

## Short Note

## Long-term adult male sociality in ring-tailed coatis (*Nasua nasua*)

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Coatis (Genus: *Nasua*) are widely distributed in Central and South America. Although some authors have studied dietary patterns and ranging behavior of ring-tailed coatis (*Nasua nasua*, Linnaeus 1766) not much was known about their social system in the wild (Beisiegel 2001, Alves-Costa et al. 2004, Beisiegel and Mantovani 2006, see also: Costa et al. 2009, Hirsch 2007a, 2009, 2010, 2011a,b). Previous authors assumed that ring-tailed coatis have similar or identical social systems to white-nosed coatis (*Nasua narica* Linnaeus 1766), which have a unique social system among carnivores in that adult males are mostly solitary outside of the mating season and females live in groups with their offspring (Gittleman 1989, Gompper 1995, Beisiegel 2001). This paper describes patterns of long-term male sociality seen during a two and a half year study of ring-tailed coatis in Iguazu, Argentina.

Various hypotheses have been used to explain sexual segregation in white-nosed coatis. Smythe (1970) hypothesized that sexual segregation could be the result of different foraging strategies between the sexes, with males eating far more vertebrate prey than females. Later studies did not support this hypothesis (Russell 1982, Gompper 1996). Russell (1981) concluded that adult males were excluded from groups by adult females protecting their offspring from infanticidal males. Infanticide is not likely to be a major factor influencing sociality because coatis do not exhibit any of the risk factors associated with sexually selected male infanticide and no other study has observed this behavior in coatis (Kaufmann 1962, Gompper 1996, Janson and van Schaik 2000, van Schaik 2000a,b). A more plausible explanation is that contest competition for fruit resources combined with sexual dimorphism leads to sexual segregation in coatis. Solitary adult male coatis have been found to have higher fruit foraging success than adult females living in

groups (Gompper 1996). At the same time, the larger body size of adult males should reduce their risk of predation, thus adult male coatis may not suffer the costs of solitary living as much as smaller coatis (Gompper 1996).

Even though adult male white-nosed coatis are primarily asocial, during the one-month mating season, adult male coatis enter social groups to breed (Kaufman 1962, Gompper 1994, Booth-Binczik et al. 2004). Adult male white-nosed coatis have occasionally been observed traveling with social groups over a period of weeks outside the mating season, but these adult males were not permanent group members (Gompper and Krinsley 1992). Because social adult males were occasionally observed traveling with their natal groups, it is not known if other adult males observed traveling with groups outside of the mating season were related to the group as well (Gompper and Krinsley 1992).

Four groups of ring-tailed coatis were studied in Iguazu, Argentina during two study periods totaling 32 months of research (Hirsch 2007a,b). During the initial study period of May–August 2001 only one animal was radio-collared (GR group) and censuses from other groups were obtained by regularly walking along trails searching for coatis. During the second study period (June 2002–December 2004) individuals from four study groups were radio-collared and regularly monitored. Animals were captured using 32×10×12 inch box traps. A total of 149 coatis were individually recognizable through the use of multi-colored plastic ear tags (Rototags, Dalton Co., Oxfordshire, UK) or radio-collars (Advanced Telemetry Systems, Isanti, MN, USA). Trapping was conducted non-randomly, and we focused our efforts on trapping group living individuals. This method resulted in an under sampling of solitary adult male coatis. Although some adult males were recognizable due to large scars or injuries, most adult males which did not have ear tags were impossible to distinguish from each other except by coat color morph (black or brown). Ear-tagged adult male coatis were either captured as sub-adults before dispersing from their natal group or when associated with a group as adults. The coati groups were usually habituated within two to three weeks and it was possible to follow the coatis within 3 m without disturbing them.

