Behav Ecol Sociobiol (2006) 61:173–182
DOI 10.1007/s00265-006-0248-3

ORIGINAL ARTICLE

Determinants of vigilance behavior in the ring-tailed coati (*Nasua nasua*): the importance of within-group spatial position

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Received: 14 February 2006 / Revised: 26 May 2006 / Accepted: 2 July 2006 /

Abstract Individuals living in social groups are predicted to live under unequal predation risk due to their spatial location within the group. Previous work has indicated that individuals located at the edge of groups have higher "domains of danger", thus are more likely to engage in vigilance or antipredator behavior. We studied the determinants of vigilance behavior in two groups of ring-tailed coatis in Iguazu National Park, Argentina. In addition to the expected pattern that coatis were more vigilant at the edge of the group, we found that individuals were particularly vigilant at the front edge of the group. This pattern conforms to predictions of differing predation risk caused by sit-and-wait predators with respect to mobile animal groups. In addition, coatis exhibited less vigilance when the number of neighbors within 5 m and group size increased. Of the three spatial variables tested, within-group spatial position was the most important predictor variable determining vigilance levels. These results confirm that spatial position has major effects on vigilance behavior, and that group directionality is an important factor which should be taken into account when measuring vigilance behavior. Coatis were more vigilant when juveniles less than 6 months old were in the groups. The presence of these young juveniles also affected the relationship between alarm response and vigilance levels. Coatis were more vigilant after strong alarm reactions, but only when young juveniles were not present in the groups. This may indicate that coatis give differential responses to alarm calls depending on the age of the caller. A comparison of antipredator vigilance between coatis and sympatric capuchin monkeys is consistent with the hypothesis that terrestriality leads to higher perceive predation risk for coatis.

Keywords *Nasua nasua* · Within-group spatial position · Vigilance behavior · Sympatric capuchin monkeys · Predation risk

Introduction

Predation is regularly cited as a major reason why animals live in groups (Krause and Ruxton 2002). Not only is predation risk expected to vary between groups of different sizes, but individuals within social groups live under different risks of predation due to age, size, and spatial factors (Elgar 1989; Janson 1990a,b). Vigilance behavior is commonly used by animals to detect predators, and the same factors which affect differential predation risk within groups are expected to affect levels of vigilance behavior.

Vigilant animals have been found to be less susceptible to predation, flee from predators before nonvigilant conspecifics, and detect predators before nonvigilant conspecifics (FitzGibbon 1989; Lima 1994; but see Cresswell et al. 2003). It is thus assumed that individuals who suffer higher predation risk will spend more time being vigilant.

Communicated by: P. Bednekoff

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This increased time devoted to vigilance behavior typically takes away from other activities such as feeding (Cords 1990; Rose 1998; Coolen et al. 2001; although see Treves 2000), and thus represents an energetic or time cost to animals.

Most models of vigilance behavior focus on how detection and dilution effects change with group size. Assuming constant levels of individual vigilance, larger groups are predicted to detect predators earlier due to the greater number of individuals scanning the environment. When a predator successfully attacks a group, the average individual risk of predation will be the inverse of group size; thus, individuals living in large groups are predicted to have lower threats of predation. Models have been developed to examine the relative effects of these two mechanisms (Dehn 1990; Beauchamp 2003) and in most cases, result in asymptotic decreases in individual vigilance levels as group sizes increase.

One factor which has typically not been incorporated into models of vigilance behavior is within-group spatial position. The original “selfish herd” theory developed by Hamilton (1971) predicted that individuals on the periphery of groups undergo higher risks of predation due to fewer neighboring conspecifics, and thus have higher “domains of danger”. This prediction has been supported in detailed studies by Viscido et al. (2001) and other studies have found that the effects of neighbor density on individual vigilance levels may be greater than group size effects (Blumstein et al. 2001a,b). These results indicate that animals may perceive individual levels of predation risk as a function of the density of neighboring conspecifics and not overall group size. In cases where a sit-and-wait predator attacks the first individual encountered, the risk of attack is predicted to be highest in individuals on the front edge of groups (Vine 1971, Krause 1994, Bumann et al. 1997). This should result in higher vigilance levels at the front edge of groups, yet most studies of vigilance in relation to spatial position have only measured centrality, and not the spatial position of the focal individual with respect to the direction of the group (see Janson 1990b, Black et al. 1992, Caro 2005 Table 5.3). These effects are predicted to be more pronounced in prey species which are terrestrial as opposed to aerial predators (Taylor 1988).

