ORIGINAL ARTICLE

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Social monitoring and vigilance behavior in brown capuchin monkeys (*Cebus apella*)

Abstract I investigated the vigilance behavior of brown capuchin monkeys (*Cebus apella*) in Iguazu, Argentina to determine the relative importance of anti-predatory vigilance versus social monitoring. Predator detection has been found to be the major factor driving vigilance patterns in other populations of *Cebus*, and a positive relationship between vigilance and the number of nearby neighbors has been found. In the Iguazu population, social monitoring is the primary function of vigilance, as indicated by a negative relationship between vigilance and neighbor density. Even if social monitoring and predator detection are totally compatible, the time trade-offs associated with vigilance behavior are mostly driven by social monitoring in this population. In addition to recording vigilance data in relation to the number of neighbors, several other variables were recorded in conjunction with vigilance behavior in order to control for possible confounding factors. After controlling for these factors, it was found that the number of neighbors within 10 m was still highly correlated with the percent of time spent vigilant. The average percent of time spent vigilant was found to be much lower in Iguazu, compared to another population of *C. apella* with higher predation pressure. The average vigilance bout was much closer in length to known social monitoring bouts than to known anti-predatory vigilance bouts. These patterns indicate that the predominate function of vigilance in this population of *C. apella* is social monitoring. In populations with low predation pressure, the time costs associated with social monitoring should increase with group size, and increasing neighbor density. The fitness costs of social monitoring have not been incorporated into current social models, and these results indicate that these models may not be appropriate for all study populations.

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Introduction

Anti-predatory vigilance has been proposed to be a major advantage of group living across several taxa. The initial model of anti-predatory vigilance (Pulliam 1973) hypothesized two major benefits to individuals living in groups. Given a constant amount of individual vigilance, an increase in group size will increase the total amount of vigilance in the group and thus increase the likelihood of predator detection. Secondly, when group numbers rise, individuals in groups are able to reduce the amount of time spent vigilant and thus spend more time engaged in other activities such as foraging. A negative relationship between individual vigilance and group size has been found in a wide variety of taxa (reviews in: Elgar 1989; Quenette 1990) although there are several exceptions to this pattern (Cords 1990; Catterall et al. 1992; Poysa 1994; Rose and Fedigan 1995; Treves 1998, 2001).

Recently, some studies have shown that neighbor density may be a more important determinant of vigilance levels than group size (Robinson 1981; Poysa 1994; Cowlishaw 1998; Treves 1998; Steenbeek et al. 1999; Rolando et al. 2001; Treves 2001). In accordance with these results, it is suggested that group density, or proximity to neighbors may be the perceptible unit of safety to group living individuals (Lima 1995; Roberts 1996; Treves 2000). Instead of investigating whether a group size effect is present, one can look at the relationship between inter-individual proximity and vigilance to gauge the effect of sociality on vigilance levels (Treves 2000). If the presence of conspecifics reduces predation risk as predicted by Hamilton (1971) individuals with more neighbors are predicted to have lower vigilance levels, which has been found in several previous studies (see above).

One of the largest problems in studies of vigilance is the difficulty in distinguishing the function or target of

vigilance, especially in primates where it may serve a wide range of functions including social monitoring, searching for food, group defense, mate defense, infanticide avoidance, and anti-predatory defense (Caine and Marra 1988; Baldellou and Henzi 1992; Rose 1998; Steenbeek et al. 1999). All of these factors may influence the relationship between vigilance behavior and group size or neighbor density. Even though the pattern of decreased vigilance in larger groups is a general pattern found across taxa, there are a variety of confounding variables such as sex, age, rank, distance from cover, spatial position within the group, feeding competition, time of day, and breeding status, all of which may affect vigilance patterns (review of birds and mammals in: Elgar 1989; Quenette 1990).

