

Spoiled Brats: Is Extreme Juvenile Agonism in Ring-Tailed Coatis (*Nasua nasua*) Dominance or Tolerated Aggression?

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Abstract

Ring-tailed coatis exhibit an extreme form of juvenile agonism not found in other social mammals. Two groups of habituated, individually recognized, coatis were studied over a 2.5-yr period in Iguazu National Park, Argentina. Dominance matrices were divided by year and group, resulting in four dominance hierarchies which were analyzed using the Matman computer program. Strong general patterns were seen in both groups during both years. Adult males (one per group) were the highest ranking individuals, followed by male juveniles, female juveniles, adult females, and male and female subadults. The pattern in which young, physically inferior individuals were able to outrank larger adults is different from other social mammal species in that the juvenile coatis aggressively defended food resources and directed aggression towards older individuals. These agonistic interactions may not reflect 'dominance' in the traditional sense, and appear to be a form of 'tolerated aggression.' This tolerated aggression leads to increased access to food, and should help juveniles during a period in which they need to rapidly gain weight and grow. Because this tolerance of juvenile aggression is reinforced through coalitionary support of juveniles by adult females, agonistic patterns are also consistent with the hypothesis that juvenile rank is being influenced by high degrees of relatedness within coati groups. Although some interesting parallels exist, there is little evidence indicating that these dominance patterns are the same as those found in other social mammals such as hyenas, lions, meerkats, or Cercopithecine primates.

Introduction

Juvenile dominance over older individuals has been reported in some species of social mammals, especially matrilineal primate species. In many macaque societies, young juvenile monkeys are able to usurp resources and direct aggression toward older, larger group members due to maternal support (Kawamura 1958; van Noordwijk & van Schaik 1999). In some species of macaques, a pattern of 'youngest ascendancy' occurs in which young female offspring are supported by their mothers over older sisters

(Datta 1988, 1991; Chapais 2004). Some primates exhibit an 'age-inversed' dominance hierarchy, where female rank is inversely related to age. In this case, young breeding females are assumed to have a greater need to obtain high dominance rank to increase their reproductive success, while older females at or near the end of their reproductive lifespan have less need to maintain a high dominance rank (Hrdy & Hrdy 1976; Jones 1980; Borries et al. 1991; Koenig et al. 2004). Authors have hypothesized both juvenile tolerance and juvenile–juvenile coalitions as the proximate mechanisms driving age

inversion in langurs (Hrdy & Hrdy 1976; Borries et al. 1991).

Tolerance for juveniles has been found in cooperatively breeding meerkats. Small juvenile meerkats are tolerated during feeding and actively supported by older group members. Clutton-Brock et al. (1999), Kokko et al. (2001) and Clutton-Brock (2002) found that larger meerkat groups are able to outcompete other groups, have lower costs of raising offspring, lower mortality, and higher breeding success. These authors conclude that meerkats likely aid young juveniles to augment group size, thus resulting in higher fitness levels for older group members.

Coatis (*Nasua* spp.) exhibit similarities to other social mammals with juvenile dominance or tolerance. Coatis are female philopatric and have the ability to form matriline-based dominance hierarchies (Gompper 1996). Coati growth rates and litter sizes (2–6) are similar to other social carnivores such as meerkats, but unlike meerkats, most or all adult females give birth (Clutton-Brock et al. 1999). Births are highly seasonal and adult females nest independent from one another. Previous authors have stated that adult female white-nosed coatis (*Nasua narica*) exhibit juvenile 'tolerance,' yet do not fully describe or quantify this behavior (Russell 1982; Gompper 1995). In addition, no authors have suggested a proximate or evolutionary mechanism for the presence of this behavior. The purpose of this report is to (1) describe the system of dominance for the ring-tailed coati (*Nasua nasua*), and (2) evaluate the possible proximate and evolutionary functions of juvenile dominance/tolerance in ring-tailed coatis.