A major complicating factor in studies of vigilance is that visual scanning can serve multiple purposes, such as looking for food or conspecifics (Elgar 1989; Steenbeek et al. 1999; Treves 2000; Hirsch 2002; Beauchamp 2003). Of particular concern is scrounging, or monitoring of conspecifics for food joining opportunities. When scrounging is incorporated into models of vigilance behavior, predictions relating vigilance levels to group size change, and in some cases do not result in a clear negative relationship between vigilance and group size (Beauchamp 2001). In some species such as nutmeg mannikins (*Lonchura punctulata*), antipredatory vigilance and scrounging are incompatible and scrounging can be controlled for when determining causes of vigilance behavior (Coolen et al. 2001). Ring-tailed coatis (*Nasua nasua*) typically discover new food sources by olfaction (BT Hirsch unpublished work); thus, visual scanning probably does not commonly function to detect scrounging opportunities. By studying vigilance in this species, we believe that producer–scrounger tactics had few, or only minor, effects on vigilance behavior in this study.

This project is part of a larger study on the socioecology and determinants of social foraging in the ring-tailed coati (BT Hirsch, unpublished work). The ring-tailed coati is ecologically similar to the better known white-nosed coati (*N. narica*). Like their close relatives, ring-tailed coatis are primarily diurnal and spend their foraging time searching for ground litter invertebrates and eating fruit. Observed group sizes in Iguazu ranged from 6–65 individuals. Groups are mainly comprised of philopatric adult females and their offspring, and in contrast to *N. narica*, groups almost always included an associated adult male (also see Resende et al. 2004)

Hass and Valenzuela (2002) have demonstrated a negative relation between group size and per capita rates of predation in *N. narica*. Previous work on coati vigilance behavior has shown a negative relation between group size and vigilance levels, and differences in vigilance levels due to age (Russell 1979, Burger and Gochfeld 1992). When coatis encounter predators or other “frightening” stimuli, they typically give alarm calls and run up the nearest tree or run away from the stimuli. The number of individuals who respond, amount of time spent in trees and off the ground, and number and intensity of the alarm calls vary with the strength of the stimuli or perceived threat.

The purpose of this study was to determine what factors influence the vigilance behavior of coatis. We predicted that coatis will have higher vigilance levels with fewer neighbors, when in larger groups, and when at the front edge of the group. Due to higher mortality rates of young individuals (Hass and Valenzuela 2002, BT Hirsch, unpublished data), we predicted that adult individuals in groups containing young juveniles (less than 6 months of age) will exhibit higher levels of vigilance for protecting their offspring. We predicted coatis would have higher levels of vigilance after alarm calls, and that vigilance levels would be affected by the activity pattern of the focal animal (similar to patterns found in comparable studies of primates). Furthermore, because the bulk of potential predators in Iguazu are terrestrial, we predicted that the vigilance levels of coatis will be higher than sympatric capuchin monkeys because coatis spend much larger amounts of time on the ground than the monkeys.

Materials and methods

The study was conducted at the Iguazu Falls National Park, Argentina (54°W, 26°S) (see Brown and Zunino 1990; Di Bitetti 2001a,b). Focal samples were taken on two groups (or bands) of habituated coatis between June 17, 2003 and March 16, 2004 (PSG group N=664, PQ group N=412). The PQ and PSG groups had similar group sizes during 2003 (9–15 individuals) and 2004 (27–29 individuals) (Table 1). These groups were generally located within a 4.5-km radius around the CIES biological station (see Di Bitetti 2001a for a map of the area). 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 using a solution of 50% Ketamine and 50% Xylazine, and 0.5 ml of atropine sulfate was injected 20 min before the anesthesia. All individuals were individually recognized by multicolored plastic eartags (Dalton Rototags), radio-collars, or the absence of the two (typically only one individual per group). The coatis were usually habituated within 2 to 3 weeks. Although the coatis were typically not alarmed when we walked inside the group and within 2 m of focal individuals, they were frightened by loud noises we sometimes produced by breaking branches, cutting vegetation with a machete, sneezing, and other assorted accidental noises. To facilitate better data collection, we typically followed the coatis from the trail system or in areas where the vegetation permitted us to walk off the trail system without the use of a machete. When recording focal samples, the observer (YDB) typically stopped movement and remained silent, thus eliminating any accidental disturbance of the animals' behavior.