In previous studies, the presence of social monitoring is typically de-emphasized, and it has been assumed that predator monitoring is the predominate function of vigilance. Some studies have used social monitoring to explain deviations from the expected pattern, but few have explicitly tested for the presence or importance of social monitoring. Jones (1998) concluded that postural differences between two marsupial species indicated that the smaller species (*Dasyurus viverrinus*) engaged in anti-predatory vigilance, while the larger species (*Sarcophilus laniarius*) was most likely monitoring conspecifics. In a study of white-faced capuchins (*Cebus capucinus*), Rose (1998) was able to determine the function of most vigilance bouts, and thus analyze differences in anti-predatory versus social vigilance scans. Although this method may be possible for some species, in most species the target of vigilance is not always clear. A third method which can be used to distinguish between anti-predator vigilance and social monitoring is investigating the relationship between group size and vigilance. Knight and Knight (1986) found that when the group size of bald eagles (*Haliaeetus leucocephalus*) rose above eight individuals, vigilance and group size were positively related. The authors concluded that this was clear evidence that eagles were monitoring conspecifics to avoid kleptoparasitism. In the absence of group size differences, one could also test whether vigilance levels increase or decrease in relation to neighbor density.

The purpose of this study was to determine whether the predominant function of vigilance in the population of brown capuchin monkeys (*Cebus apella*) in Iguazu, Argentina is predation avoidance or social monitoring. It is important to determine the predominant function of vigilance in order to predict the patterns and distribution of vigilance levels within a group. This is in turn important for determining which individuals undergo higher fitness costs associated with being vigilant, as opposed to engaging in other fitness enhancing behaviors. If social monitoring is the predominant function of vigilance, it is predicted that vigilance and the number of nearby neighbors will be positively correlated. Conversely, if vigilance is primarily anti-predatory in function, number of neighbors and vigilance should be negatively related because individuals with lower numbers of neighbors should undergo a higher threat of predation (Hamilton 1971; van Schaik and van Noordwijk 1989; Poysa 1994; Cowlishaw 1998; Steenbeek et al. 1999; Treves 1999). Because previous work has shown that vigilance levels can be determined by a large number of factors, additional ecological and social variables were recorded in order to determine their effect on vigilance levels. In addition, it is important to control for the effects of these variables when determining the function of vigilance behavior. I recorded time of day, canopy cover, age, sex, rank, group speed, individual behavior, height, number of neighbors within 10 m, position in group, group spread, and time since last alarm call in conjunction with vigilance behavior.

Methods

Study subjects and area

The study was conducted at the Iguazu Falls National Park, Argentina (54°W, 26°S) (see: Brown and Zunino 1990; Janson 1996; Di Bitetti 2001). The capuchin habitat is in a highly seasonal subtropical forest, with a maximum tree height of only 27 m (Janson, unpublished data). A very high density of fruit trees is found in Iguazu forest (3–5/ha; Janson, unpublished data). Two non-adjacent groups of *C. apella* were studied. The Macuco group (which has been the subject of previous studies: Janson 1996; Janson and Di Bitetti 1997; Janson 1998; Di Bitetti 2001) had 25–29 individuals, and the Silver group had 23 individuals, thus group size was similar between the two groups. A series of demographic changes in the Macuco group occurred during the study, which led to the loss of the alpha and gamma males, one subadult male and one infant. These factors caused the group size of the Macuco group to decrease by four individuals during the course of this study, and the shift in alpha male status had to be taken into account during analysis.

At Iguazu there are six species of felids (*Felis pardalis*, *F. concolor*, *F. onca*, *F. yagouarundi*, *F. cf. tigrina* and *F. wiedi*, the last three of which are presumably too small to pose a serious predation threat), two species of raptors (*Spizaetus ornatus*, *S. tyranus*, both of which are rarely seen) and one species of tayra (*Eira barbara*, which is a potential predator) (Di Bitetti, personal communication). The threat of predation in Iguazu is much lower than at Manu, Peru where similar studies of brown capuchin behavior and vigilance have been conducted (van Schaik and van Noordwijk 1989). In Manu, groups of *C. apella* were attacked by predators approximately every 2 weeks, whereas in Iguazu only two predation attempts have been observed in over 750 contact days (Janson, unpublished data).

The bulk of samples (90.7%) analyzed in this study were from the Macuco group, which has been the subject of a series of foraging experiments since 1992 (Janson 1996). These ongoing experiments involve five sets of artificial feeding platforms where the monkeys receive bananas and tangerines once a day. These platform sites are used to mimic fruit trees during fruit shortages during the Argentine winters. The monkeys spent approximately 5–15 min feeding at each experimental platform array and were generally finished visiting the feeding platforms by 1100 hours. The rest of the day was spent visiting natural fruit trees and foraging for insects and bamboo shoots. Since group spread decreases, number of neighbors increases, and levels of aggression increase during platform feeding bouts, the time since food was placed in the platform was recorded in conjunction with the vigilance data in order to control for any potentially confounding effects of the feeding experiments.