Methods

The study was conducted at the Iguazu National Park, Argentina (see Brown & Zunino 1990; Di Bitetti 2001a,b). Dominance interactions were recorded opportunistically from the PQ and PSG groups between Jul. 2002 and Dec. 2004 (Table 1). In order

Table 1: Group structure of the PQ and PSG groups. Absence of PQ subadults during 2004 was due to premature emigration not mortality

Group	Year	Adult males	Adult females	Subadults	Juveniles	Total group size
PQ	2001	1	1	0	6	8
	2002	1	1	3	3	8
	2003	1	3	2	9	15
	2004	0–1	5	0	19–25	25–30
PSG	2003	0–1	5	0	6	12
	2004	1	5	6	15–17	27–29

to place radio collars and mark animals, the coatis were captured using 32 × 10 × 12 inch Tomahawk or similar traps. The coatis were anesthetized with the assistance of a veterinarian. All individuals were individually recognized by multi-colored plastic ear-tags (Dalton Rototags, Dalton I.D. Systems, Henley-on-Thames, England), or radio-collars. Ear-tags were not placed on juveniles less than 4 mo of age. The coati groups were usually habituated within 2–3 wk. We were able to follow habituated individuals within 2 m without disturbing them in areas of open forest. Because the coatis were scared by loud noises such as broken branches, the observers followed the groups as quietly as possible.

Coatis spent most of their time foraging for ground litter invertebrates, which is consistent with another study of ring-tailed coati diet (Alves-Costa et al. 2004, 70–92% of all group scans; Hirsch 2007). Fruit and invertebrate food availability is lower during the winter months (Di Bitetti 2001b; Beisiegel & Montovani 2006; Hirsch 2007). The most important fruit species for coatis in Iguazu are pindo fruits which are available year round, but typically peak during February–May (Di Bitetti 2001b). Coatis fed on pindos during 44% of all scan samples in which fruit was being eaten (Hirsch 2007). Both groups would occasionally use areas which overlapped with human visitors. During these periods, trash or human foods were sometimes available inside the group spread (<3–4% of scan samples). When coatis were in these areas, we guarded trash cans or any non-natural food to prevent the coatis from attempting to feed.

Coatis were divided into three age classes: juveniles, subadults, and adults. When young coatis (7–8 wk of age) descended from their nests and first join the groups they were defined as juveniles, and were two to four times smaller in weight than subadults and adults (Hirsch 2007). By this age they were weaned and ate fruit and ground-litter invertebrates. During October, when pregnant adult females leave their groups to give birth, the previous year's juveniles are then 12 mo old. Subadults are defined in this study as male and female coatis between 12 and 24 mo of age. This definition is not perfect, but appears to reflect true behavioral differences. Subadult female coatis are able to conceive at 24 mo of age. At 24 mo of age, the 'newly adult' males disperse from their natal groups and become solitary. Despite being defined as 'adult' these 24-mo-old male coatis were never seen mating with an adult female, and they did not reach typical adult male body weights until 26–30 mo of age (Hirsch 2007). Unlike white-nosed coatis (*Nasua narica*), ring-tailed

coati groups typically have one adult male associated with each group (Resende et al. 2004; Hirsch 2007; C. P. Alves-Costa, pers. comm.). In cases where age could be determined, these group living adult males were all over 28 mo of age ($n = 4$). During the mating season, some groups were followed by several solitary males and adult females likely mated with multiple males. During this 2.5-yr study period female ring-tailed coatis were never observed or suspected of changing or entering other groups. This pattern of 100% female philopatry in Iguazu differed from Gompper et al. (1997) who found several examples of white-nosed coati adult females that were not related to other group members.

All agonistic interactions were recorded *ad libitum* by the author, or by field assistants trained for at least 2 mo. When both myself and one of the four field assistants simultaneously recorded an agonistic interaction, over 95% of the samples were identical ($n = 63$). When an agonistic interaction was observed, the initiator, recipient, winner, context of the aggression, and type of agonism were recorded. In some cases, the individual who initiated the interaction was not seen, but the winner and loser were observed. The winner was defined as in Gompper (1996). If one individual directed agonism toward a conspecific, and the recipient did not defend themselves, the recipient was considered the loser. If an individual gained or maintained possession of a food item after an agonistic interaction, they were defined as the winner.