At Iguazu, there are six species of felids (*Panthera onca*, *Puma concolor*, *Leopardus pardalis*, *L. tigrinus*, *L. wiedii*, and *Herpailurus yaguaroundi*); the first three of which are presumed to be the major predators of coatis over 3 months of age. The tayra (*Eira barbara*) is also a potential predator (Di Bitetti, personal communication). The two species of raptors (*Spizaetus ornatus* and *S. tyranus*) are rare and probably not normal predators of coatis in this field site. Ground predator presence was based on the results of a camera trap study in Iguazu National Park undertaken concurrently with the coati project (Di Bitetti and Paviolo, unpublished data). Raptor presence was based on communications with scientists working in the area during the past 15 years (Janson, Di Bitetti, and Amfuso, personal communication).

Recording vigilance

Vigilance was defined in this study when a coati stopped all body movement, and silently looked with their head raised from the ground. Ten second continuous focal samples were taken by YDB and the time spent vigilant during the sample was recorded (Martin and Bateson 1996). The percentage of time spent vigilant was calculated as the summed duration of all vigilance bouts in a 10-s sample, divided by ten. Vigilance bouts were recorded to the nearest 1.0 s interval using a stopwatch that beeped at 1 s intervals. Short focal samples were recorded due to: (1) the rapid rate at which some behavioral and ecological variables changed, (2) difficulty in maintaining continued visibility of a focal individual for longer periods, and (3) to be directly comparable to a previous study of sympatric capuchin monkeys (Hirsch 2002). Taking data on individuals in a preordered manner was nearly impossible, thus samples were taken opportunistically on visible animals and preferentially on adults and undersampled individuals. Vigilance samples were taken at least 2 min apart, and individuals were never resampled within 10 min. The independence of consecutive samples was tested using the method reported in Schoener (1981, Appendix 2).

The definition of vigilance in this study is similar to other studies of coati vigilance (Russell 1979; Burger and Gochfeld 1992; Burger 2001), but we have limited our definition to times when the coatis were motionless to differentiate between vigilance and when the coatis hold their heads steady during travel. Typically, when a coati is vigilant, the animal will stop whatever behavior it is engaged in, freeze body movement, and hold its head in an upwards position for approximately 1–3 s. Using these criteria, vigilance is mutually incompatible with feeding, traveling, and other behaviors. For example, when traveling, coatis would often stop, stand motionless with their head upwards, and afterwards continue traveling. As in Hirsch (2002), vigilance bouts were classified as social monitoring when the bouts were clearly and obviously directed towards conspecifics, a noise produced by a conspecific (alarm calls not included), or followed the bodily movement of a conspecific. In the present study, all social monitoring bouts were excluded from the analyses (social monitoring was present in 8.23% of focal samples N=87).

Ecological and behavioral variables

Seventeen associated ecological and behavioral variables were recorded in association with the vigilance samples. Date, time, group, and individual ID were recorded for all samples. The individual IDs were then grouped by age and sex for the analyses. The number of juveniles (3–12 months old), subadults (13–24 months old), and adults (greater than 24 months) within 5 m from the focal individual were recorded during the sample. The within-group spatial position of the focal sample was recorded as in Janson

(1990a,b) and Hall and Fedigan (1997). These distinct spatial positions were pooled into seven different spatial categories for the purpose of analysis (1. front edge, 2. front middle, 3. center, 4. back middle, 5. back edge, 6. side periphery, and 7. side middle). The behavioral activity of the focal individual and the group during the sample was recorded (terrestrial food search, eating fruit, travel, rest, and play). The category of substrate use (terrestrial or arboreal) was recorded both for the focal individual and the group. The travel speed of the group was recorded and graded on a scale of 0–4 (0 = no movement, 4 = rapid travel). The presence of alarm calls within 10 min of the focal sample was recorded, as well as the type of alarm response. Alarm responses were graded on a scale of 0–3 based on the strength of the initial response to an alarm call (0 = no alarm call within 10 min of the focal sample, 1 = <33% of the group climbed a tree after the alarm call, 2 = 33–66% of the group climbed a tree, and 3 = >66% of the group climbed a tree). The number of individuals present in the focal animal's group and the presence or absence of juveniles less than 6 months of age were also used as predictor variables.