Two of the coati groups were contacted multiple times per month, typically for 10–15 days per group (PSG and PQ). The other two groups were contacted less often, but generally at least once per month. Group censuses were recorded from a total of 94 group/months and groups ranged from 8 to 65 individuals. A total of 14 recognizable adult males were seen in the study groups during this time. Several unrecognizable adult males were seen ranging alone during the course of the

study. The exact sex ratio of this population is not known because it was not possible to determine the number of solitary adult males. Adult males were found associated with coati social groups during 87.2% of the monthly censuses (82 out of 94 group/months). If all samples taken during the August breeding season are excluded, the percentage of group/months with social adult males is similarly high 85.2% (69 out of 81). Adult males were found in all four social groups and some males were seen in groups for several continuous months outside the mating season (Table 1). In one extreme case of long-term male residency, an adult male was observed with a group for over 22 months (VI in the PSG group). All four coati groups typically, but not always, contained a single adult male. Multiple adult male coatis were never observed simultaneously living in a group outside of

the mating season. In some cases, rapid male turnover was observed and males were only present in a group for a few days. Within-group males were observed grooming other group members, sleeping in the same sleep sites, and appeared to be fully incorporated into the social group. This pattern contrasts sharply to patterns observed in white-nosed coatis (Gompper and Krinsley 1992). The frequency and duration of social adult male coatis in Iguazu has not been reported in any previous study (Gompper and Krinsley 1992, Costa et al. 2009).

In four cases, it was possible to determine the natal group of adult males. IK and TV were originally tagged as sub-adults in the GR group (born in 2000), and Dr. H and NR were originally from the SF group (born in 2001). These males ranged from 29 to 42 months of age when they were

**Table 1** Adult male residency in four coati groups.

Group	PQ	PSG	SF	GR
2001				
June	Brown male	–	Brown male	SF
July	Brown male	–	Brown male	SF
August	Brown male	–	?	SF, Black male
2002				
June	Brown male	–	?	Black male
July	Brown male	–	WW	?
August	Brown male	–	Brown male	Black male, VI
September	EH	–	WW, BF	MD
October	None	–	?	MD
November	None	–	?	MD
December	None	–	?	MD
2003				
January	None	–	WW	MD
February	None	–	?	MD, VI
March	IK (29)	VI	?	?
April	IK	VI	?	?
May	IK	VI	?	None
June	IK	VI	?	Brown male
July	OB1	VI	WW, BF	MO
August	OB1	VI	VV, WW, VI, BF, MP	MO
September	OB1	VI	IK, WW	?
October	None	VI	?	MO
November	OB1	VI	IK	?
December	None	VI	IK	None
2004				
January	None	VI	IK	None
February	IK	VI	IK	None
March	IK	VI	?	None
April	IK	VI	TV (42)	BF
May	IK	VI	TV	?
June	IK	VI	?	Dr H (32), BF, NR (32)
July	IK	VI	?	NR
August	IK	VI, BF	TV, Brown and Black male	NR, VI, Black male
September	IK	VI, Black male	?	?
October	?	?	?	?
November	?	?	?	?
December	IK	VI	TV	?

Initials represent recognizable adult male coatis. – Denotes that the group had not yet split off from the GR group. A question mark indicates that the group was not censused during that month. Unmarked adult males were recorded as brown or black males depending on coat color. Numbers in parentheses are the age in months of males when first entering a group. These latter males were tagged when they were sub-adults residing in their natal group. The mating season was in August.

first observed in another (non-natal) group. These males presumably lived alone for 6–20 months before entering their social group. It is plausible that adult males need to reach a certain age or body size before they are allowed into social groups. Males may need to reach a certain size before they are able to fight away other males trying to enter the same social group. All four study groups were spatially close and had overlapping home ranges, thus these four males did not disperse very far from their natal groups (Hirsch 2007b). Behavioral and genetic evidence suggests that males typically entered non-kin groups (BT Hirsch and JE Maldonado, unpublished data).