All interactions with unknown individuals were not used in the dominance hierarchy analyses. A larger data set ($n = 1575$) which also included unknown individuals was used in an analysis of effects of age, sex, context, and type of agonism. In this larger data set, some individuals were recognizable by age class but not by individual ID. Six types of agonism were recorded (in order from least to most aggressive); avoidance, displacement, aggressive vocalization, lunge, bite, chase, and escalated fighting. The most common type of agonism, lunging, occurred when one coati would lunge their head in the direction of another. This type of interaction was typically, but not always, accompanied by a sharp aggressive vocalization. Any interaction which involved more than two individuals was noted and used in a separate analysis. Polyadic interactions were often difficult to fully observe, thus the percentage of coalitionary interactions in the data set is likely an underestimate. Agonistic events were classified as coalitions when two individuals directed

agonism at a third, or a third individual came to the aid of another during an agonistic event.

Dominance matrices of dyadic interactions were constructed using two groups (PQ and PSG), with the 2003 and 2004 seasons separated (Nov. 2002–Oct. 2003, Nov. 2003–Oct. 2004). The four dominance matrices were reordered and all matrix statistics were determined using the Matman program version 3.1 (de Vries et al. 1993; de Vries 1995). Average dominance ranks were adjusted for group size. The rank of each individual was divided by group size, and then averaged by age/sex class. This resulted in a value between 0 and 1 for each age sex class, which was then multiplied by the average group size (20.75). The resultant values represent the average rank per age/sex class in a standardized average group of 20.75 individuals. Any agonistic interaction that simultaneously involved more than two individuals was classified as a coalitionary interaction. These interactions were not necessarily coordinated. For example, if two juveniles simultaneously attacked an adult male, it was recorded as a coalition. If the two juveniles attacked the adult male sequentially, they were recorded as two separate dyadic interactions. Coalitionary interactions were broken down by age/sex class. In the analysis of adult female support for juveniles, maternity was assigned using grooming data (Hirsch, unpubl. data). All observed grooming interactions were entered into a similarity matrix, and juveniles were assigned maternity based on the number of grooming bouts received by each adult female (which were highly skewed toward the presumed mothers). Only individual juveniles that were groomed significantly more by one female than any other females was assigned a mother. Maternity of juveniles in the PQ group during the 2003 season were excluded from the analysis because the grooming data were not sufficient to statistically determine maternity.

Results

Dominance Patterns

A total of 1079 dyadic interactions were used in the dominance matrix analyses (PQ 2003 = 93, PQ 2004 = 266, PSG 2003 = 184, PSG 2004 = 539). A representative dominance matrix is shown in Table 2, and the other three dominance hierarchies can be found in Hirsch (2007). Adult males had the highest average rank of any age/sex class (4.3), followed by male juveniles (5.9), female juveniles

Table 2: Dominance hierarchy for the PQ group during 2003

	Age/sex	IK	CL	LW	PB	PU	AK	TC	SB	AA	MA	AY	GZ	AN	DA	CC	Total
1	IK AM	–	2	1	1	1	0	0	2	1	2	0	1	0	0	2	13
2	CL JM	0	–	2	1	0	0	0	0	0	1	0	1	0	0	1	7
3	LW JM	0	0	–	1	1	0	0	0	1	1	0	1	0	0	0	6
4	PB JM	0	0	1	–	2	1	0	0	0	0	0	1	0	0	0	5
5	PU JM	1	1	0	0	–	1	0	0	0	0	1	1	1	1	2	9
6	AK JM	0	0	1	0	0	–	1	1	1	0	0	3	0	0	1	8
7	TC JM	0	0	0	3	0	0	–	0	0	0	0	1	0	0	1	5
8	SB JF	0	0	0	0	0	0	0	–	0	0	1	0	0	0	0	1
9	AA JF	0	0	0	0	0	0	0	0	–	0	0	0	2	0	1	3
10	MA AF	0	0	0	0	0	0	0	0	0	–	0	0	5	1	0	6
11	AY AF	0	0	0	0	0	0	0	0	0	0	–	1	1	2	0	4
12	GZ AF	0	0	1	1	0	0	0	0	0	0	1	–	12	1	1	17
13	AN SF	0	0	0	0	0	1	0	0	0	0	1	1	–	0	1	4
14	DA SF	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0
15	CC JF	0	0	0	0	0	0	0	0	1	0	0	1	0	0	–	2
Total		2	3	6	7	5	4	1	3	4	5	4	12	21	5	10	93

Rows represent winners and the columns the losers in agonistic encounters. Age/sex classes are coded as follows: AM, adult males; JM, juvenile males; JF, juveniles females; AF, adult females; SF, subadult females.