Analyses

Because of significant effects of age on vigilance behavior in the original database (logistic regression λ^2=14.179, P<0.0002, N=1,815), samples from all coatis less than 24 months old were excluded. All samples taken when focal animals were playing were excluded due to low sample sizes (N=12). The distribution and duration of vigilance bouts was similar to a previous study (Hirsch 2002). Most vigilance bouts were less than 3 s in duration (79.7%) and only 8.7% of samples were truncated while the focal animal was vigilant. It was rare for the coatis to be vigilant for extended periods of time (>10 s); thus, the use of short samples was deemed appropriate. The independent variables were entered into a Generalized Linear Model (GdLM) and analyzed using Akaike's information criterion (AIC) in STATISTICA (version 5.5, StatSoft, 2000). The dependent variable was the presence or absence of vigilance (excluding known social monitoring bouts) in the 10-s bout, modeled as a binomially distributed logistic variable. The presence or absence of vigilance in the samples was positively correlated to the percentage of time spent vigilant (logistic regression λ^2=995.216, P<0.001, N=1,039), and thus represents an accurate proxy of the percentage of time spent vigilant. The AIC analysis resulted in a best-subset model with ten significant predictor variables and three variable interactions (df=28, AIC=1,021.223, λ^2=173.256). A new GdLM analysis was performed with this subset of variables.

Using multiple observations from the same individuals can lead to pseudoreplication. The AIC analysis indicated that the effects of individual ID on the results were minimal. Unfortunately, both individual ID and sex could not be entered into the GdLM simultaneously as main effects. To detect possible individual effects on the results, another GdLM model was created which included individual ID nested into sex. The nested individual ID variable was not significant in the resulting model (type one likelihood ratio, df=15, λ^2=22.489, P=0.096). In addition, the magnitude and direction of parameter estimates for all other predictor variables (except time of day, terrestriality, and alarm call interactions) were similar to the previous GdLM which did not include individual ID. These results indicate that individual ID had a minor influence on the statistical conclusions.

Levels of antipredatory coati vigilance were compared to overall vigilance levels of sympatric capuchin monkeys from a previous study (Hirsch 2002). The arcsine-transformed percentage of time spent vigilant for both species was entered into a Wilcoxon test for variance of means. Overall levels of antipredatory vigilance for brown capuchin monkeys were calculated by extrapolating the percentage of time spent engaged in antipredatory vigilance during known vigilance bouts times the overall amount of time spent vigilant (Hirsch 2002). Because levels of capuchin antipredatory vigilance had to be extracted from the data, they could not be directly compared to levels of coati vigilance.

Results

The best AIC model yielded significant effects of time of day, sex, number of neighbors within 5 m, within-group spatial position, individual behavior, group velocity, group

Table 1 Demography of two coati groups, PQ and PSG

Group	Year	Adult males	Adult females	Subadults	Juveniles	Total group size	N
PQ	2003	1	3	2	9	15	45
	2004	0–1	5	0	22–24	27–29	352
PSG	2003	0–1	3–5	0	6	9–12	477
	2004	1	5	6	15–17	27–29	165

Subadults are individuals between 12 and 24 months of age. Juveniles are between 2 and 12 months old.
N The number of vigilance samples taken from each group/year.

size, presence of juveniles less than 6 months of age, type of alarm call within 10 min of the sample, the interaction between presence of juveniles <6 months and alarm call type and the interaction between time of day and individual behavior (Table 2). Correlation coefficients among most continuous predictor variables were low (Table 3), so it is unlikely that the results were strongly affected by collinearity among the predictors. Date, terrestriality of the focal

Table 2 Generalized linear model for the presence of vigilance

Variable	*df*	Estimate	Standard error	*P*
Sex (female)	1	0.441	0.130	<0.001***
Spatial position	6			
Front edge		1.234	0.193	<0.001***
Front middle		−0.168	0.240	0.484 ns
Center		0.000	–	
Back middle		0.018	0.189	0.924 ns
Back edge		0.127	0.187	0.497 ns
Side edge		0.434	0.183	0.018*
Side middle		−0.450	0.211	0.033*
Individual activity	3			
Invertebrate foraging		0.000	–	–
Fruit eating		0.591	0.890	0.507 ns
Rest		1.572	0.769	0.041*
Travel		−1.120	0.747	0.134 ns
Terrestriality (on the ground)	1	3.659	0.480	<0.001***
Group speed	3			
No movement		0.000	–	–
Slow movement		0.287	0.209	0.170 ns
Moderate movement		0.252	0.252	0.317 ns
Rapid travel		−1.106	0.524	0.035*
Alarm call type within 10 min	3			
No response		0.000	–	–
Low response		−4.375	0.565	<0.001***
Medium response		−3.675	0.221	<0.001***
High response		4.471	0.192	<0.001***
Presence of juveniles <6 months	1	1.647	0.512	0.001**
Number of neighbors within 5 m	1	−0.055	0.024	0.022**
Group size	1	−0.174	0.058	0.003**
Time	1	−0.011	0.004	0.003**
Presence of juveniles × alarm calls	3			
No response no juveniles		0.000	–	–
No response with juveniles		0.000	–	–
Low response no juveniles		−0.088	0.182	0.629 ns
Low response with juveniles		–	–	–
Medium response no juveniles		−0.088	0.222	0.690 ns
Medium response with juveniles		–	–	–
High response no juveniles		0.499	0.191	0.009**
High response with juveniles		–	–	–
Terrestriality × alarm calls	3			
Arboreal no response		0.000	–	–
Arboreal high response		3.977	0.528	<0.001***
Time × individual activity	3			
Invertebrate foraging		0.000	–	–
Fruit eating		−0.014	0.009	0.095*
Rest		−0.009	0.007	0.186 ns
Travel		0.015	0.007	0.020*