Recording vigilance

Vigilance in this study was defined as looking at areas beyond the immediate substrate. Each such scan was termed a "vigilance bout." I took vigilance data using 10 s continuous focal samples (Martin and Bateson 1996). Time spent vigilant was calculated as the summed duration of all vigilance bouts in a 10 s sample, divided by ten. If a portion of a vigilance bout fell outside the 10 s sample, only the portion of the vigilance bout that fell within the 10 s sample was used to calculate percentage of time spent vigilant. To determine average bout length, I measured the total duration of every vigilance bout initiated within a 10 s sample, whether or not it ended within the sample. Vigilance bouts were recorded to the nearest 0.5 s interval using a stopwatch which beeped at 1 s intervals. In some cases, vigilance bouts were shorter than 0.5 s, and were recorded as "glances." All glances were treated as 0.25 s in length in the analysis, which was supported by videotape analysis of vigilance glance length. Vigilance samples were taken at least 2 min apart, and individuals were never resampled within 6 min. Samples on one individual were typically separated by 10 min or more. The independence of consecutive samples was tested using the method reported in Schoener (1981, Appendix 2). All adult individuals were recognized by distinctive facial and morphological characteristics. Samples were taken opportunistically on visible animals, and preferentially on undersampled individuals. At least 105 samples were recorded for all adult females in the main study group. These data were recorded between 6 June and 16 August 1999 (n=2,297, 10 s vigilance samples).

Determining the direction of gaze was not overly difficult because of the short height of most trees, the clear forest understory, and the short length of the vigilance samples. When the monkeys were located in dense high canopy, the determination of vigilance behavior was not always clear, in which case samples were aborted. If the individual was moving and its head was pointed down or level in the direction of travel, a vigilance bout was not recorded due to the high probability that it was looking at branches for locomotion. If the individual was moving and turned its head up or away from the direction of travel, it was scored as a vigilance bout. Unlike many previous studies, I did not exclude vigilance bouts toward conspecifics. If at all possible, the target of the vigilance bout was recorded. If the bout was in response to a noise, conspecific's alarm call, potential predator, or observer, it was classified as anti-predator vigilance. If the vigilance was clearly directed at a conspecific, or the non-alarm call vocalizations of a conspecific, the bout was classified as social monitoring. A typical example of the former was when a focal individual's direction of gaze followed the travel path of a conspecific. If the focal individual disappeared from view, or moved into a position where the observer's visibility of scanning was obscured, the sample was discarded.

The definition of vigilance used in this study differs from most studies of vigilance behavior, in that I included both short glances and scans towards conspecifics. Given that the purpose of this study is to determine whether vigilance functions primarily for predator detection or to monitor conspecifics, the inclusion of social monitoring bouts is necessary. By recording short glances, I measured a behavior fundamentally different from that recorded by Rose (1998) and Rose and Fedigan (1995) on *C. capucinus*. Rose (1998) reported an average bout length of 28 s for adult females. I believe the finer grain measurement used in this study may be a better reflection of the actual percentage of time spent scanning, and thus providing a closer measure of the opportunity costs to vigilance behavior. The methods used by van Schaik and van Noordwijk (1989) closely resemble the present study with the exception that the authors excluded glances towards conspecifics.

Ecological and behavioral variables

Fifteen variables were recorded in conjunction with vigilance in this study: time of day, group identity (Macuco or Silver), environment (open canopy or continuous canopy), age (subadult, adult: for males only), sex (male or female), rank (alpha, or non-alpha), group speed (scored from 1 to 4, with 1 being little-to-no group movement, and 4 indicating that the group was traveling rapidly, corresponding to 20 m/min or more, as in Janson and Di-Bitetti 1997), individual behavior (groom, rest, investigate substrate, nurse, ingest, move, play), height (0–3 m, 3–6 m, 6–13 m, >13 m), number of neighbors (within a 10 m radius), within-group spatial position (center or edge), group spread (distance between the farthest members of the group rounded to the closest 25 m), time since last alarm call (up to 30 min), and time since last feeding platform was baited (up to 30 min). Neighbor density was recorded within a 10 m radius because the maximum tree crown diameter is approximately 20 m, and this has been shown to be a relevant measure for food competition (Janson 1996). Although the time since feeding platforms were raised was not initially planned as a variable in this experiment, the data were collected and analyzed due to possible confounding effects on the other variables. If possible, a vigilance category (social, anti-predatory, or unknown) was assigned to each vigilance bout within a sample (only 34.5% of bouts were classifiable). Since a 10 s sample could contain both social and anti-predatory vigilance bouts, 10 s samples were not assigned vigilance categories. Because of this, I was not able to analyze vigilance category in relation to percentage of time spent vigilant.