Table 3: Dominance hierarchy statistics

Group/year	PSG 2003	PSG 2004	PQ 2003	PQ 2004
Matrix total	184	539	93	266
Landau's linearity index (h)	0.629	0.270	0.125	0.125
Landau's corrected index (h')	0.675	0.306	0.221	0.185
Expected value of h or h'	0.231	0.107	0.176	0.100
Directional consistency index	0.630	0.703	0.785	0.752
% of unknown relationships	19.70	33.62	54.17	59.61
% of one-way relationships	46.97	47.86	37.50	32.51
% of two-way relationships	33.33	18.52	8.33	7.88
% tied relationships	1.52	6.84	7.50	3.94
Improved linearity test (R-tailed probability)	<0.001	<0.001	0.296	0.019

(11.3), adult females (16.3), subadult females (17.6), and subadult males (18.4). With the exception of the PQ group during the 2003 season, all dominance hierarchies were significantly linear (Table 3). The directional consistency indexes varied from 0.63 to 0.78, and a high proportion of two-way interactions were recorded (Table 3). Even though the number of reversals was relatively high, the patterns found by age/sex class were still robust. Adult males won 68.0% ($n = 100$) of interactions against juveniles, 85.5% ($n = 62$) against adult females and 92.3% ($n = 52$) against subadults. Juveniles (both male and female) won 84.2% ($n = 234$) of interactions with adult females and 82.8% ($n = 87$) against subadults. Juvenile dominance over adult females did not vary in relation to the adult female:juvenile ratio

(percentage of interactions won and adult female:juvenile ratios; PSG 2003 = 80.7%, 5:6, 2004 = 89.0%, 5:15; PQ 2003 = 82.4%, 3:9, 2004 = 82.2%, 5:23) ($p = 0.730$, linear regression). Juveniles directed aggression toward their presumed mothers in 19.9% of interactions toward adult females (33 of 166). Because the PQ and PSG groups during years in which maternity could be assigned contained five adult females, juveniles were not directing more or less aggression toward their mothers than at random (G -test, $df = 1$, $\chi^2 = 0.001$, $p = 0.975$).

Adult females won 78.8% ($n = 118$) of interactions against subadults. These interactions were more common when juvenile coatis were less than 6 mo old. A total of 83 cases of adult females winning agonistic interactions vs. subadults were observed (from the PQ 2003 and PSG 2004 group years). Of these interactions, 83.13% occurred when juvenile coatis were 6 mo of age or less (December–May). Few or no interactions were recorded from October and November when most groups had disbanded. The lopsided pattern was further evident when compared with the total number of agonistic interactions recorded (December–April = 274, May–September = 488). Adult female domination of subadults represented 25.18% of all agonistic interactions during the first time period, and then dropped to 3.07% when juveniles were older than 6 mo of age. Although average rates of aggression could not be assigned because of the ad libitum sampling protocol, it appears that rates of aggression between

adult females and subadults vary significantly over time.

Context and Type of Agonism

Almost all agonistic interactions where the context was known occurred during feeding and foraging (96.8%). A small fraction (3.2%) occurred in social contexts such as grooming, rest, or play. It was not possible to accurately determine the context in 14.6% of the interactions. These indeterminate samples were often observed after the initiation of the agonistic interaction or the context appeared ambiguous to the observer. Differences were found in the type and context of agonism by age class. When an agonistic interaction was instigated by a juvenile, it typically occurred during fruit feeding (51.1%). Adults and subadults instigated agonism during fruit feeding much less than juveniles (28.6% and 26.4% respectively). When juveniles initiated an agonistic encounter, they were more likely to lunge at their opponents (78.4%) than subadults and adults (57.6% and 42.4% respectively), and less likely to chase or fight with their opponent (juveniles = 13.5%, subadults = 26.3%, adults = 40.5%). Fights between adults and subadults were particularly violent, and 47.1% involved chasing or escalated fighting (Table 4). Additionally, in 18.9% of the interactions between adults and subadults, the subadults actively avoided the adult. This high number of avoidances compared with other age/sex classes probably reflects a strategy of the subadults to escape aggression from adults by using spatial avoidance. There were no significant differences between the sexes in the type of agonism used.