If predation risk is significantly higher in Iguazu compared to other coati populations, this could shift the costs and benefits of sociality and thus lead adult males to live in groups (Hass and Valenzuela 2002). The major predators of weaned coatis in Iguazu are likely medium and large felids such as jaguars (*Panthera onca*), puma (*Puma concolor*), ocelots (*Leopardus pardalis*) and one mustelid which is an aggressive predator, tayra (*Eira barbara*) (Crawshaw 1995, Di Blanco and Hirsch 2006, Di Bitetti et al. 2006, 2008). Compared to other sites where coatis have been studied (Nunez et al. 2000, de Villa Meza et al. 2001, Hass and Valenzuela 2002, Moreno et al. 2006) felid population densities in Iguazu were low (jaguar=0.93–1.74 individuals per 100 km<sup>2</sup>, puma=1.55–2.89 individuals per 100 km<sup>2</sup>, ocelot=11.9–18.9 individuals per 100 km<sup>2</sup>) and it appears that predator population densities are relatively stable over time (Di Bitetti et al. 2006, 2008, Paviolo et al. 2008, 2009). Survival rates of coatis in Iguazu were generally higher than other coati study populations, thus predation risk is likely to be lower in Iguazu (Hirsch 2007a). In addition, if predation was the primary factor driving adult male sociality, one might predict that all adult males should be social, and groups should contain more than one adult male. This was not the case, and it is likely that most adult males in the population are solitary. For these reasons, it is unlikely that increased predation pressure was driving adult male sociality in this population.

It appeared that adult male coatis in Iguazu also had incentives to forage alone (Hirsch 2011a). Although no foraging data were recorded for solitary adult male coatis, group size was inversely related to invertebrate foraging rates (Hirsch 2011a). When feeding on fruit, adult males had similar intake rates to other age/sex classes, but adult males were found at fruit trees significantly less frequently than all other age/sex classes (Hirsch 2011a). Even though adult males were the highest ranking age/sex class in coati dominance hierarchies, there was a trend for adult males to be lower ranking in larger groups (Hirsch 2007b). This pattern suggests that adult males may be vulnerable to coalitionary aggression from teams of related females, which could explain their avoidance of fruit trees relative to other age/sex classes (e.g., Gompper et al. 1997, Hirsch 2011a,b). This problem might be solved if adult male coatis entered groups with a brother or other close relative, but the presence of two adult males in a group was never observed outside the mating season.

It is plausible that adult males live in groups for other reasons such as parasite reduction or access to females

(Gompper 2004, Monello and Gompper 2010). Living in a group may make it easier for an adult male to gain access to females during the mating season. This increased access to females is probably a major factor leading to increased mating success for social males (Hirsch and Maldonado 2011). Group living adult male coatis often fight with solitary males, and the ability to remain in a group may be a sign of strength or fitness. Alternately, female choice may play a role in allowing certain males to join the social group while excluding others. Group living males sire a large proportion of offspring despite highly promiscuous mating by females (Hirsch and Maldonado 2011). This pattern is likely driven by female mate choice, although it is not clear whether females are choosing to mate with strong males that are able to drive solitary males away from their group, or whether females choose to allow particularly desirable males to enter their group. It is also noteworthy that social males were sometimes observed leaving their groups during the mating season and mating with females from other groups.

Even though there was flexibility in male sociality in the Iguazu population, and some groups did not have adult males present for several months in a row, the degree of adult male sociality in this population was far higher than previously assumed. Observations of other ring-tailed coati populations have demonstrated that male sociality might be a species-wide behavioral pattern. Adult males have been observed in groups outside the mating season in five different coati populations in Brazil; Mangabeiras Park, Minas Gerais; Tiete Ecological Park, Sao 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 and J. Bonatti personal communication). Even though the ecology of these field sites is very different, adult male sociality has been observed in all five sites. These patterns are consistent with the hypothesis that a higher degree of adult male sociality is a species-wide trait, and not a behavior exclusively influenced by localized costs and benefits.

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