Analysis

Due to the small sample size (n=2), play behavior was excluded from the analysis. Comparisons between groups had to be omitted from multiple regression analysis because of missing effects in the ANOVA. Since the fastest group speed (speed 4) was observed almost exclusively in the context of traveling to an experimental feeding platform, and the Silver group did not participate in the feeding experiments, there were no instances where the Silver group had a group speed of 4.

The remaining 13 variables were entered into stepwise multiple regressions using the JMP statistical package (version 3.2.2, SAS Institute 1997) with arcsin transformed percentage of time spent vigilant being entered as the dependent variables in separate analyses. The variables were entered using both forward and backward stepwise regressions. Variable interactions were also entered into the model. The percentage of time spent vigilant was arcsin-transformed to conform to assumptions of normality (Sokal and Rohlf 1997). Continuous variables that were significant in the multiple regressions were further analyzed using standard beta slopes. Standard beta slopes are reported here to control for different variances between variables, thus making comparisons of the relative importance of the variables possible.

Results

The stepwise multiple regression analysis for percent of time spent vigilant yielded significant effects of group speed, individual behavior, height, number of neighbors within 10 m, and time since alarm call (Table 1). Only when a one-tailed test was used for the alarm call variable was it significant in the multiple regression model. A one-tailed test was used for analysis of the alarm call variable because no plausible alternative hypothesis could be identified for why vigilance would decrease after an alarm call. Correlation coefficients are reported in Table 2. Rank, time of day, canopy cover, age, sex, position in group, group spread, and time since feeding experiment, were not found to be significant predictors of vigilance levels when entered into the final multiple regression test. All variable interactions were either non-

Table 1 Significant factors in a stepwise regression of percentage of time spent vigilant by brown capuchin monkeys (*Cebus apella*) (R^2=0.187) All reported *P*-values are two-tailed except for the time since alarm call variable which is one tailed

Variable	df	F Ratio	P>F
Group speed	1	9.820	0.0017
Activity Pattern	5	66.112	<0.0001
Height	1	45.494	<0.0001
Number of neighbors	1	21.225	<0.0001
Time since alarm call	1	3.719	0.0270

Table 2 Pearson correlation coefficients of statistically significant vigilance determinants (*P*<0.05)

Variables (pairwise *n*)	Speed (2,301)	Height (2,301)	No. of neighbors (2,301)
Height	0.115	–	–
No. of neighbors	–0.248	–0.159	–
Alarm call	0.137	0.027	–0.072

Fig. 1 Height in canopy effect on percentage of time spent vigilant by brown capuchin monkeys (*Cebus apella*), +/–SE. *n* Sample size

Fig. 2 Number of neighbors within 10 m effect on percentage of time spent vigilant, +/–SE

significant, or the inclusion of variable interactions resulted in lower significance levels for the individual variables.

Levels of vigilance decreased when the group was traveling faster (standard beta slope=–0.066). Vigilance levels varied markedly with activity. The highest levels of vigilance were found when monkeys were nursing or resting (least squared means; nursing=0.582, resting=0.457), intermediate levels were found when ingesting and moving (least squared means; ingesting=0.291, moving=0.222), and the lowest levels of vigilance were found when grooming and investigating substrates (least squared means; grooming=0.150, substrate=0.132). The lowest levels of vigilance were found at the highest levels in the canopy (13 m or more), and the highest levels of vigilance occurred when the monkeys were 0–3 m high (Fig. 1; standard beta slope=–0.129). When samples where the focal animal was on the ground (0 m) were excluded, this result remained. Although the number of neighbors within 10 m is highly correlated with group spread and position in the group, only the number of neighbors is a significant variable in the multiple regression tests. Individuals spent more time vigilant as the number of neighbors within 10 m increased (Fig. 2; standard beta slope=0.091). Individuals were more vigilant in the 30 min following an alarm call than at other times (standard beta slope=–0.037).