Pindo palm fruits were the most common resource at which food-related agonism took place (33.6% of all agonistic interactions). Coatis were observed feed-

ing on pindo fruits during 8.45% of foraging scan samples, and pindo made up 43.76% of fruit foraging time. The amount of agonism observed during pindo foraging was statistically more than expected based on foraging time (G-test, $df = 1$, $\chi^2 = 540.65$, $p < 0.001$). Although some coatis would climb into palm tree fronds to eat fruit (typically one to five individuals at one time), the bulk of the group usually consumed fallen fruits in the fruit shadow (which typically ranged from 1.5 to 3.5 m in diameter). When feeding below these fruit trees, juveniles and adult females were rarely forced to leave the fruit shadow, but would aggressively compete for individual fruits. On the other hand, older individuals, especially subadults, were sometimes chased out of these feeding patches or avoided them altogether (Hirsch, unpubl. data). The common usage and clumped distribution of pindo fruits may be important in driving the type of agonistic encounters found. These dietary patterns appear analogous to the reliance of *N. narica* on *Scheelea* fruits on BCI. There were no differences in agonistic patterns when coatis fought over non-natural foods. There was also no indication that agonistic patterns changed during the peak tourist season (July and August), which also corresponded to the period of lowest natural food availability.

Coalitionary Patterns

Coalitionary interactions occurred at similar levels as recorded in *N. narica* (Gompper et al. 1997) ($n = 79$, 6.8% of all interactions with known individuals). Coalitions occurred in almost every age/sex class combination possible. Thirty-three of these coalitionary interactions involved adult females supporting juveniles. Adult females aided juveniles against subadults ($n = 6$) and adults, both male and females

Table 4: Percentage of different types of aggression recorded during dyadic encounters separated by age class. Type of aggression is ordered from least to most aggressive

Winner-Loser	Avoidance	Displacement	Vocalization	Lunge	Bite	Chase	Fight	n
Adult-adult	6.45	1.08	8.60	43.01	1.08	35.48	4.30	93
Adult-juvenile	5.13	3.42	17.95	58.12	0.00	14.53	0.85	117
Adult-subadult	23.40	6.38	3.55	17.73	1.42	42.55	4.96	141
Subadult-adult	9.09	0.00	3.03	33.33	9.09	39.39	6.06	33
Subadult-juvenile	6.06	0.00	3.03	69.70	15.15	6.06	0.00	33
Subadult-subadult	0.00	0.00	0.00	73.08	3.85	19.23	3.85	26
Juvenile-adult	1.16	1.54	14.29	59.07	5.41	17.37	1.16	259
Juvenile-juvenile	0.48	0.73	3.15	84.99	4.36	5.57	0.73	413
Juvenile-subadult	1.15	1.15	1.15	73.56	1.15	19.54	2.30	87

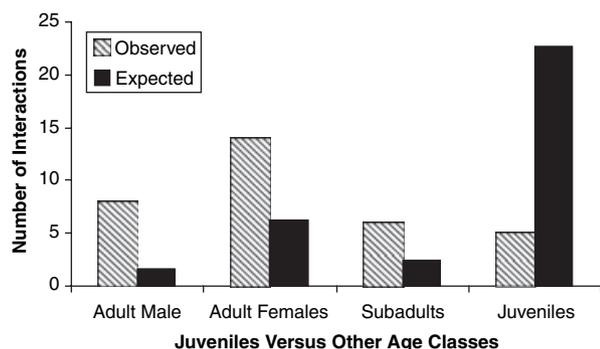


Fig. 1: The number of fights in which adult females supported juveniles. Columns separated by age/sex class of opponent with whom the juvenile fought against (G-test, $\chi^2 = 43.47$, $p < 0.001$)

($n = 22$), more frequently than against juveniles ($n = 5$) (G-test, $\chi^2 = 43.47$, $p < 0.001$) (Fig. 1). Of these 33 cases, the maternity was known/suspected in 19 cases. In 12 of the 19 cases, the supported juvenile was not the offspring of the adult female who helped. The females who supported juveniles were likely their aunts or grandmothers. In one case a subadult female was observed supporting a juvenile vs. an adult male. No other instance of a juvenile being aided by subadults, or an adult male was seen. No coalitions were recorded which only involved juveniles and not at least one older individual. Juveniles formed coalitions among themselves toward older individuals a total of 14 times, 8 times against adult females, 4 times against subadults, and 2 times vs. adult males.