df=28, AIC=1,021.223, λ^2=173.256

**P*<0.05

***P*<0.01

****P*<0.001

Table 3 Correlation coefficients for the significant continuous variables

Variables	Sex	Neighbor density	Group size
Neighbor density	−0.110		
Group size	−0.164	0.053	
Time of day	−0.027	0.012	−0.009

individual, and group, behavior of the group, and the presence/absence of alarm calls within 10 min of the focal sample were not significant when entered into the GdLM.

Adult females were more vigilant than males (males=22.39%, females=31.60%, slope=0.441, P=<0.001), and had more neighbors within 3 m than adult males (λ^2=14.86, P=<0.001). Coatis were less vigilant as the number of neighbors within 5 m increased (slope=−0.055, P=0.022), and group size increased (slope=−0.174, P=0.003). The coatis were more vigilant at the periphery of the group, and in particular, the front periphery of the group (Fig. 1, slope=1.234, P=<0.001). Coatis were less vigilant earlier in the day (slope=−0.011, P=0.003). Coatis that were resting were more likely to be vigilant than individuals that were feeding (rest = 41.00%, terrestrial foraging = 28.71%, slope=0.014, P=0.031). The presence of juveniles less than 6 months of age had a strong positive effect on vigilance levels (slope=1.647, P=0.001). The effect of alarm type within 10 min of the focal sample was only significant when juveniles less than 6 months were not in the group (λ^2=14.621, P=0.002; when juveniles less than 6 months were present, λ^2=2.334, P=0.506) (Fig. 2). Capuchins spent slightly more time vigilant than coatis (coatis=11.3%, capuchins=12.7%, Wilcoxon test, P<0.001, R^2=0.006), but less time once social monitoring was excluded (coatis=11.3%, capuchins=2.9%).

Discussion

Neighbor density and within-group spatial position

The effects of neighbor density (the number of individuals within 5 m), and within-group spatial position on vigilance conformed to predictions regarding predation risk within social groups. The result that individuals were less vigilant as the number of neighbors within 5 m increased conforms to assumptions of Hamilton's (1971) theory of "domains of danger". The effect of within-group spatial position on vigilance levels conforms exactly to previous predictions (Krause 1994; Bumann et al. 1997; Krause and Ruxton 2002) and are similar to results of a previous study of the effects of spatial position on the behavior of brown capuchin monkeys (Janson 1990b). Vigilance levels were lowest in the central spatial position (Fig. 1) and highest in peripheral spatial positions, particularly the front edge of the group. Although both independent variables were positively correlated (Wilcoxon test, P<0.001), they both independently predict vigilance levels as shown by their significant contributions to the logistic regression. Of particular interest are the parameter estimates, which are lower for neighbor density than within-group spatial position (Table 2). This result indicates that the spatial position within the group predicts vigilance levels better than neighbor density. For example, vigilance levels were higher at the front of the groups (front periphery = 52.59%, back periphery = 31.55%), even though the average number of neighbors for individuals at the front edge was higher than at the back edge (average number of individuals within 5 m at the front periphery = 2.69, back periphery = 1.96). This result is consistent with the hypothesis that the risk of predation is higher at the front edge of groups, and that this increased predation risk is expressed as higher vigilance in ring-tailed coatis (Bumann et al. 1997).

