a function of species-level differences or population-level plasticity reflecting resource abundance and distribution. For example, outside of Barro Colorado and Iguazú, no other studies have reported data on both genetic relatedness and dominance interactions (although see captive studies by Romero and Aureli 2007, 2008). If models linking social behaviour to local environmental conditions hold true, coati social patterns will vary between field sites both within and between species. However, it appears that the extent of adult male sociality varies by species, which contradicts predictions arising from socio-ecological models. Social dominance patterns found by Hirsch (2007b) showed little or no evidence of despotism, and strongly diverged from predicted patterns. What is still unclear is whether the unusual social patterns found in one ring-tailed coati population are representative of the species. Additional detailed studies of social structure in relation to the types of ecological and morphological variables we detail in this chapter need to be undertaken on additional coati populations to understand the extent to which coatis fit existing socio-ecological models. We have detailed here examples of how coati social behaviour is linked to environmental forces, but also the possible presence of phylogenetic inertia, whereby male sociality varies by species and not according to the environment. To further address these questions, detailed studies of other ring-tailed coati populations are badly needed. Additionally, the lack of information about *Nasuella* ecology and social behaviour is a major gap in our understanding of the Procyonidae. We posit that the Procyonidae are an ideal taxonomic group for additional research that can provide critical tests for understanding the evolution and maintenance of sociality in mammals.