Discussion

Despite a high number of reversals, patterns of coati dominance were clear. Adult males were the highest ranking on average, followed by juvenile males, juvenile females, adult females, and subadults. The patterns found with respect to adult females and juveniles are different compared with previously studied dominance patterns in primates and other social mammals, but may fall somewhere between the nepotistic aggressive social systems of macaque societies, and the tolerant cooperative breeding system of meerkats. The relationship between adult females and subadults was particularly hostile when juveniles were 6 mo of age or less. During this period, there were a large number of escalated aggressive interactions between adult females and subadults, and subadults were commonly seen avoiding adult females. This agonism likely played a large factor in the premature emigration of the PQ subadults during 2004.

Possible Mechanisms Leading to Juvenile 'Dominance'

Matrilineal support

The patterns of dominance found in ring-tailed coatis were not similar to female bonded primate and hyena societies with matrilineal dominance hierarchies. In these social systems, juveniles typically rank just below their mothers, and above females of lower ranking matriline (Cheney 1977; Hausfater et al. 1982; Chapais 1992; Holekamp et al. 1996; Engh et al. 2000; Chapais et al. 2001). In ring-tailed coatis almost all juveniles were ranked above all adult females, a pattern unlikely to be produced through maternal coalitionary support. Even though support from mothers could not have been the sole mechanisms driving juvenile dominance in ring-tailed coatis, the pattern in which all adult females supported all juveniles appeared to play an important role in shaping the dominance system. Females did not preferentially support their own offspring, but did support juveniles over older individuals more than expected by chance. Adult female white-nosed coatis have been found to direct more aggression toward unrelated females (Gompper et al. 1997), but it is unclear if this behavior would transfer to within-group offspring of unrelated females as well. In order to properly test the effects of inclusive fitness on juvenile support and tolerance, it would be ideal to study a group where at least one of the adult females had immigrated into the group and was not closely related to the other adult females.

Juvenile coalitions and mobbing

Juvenile coatis may be able to form coalitions with each other in order to dominate older individuals (Chapais & Gauthier 2004). Little evidence was obtained to support this hypothesis. Only 14 coalitions of juveniles against older individuals were recorded. Even if juveniles do not actively form coalitions against older individuals, their sheer numbers in the group might allow them to 'mob' other group members. In several cases, we observed an adult female run away from small concentrated food patches (such as pindo fruit shadows) after being repeatedly attacked by several juveniles acting independently. It appeared that the aggression directed toward the adults and subadults was so bothersome and annoying that the costs of aggression outweighed the benefits gained by feeding. If this mobbing hypothesis is correct, juvenile dominance

patterns should vary depending on the relative numbers of adult females and juveniles. However, the patterns of juvenile dominance were the same for all group years despite wide variance in the adult female/juvenile ratio (from 5/6 to 5/25). Juveniles in the group with the highest adult female to juvenile ratio (PSG 2003 = 5/6) won a similar percent of interactions vs. adult females compared with other group years, thus there was no discernable effect of adult female juvenile ratios on patterns of juvenile dominance.

Female tolerance for group augmentation

If group augmentation is driving female tolerance, one would expect to find similar circumstances to those found in meerkats. However, coatis are not cooperative breeders, thus most adult females have offspring in the group and would be predicted to act in their offspring's interest over that of others. Although longer term demographic data would be ideal for hypothesis testing, it appears that no clear relationship is present between group size and mortality or breeding success, thus group augmentation does not appear to be a plausible reason for juvenile dominance in ring-tailed coatis. In addition, juvenile coatis regularly attacked and were aggressive toward older individuals, which is not a pattern predicted by the group augmentation hypothesis. One parallel between ring-tailed coatis and meerkats is that both species have relatively rapid life histories compared with primates and hyenas. Because juveniles in species with faster life histories are particularly vulnerable, and need to rapidly gain weight, the relative value of food items may be greater for juveniles vs. older, more self sufficient individuals.