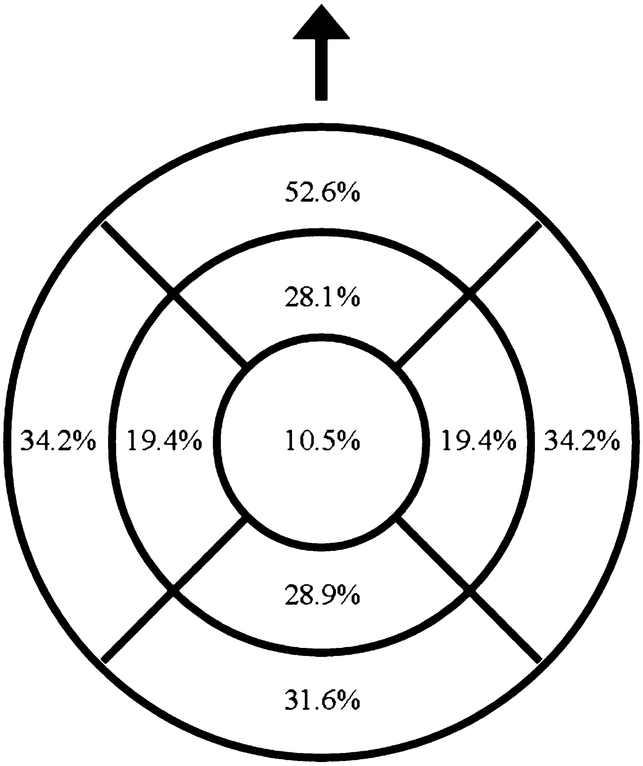

Fig. 1 The percentage of focal samples in which coatis were vigilant as a function of within-group spatial position. The *top of the circle* represents the front of the group

The results relating within-group spatial position and neighbor density to vigilance behavior are particularly important in light of the lack of studies on within group spatial position (but see Inglis and Lazarus 1981; Krause 1994; and Krause and Ruxton 2002). A diversity of studies on vigilance has demonstrated a variety of environmental variables that affect levels of vigilance, including neighbor density (Treves 1998; Hirsch 2002) and group size (review

Elgar 1989). Few of these studies have included spatial position along with other variables; thus, there have been few studies explicitly examining the separate effects of spatial position vs other vigilance predictor variables. Even when spatial position is recorded, the vast majority of studies do not indicate the directionality of group movement, which in this and other studies (Janson 1990b and Black et al. 1992), has been shown to be an important determinant of vigilance behavior. Given the importance of within-group spatial position on competitive regimes (Janson 1990a,b), vigilance (Janson 1990b), and social foraging (Giraldeau and Caraco 2000), and the fact that this is a little studied area, we suggest that more work be done in the future to determine the effects of an individuals' spatial position on the behavior of individuals and the costs and benefits of sociality.

Group size and the presence of young juveniles

As predicted, individuals in larger groups were less vigilant than in smaller groups. This negative effect of group size was outweighed by the effect of the presence of young juveniles on vigilance levels. Both study groups substantially increased in size after the 2003 breeding season (Table 1). After the groups reformed and contained large numbers of juveniles less than 6 months old, overall vigilance rates increased despite higher group sizes. Juveniles less than 6 months old are probably more susceptible to predation than older juveniles (BT Hirsch, unpublished data), and these data are consistent with the hypothesis that coatis increase vigilance levels to protect young offspring. These results are consistent with those of a previous study by Treves et al. (2001).

Alarm reactions

Coati vigilance was significantly higher depending on the level of alarm response given within 10 min before the focal sample, but only when juveniles less than 6 months were absent (Fig. 2). We interpret these results as being evidence that adult coatis do not treat the reactions of young juvenile coatis equally to those of adults. Previous work has shown that adult monkeys and marmots are less vigilant after young individuals have given alarm vocalizations as compared to when adults do (Seyfarth and Cheney 1980; Blumstein and Daniel 2004; McCowen et al. 2004). Unfortunately, there was no way to determine who gave the alarm calls recorded in this study. To test if our interpretation is in fact correct, experimental playback studies would need to be conducted.

Terrestriality

Coatis were more likely to be vigilant when on the ground, which is consistent with the higher predicted threat of