Female tolerance for inclusive fitness benefits

Demographic patterns appear to provide ideal conditions for high r values between adult females (Hirsch 2007). If this is correct, the high degree of relatedness between adult females and assorted juveniles may influence the costs and benefits of aggression. If this is true, it is predicted that ring-tailed coati groups will exhibit degrees of relatedness far higher than similar matrilineal mammals such as cercopithecine primates, white-nosed coatis, and hyenas. In order to properly test this hypothesis, a comprehensive analysis of the DNA samples taken from the PQ and PSG groups will need to be conducted.

Further discussion

Why do adult females support juveniles but not subadults? Presumably, subadults and juveniles are equally related to the adult females. In some species of primates, adult females support their younger offspring over older offspring (Kawamura 1958; van Noordwijk & van Schaik 1999). This pattern has been ascribed, in part, to the higher reproductive values of younger siblings (once they have reached the age of first reproduction) compared with their older sisters (Schulman & Chapais 1980). In some cases, juvenile dominance can occur due to the support of non-kin allies (Chapais & Gauthier 2004). In these cases, non-kin were forming bridging alliances vs. older sisters (i.e. in an $A > B > C$ rank order, A helps C outrank B). This hypothesis is an unlikely explanation for the evolution of juvenile dominance/tolerance in coatis because juvenile coatis are not likely to be consistent or effective coalition partners which would allow bridging coalitions against higher ranking individuals. Although juveniles and adult females sometimes formed coalitions vs. subadults, the major source of aggression toward subadults was direct dyadic aggression from adult females and juveniles. These agonistic interactions were concentrated in periods when the juveniles were particularly young (<6 mo of age). The increased aggression toward subadults during this time period could either coincide with the period in which the juveniles have the highest nutritional needs or be a result of the adult females reinforcing the new dominance relationships between subadults and their conspecifics.

Juvenile support may be the result of the greater relative nutritional requirements and higher vulnerability of juvenile coatis (cf. Datta 1988). It is presumed that high juvenile growth rates need to be accompanied by high energy intake, thus the need for food may be higher in juveniles compared with subadults. Support of juveniles would thus serve to increase a female's long-term reproductive value (Kaufman 1962; Gittleman & Oftedal 1987). Tolerance of juvenile aggression by adult females may allow coati juveniles to force their way into spatial positions with the highest foraging success, and effectively give the juveniles priority access to resources (Hirsch, unpubl. data). The pattern of increased aggression toward subadults when juveniles are 6 mo or less may provide additional support for the hypothesis that adult females are aiding juveniles when they have greater nutritional needs.

Why don't other social mammals exhibit similar dominance patterns to ring-tailed coatis? Despite observations of youngest ascendancy and age-inversed hierarchies in primates, and juvenile tolerance in meerkats, no other known social animal has a system of dominance exactly like ring-tailed coatis. Coatis may fall somewhere between macaques and meerkats. In some macaque species juveniles aggressively fight over food against older larger individuals. The success of these interactions depends on coalitionary support from other group members, particularly close kin (Chapais et al. 2001). The resultant macaque dominance hierarchies are in large part organized by matriline, with daughters being ranked just below their mothers. On the other end of the spectrum, cooperatively breeding animals exhibit juvenile tolerance with little or no matrilineal basis. In the case of meerkats, large cohorts from one female are present in the group, and juveniles are tolerated by all group members (Brotherton et al. 2001). These juveniles can then non-aggressively steal food from others at will. This tolerance of juveniles during feeding is also found in cooperatively breeding primates (Goldizen 1987). Lion social systems are a useful comparison because they can contain multiple juveniles and subadults from different mothers, which is similar to coatis. In this case, adult females are dominant over both age/sex classes but cubs may gain access to carcasses because the dominant adult male tolerates their presence (Schaller 1972a,b). This behavior is not seen in ring-tailed coatis and is consistent with the pattern that group living adult males are unlikely to have fathered many juveniles currently in the group (although it may have occurred in the PSG group 2004).

The social system of ring-tailed coatis differs from both of the previous examples in that coati juveniles are actively and aggressively fighting for food items, rather than being passively tolerated by older individuals, yet, unlike macaques, this system is not based on direct matrilineal support. Despite the lack of matrilineal dominance hierarchies, coalitionary support from closely related adult females may drive, or at least help reinforce juvenile dominance. Demographic factors could lead to high r values between adult females and juveniles which could lead to adult female tolerance during aggressive interactions.

The presence of juvenile 'dominance' in ring-tailed coatis could be influenced by their feeding ecology. Unlike many small-medium sized social carnivores such as meerkats and mongoose, coatis spend a significant percentage of their foraging time eating fruit (Hirsch 2007). Fruit trees are often

found in clumped defensible patches which promote contest competition, wherein dominant individuals could defend the resource and prevent subordinates from feeding (Vogel 2005). Small ephemeral items such as leaf litter invertebrates are not predicted to promote contest competition (unless long handling times are necessary) and should thus result in scramble competition (van Schaik 1989). The patterns of coati aggression do not precisely fit into these two categories. Coatis were often observed fighting while foraging on leaf litter invertebrates. These fights typically occurred when a coati was digging a large pit to extract an invertebrate, after which the victorious coati usurped the hole and resumed pursuing the prey. In other cases, coatis fought over large invertebrates such as annelid worms or large crickets which could not be eaten in one bite. Although aggression occurred during invertebrate foraging, fruit feeding was the most common context in which aggression was recorded (pindo fruits in particular). The distribution of fruits underneath and on pindo trees is spatially clumped and thus predicted to promote contest competition. When a group arrived at a pindo tree, the juveniles would often aggressively defend individual fruits and their immediate personal space. Unlike some species of primates, dominant coatis did not regularly defend entire fruit patches, and most aggression occurred within the fruit patch. In a study of *N. narica*, Gompper (1996) found that subadults had lower foraging success than adult females when feeding on *Scheelea* fruits which is probably related to aggressive competition. Because juvenile coatis did not exclude older individuals from the foraging patches, the feeding success of adult females was not predicted to have been substantially reduced due to juvenile aggression. Pindo foraging rates of the different age/sex classes were all similar, but the total time spent feeding on Pindo was lower for subadults than adult females and juveniles (Hirsch 2007). This pattern is consistent with the hypothesis that subadults are either being pushed out of fruit patches, or actively avoid them to reduce their level of received aggression. These patterns indicate that their may be very little cost to adults for tolerating juvenile aggression, while subadults are suffering a reduction in feeding due to their subordinate status.

Conclusion

The patterns of dominance exhibited by ring-tailed coatis are different from any previously published

social animals. Whether this behavior only occurs in Iguazu, or is a species-wide phenomenon is currently unknown. Although previous work on white-nosed coatis has suggested that adult females are 'tolerant' of juveniles, nothing resembling the patterns described here has been reported. It is unclear if these patterns have not been described because no researchers have collected data on juvenile dominance, or because it does not occur. Because patterns of juvenile dominance are so visibly obvious in ring-tailed coatis, I believe the latter is more plausible, and white-nosed coatis simply do not exhibit this pattern. If high within-group relatedness is helping to drive juvenile dominance, it is predicted that this social system might not be found in every population of *N. nasua*. In order to test these hypotheses further, it would be ideal to study populations with higher predation rates, occasional female transfer, or lower reproductive rates.

It is not surprising that adult females would support offspring and close kin, but it is not clear why coati 'tolerance' is actually quite violent. Even though juvenile coatis were less aggressive during dominance interactions than older individuals, they still attacked older individuals during feeding (passive interactions like avoidance and displacements occurred in only 2.6% of the dominance interactions that juveniles won). If adult females coatis choose to tolerate juveniles and allow them to have priority access to food, why do the juveniles regularly attack the adult females? In order to fully test questions regarding the origin of these patterns it is first necessary to confirm that the coatis in the Iguazu study groups are in fact closely related. Tissue samples taken from the coatis during the trapping procedure can be used for a genetic analysis to determine the degree of relatedness between females and confirm suspected/inferred matrilineal relationships. In the future it would then be ideal to investigate patterns of dominance in groups where at least one adult female is not closely related to the other group members. If so, this could provide a strong test of the theory that inclusive fitness is helping drive the evolution and maintenance of juvenile dominance in ring-tailed coatis. Another useful experiment would be to change the costs of feeding competition. There currently appears to be little evidence that adult females are suffering a reduction in food intake because of their tolerance of juveniles. It is currently unknown if adult females would tolerate food theft and aggression from juveniles during a period of extreme food scarcity.

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