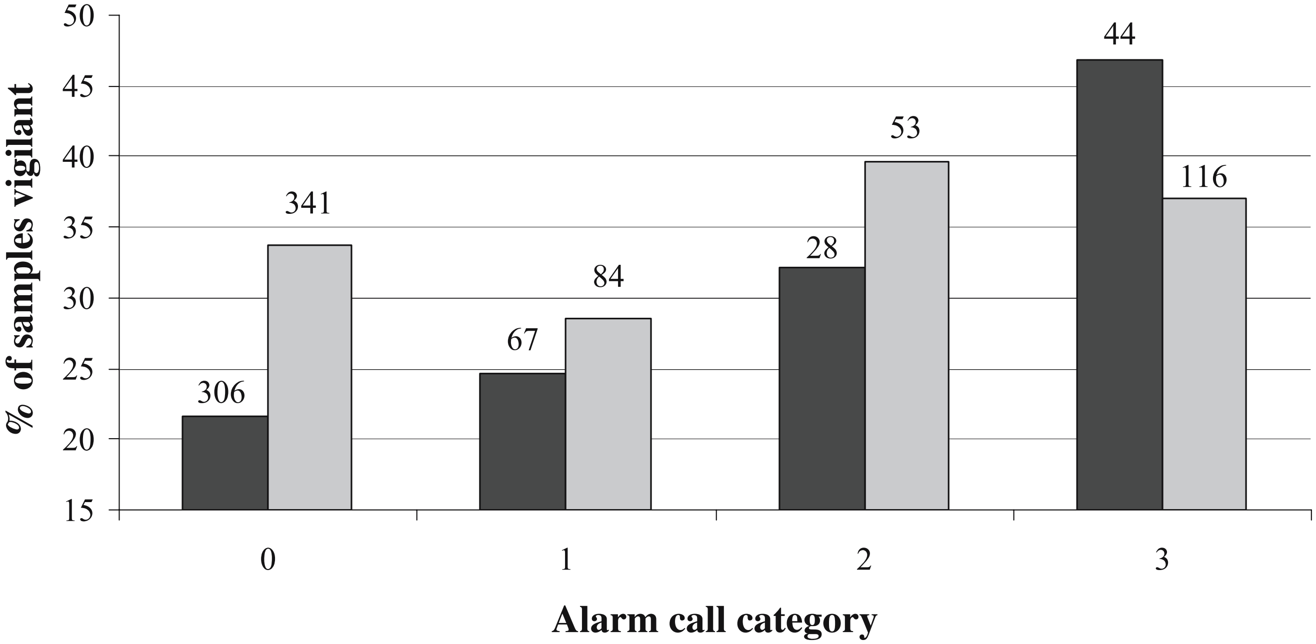

Fig. 2 Effect of alarm call response on vigilance levels. 0 = No alarm call within 10 min of the focal sample, *1* <33% of the group climbed a tree after an alarm call within 10 min of the focal sample, *2* 33–66% of the group climbed a tree, and *3* >66% of the group climbed a tree. *Dark bars* indicate no juveniles <6 months found in group and *light bars* indicate juveniles <6 months are present in the study groups. *n* Numbers above bars. Effects of alarm call are significant when no juveniles less than 6 months (λ^2=14.621, P=0.002) but not when juveniles less than 6 months were present (λ^2=2.334, P=0.506)

predation on the ground. This pattern was also found in conspecific capuchin monkeys (Hirsch 2002). The interaction between alarm call response and terrestriality was also a significant predictor variable. After a strong alarm response, arboreal coatis were more vigilant than terrestrial individuals. This pattern reflects the two common post-detection predator responses; climb a tree and look for predators, or quickly flee the area.

Time of day, activity patterns, and travel speed

The activity pattern of the focal individual had significant effects on vigilance levels (Table 2). Coatis were more vigilant while resting, and less vigilant while traveling. There was a negative relationship between travel speed and vigilance levels, which is consistent with previous results (Hirsch 2002). Coatis were slightly less vigilant earlier in the day in the final GdLM model, but this pattern was not significant in the model with individual ID nested in sex. In addition, there was a significant interaction between the time of day and the activity pattern of the focal individual, but all of these effects were weak (slope = <0.015).

Effects of sex

In contrast to the other well-studied species of coati (*N. narica*), groups of *N. nasua* in Iguazu regularly had adult males associated with the groups during most of the year (BT Hirsch, unpublished work). Because various hypotheses relating sex and vigilance produce contradictory patterns, no a priori predictions were made. Despite being located in areas of the group with higher threat of predation, males were less vigilant than females. There are two possible reasons for this result: (1) inclusive fitness benefits and (2) sexual dimorphism. Females may be more vigilant to provide inclusive fitness benefits to offspring and close relatives in the group, whereas males might not have offspring in the group. The paternity of the offspring in these groups is not currently known, but it is likely that these males sired few if any offspring during the course of this study, with the exception of group PSG in 2004.

The other plausible hypothesis for why males are less vigilant is that males are less susceptible to predation than females due to their larger body sizes (average body weight in adult males 6.11 kg, *N*=6, adult females 4.22 kg, *N*=22). Some medium-sized predators such as ocelots and tayra may have more difficulty attacking and killing a large adult male than an adult female (ME Gompper, personal communication). Some evidence to support this hypothesis is the fact that all adult males tend to be more peripheral even though they generally win contests over food and thus have little reason to avoid the center of the group spread (BT Hirsch, unpublished data).

Coati–capuchin comparisons

The methods in this study were designed to be directly comparable to a previous study on sympatric capuchin monkeys (Hirsch 2002). Because predation threat is typically higher when animals are on the ground, we predicted that coatis would spend more time vigilant than sympatric capuchin monkeys. The overall levels of coati vigilance were slightly lower than those found in brown capuchin monkeys (coatis = 11.3%, capuchins = 12.7%). We believe that this pattern is not due to differences in group sizes because the capuchin group had between 25–29 individuals during the duration of the study. A possible reason for this result is that the majority of vigilance in capuchin monkeys functioned to monitor conspecifics, and was not directed at predator detection. By using the percentage of samples of capuchin vigilance in which the target of vigilance was known, we recalculated the overall percentage of time capuchin monkeys spent engaged in antipredator vigilance as 2.9%. If we only compare the percentage of time spent vigilant for predator detection, the percentage of time spent vigilant by coatis is almost four times higher than the monkeys, which is consistent with the previous prediction that coatis live under a higher predation threat due to their higher degree of terrestriality. This interpretation agrees with the fact that capuchins are more vigilant when they approach within 3 m of the ground (percentage of time spent vigilant = 17.4%, Hirsch 2002).

Conclusion

The results of this study are largely consistent with the hypothesis that social groups reduce predation risk to individuals (see also Gompper 1996, Hass and Valenzuela 2002). More specifically, the within-group spatial position of social animals is an important determinant of their perceived risk of predation. This study is consistent with previous predictions that individuals are at highest risk of predation when in peripheral spatial positions, at the front edge of the group, and when their “domains of danger” increase. To understand the evolution and maintenance of group structure and spatial organization in social animals, it is important to determine what the costs and benefits to within group spatial position are (Krause 1994, Krause and Ruxton 2002). The results of this study can be combined with detailed measures of feeding rates in relation to within group spatial position, and scrounging behavior to understand the determinants of group spatial structure in this species (BT Hirsch, unpublished data).

The result that individuals were less vigilant during rapid travel than while foraging is similar to previous work on sympatric capuchin monkeys which found lower rates of vigilance and food detection as travel speed increased (Janson and Di Bitetti 1997; Hirsch 2002). Coatis are the only diurnal genera of procyonids and have poor visual abilities compared to birds and primates (the two organisms in which vigilance has been most regularly studied). Coatis may be able to smell or hear predators at greater distances than by sight. Boinski et al. (2003) pointed out that squirrel monkeys in dense habitats spend less time vigilant than in more open habitats in part because when the visibility is extremely poor, any scanning of the environment will not likely result in the detection of predators. Because of the coatis' poor eyesight and the dense understory vegetation, visual scanning by coatis is unlikely to be an effective method for detecting predators in this study site. If coatis are unlikely to discover predators by sight, why are they vigilant? The low percentage of social monitoring and other results of this study indicate that vigilance in this population is primarily antipredatory in function (as opposed to social monitoring or monitoring scrounging opportunities Coolen et al. 2001, Hirsch 2002). By standing still and directing their attention towards the surrounding environment, coatis may be able to smell or hear predators at longer distances than nonvigilant animals (Kramer and McLaughlin 2001; Clark and Dukas 2003). In particular, we believe that the noise made by coatis when running or walking on dry leaves (this study coincided with a drought period) disrupts their ability to hear predators. By stopping locomotion, these animals may be better able to hear noises.

Acknowledgements The authors would like to thank Santiago Escobar, Carolina Ferrari, and Fermino Silva for help and assistance during the course of the field work. We would also like to thank Viviana Muñoz for her veterinary assistance. The authors are particularly grateful to Charles Janson for the immeasurable amount of advice he gave us during all aspects of this project, and letting us borrow several pieces of much needed field equipment. The authors are also very thankful for the consistently helpful comments and advice from Mario Di Bitetti. We would like to thank Barry Hirsch for statistical advice and help using SAS. This paper has benefited tremendously, thanks to comments by Mario Di Bitetti, Dan Blumstein, Joanna Burger, Matt Gompper, Charles Janson, Roland Kays, and Abe Ruttenburg. We thank the APN for the permission to carry out work in Iguazu. This study was funded in part by a NSF DDIG grant.

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