Vigilance levels were significantly higher when monkeys had more neighbors (χ^2=79.93, *df*=16, Kruskal-Wallis *P*<0.0001), were more central in the group (χ^2=32.17, *df*=1, *P*<0.0001), and when the group spread decreased (χ^2=104.55, *df*=7, *P*<0.0001). Despite these univariate results, only the number of neighbors remained a significant predictor variable in the multiple regression model. In contrast to other studies (van Schaik and van Noordwijk 1989; Rose 1998), there was no significant difference in vigilance levels between the sexes
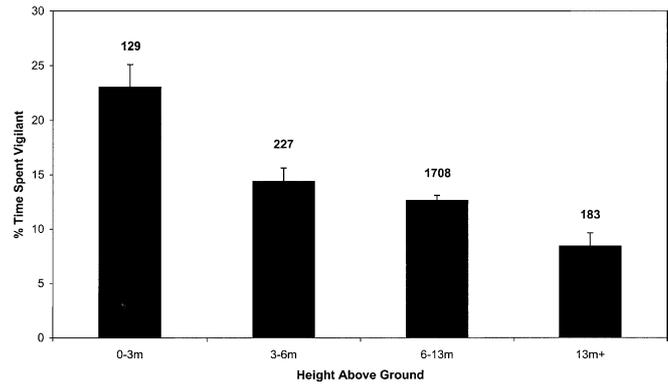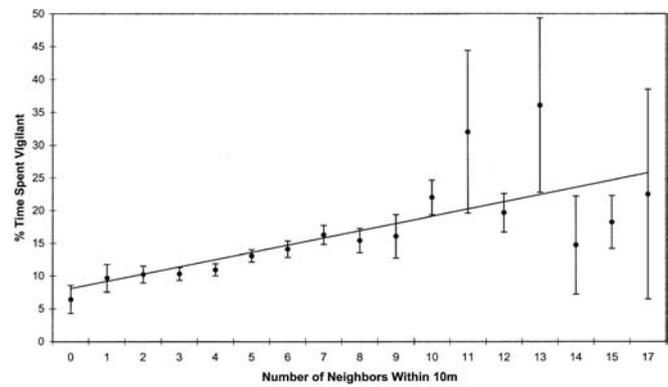
(χ^2=1.25, *df*=1, Kruskal-Wallis *P*<0.2637). However, sex was correlated to other significant predictor variables. Males were more likely to be lower in the canopy (χ^2=7.81, *df*=1, Kruskal-Wallis *P*<0.0052), have more neighbors (χ^2=27.69, *df*=1, *P*<0.0001), and travel faster than females (χ^2=15.46, *df*=1, *P*<0.0001). Although not significant in the final multiple regression model, in an alternate model with a lower R^2 value, rank was a significant predictor variable, and alpha individuals spent more time vigilant than subordinates (*P*<0.0459, standard beta slope=–0.041).

Discussion

The results of this study are consistent with the hypothesis that vigilance in this population functions for both predator detection and social monitoring. A positive relationship between the number of nearby neighbors and vigilance levels supports the hypothesis that vigilance has a social monitoring function. Low overall levels of vigilance and an analysis of vigilance bout lengths indicate that social monitoring is the primary function which drives vigilance patterns in this population. Increased

vigilance close to the ground and after alarm calls are evidence that vigilance serves an anti-predation function.

Number of neighbors

Understanding the determinants of vigilance behavior, and thus what drives the time tradeoffs associated with vigilance, is important for determining how social and ecological pressures shape group size and structure. If predator detection is the primary function of vigilance, one predicts that vigilance will decrease as the number of neighbors increase. Alternatively, if vigilance primarily functions as social monitoring, a positive correlation between vigilance and number of neighbors is predicted. I found that vigilance increased as the number of neighbors increased, thus supporting the social monitoring hypothesis, and rejecting the anti-predation function of vigilance (Fig. 2). The result that the number of neighbors was significant in the multiple regression analysis while group spread and spatial position were not significant may indicate that neighbor density is the perceptible unit by which individuals determine appropriate vigilance levels. These data reinforce conclusions of other studies which have demonstrated the importance of the number of neighbors in determining vigilance levels (van Schaik and van Noordwijk 1989; Poysa 1994; Lima 1995; Roberts 1996; Cowlishaw 1998; Treves 1999).

Another factor that can be used to determine the relative importance of social monitoring versus anti-predatory vigilance is the difference in bout length by vigilance category. Despite the high number of vigilance bouts whose function is unknown, the number of social vigilance bouts was over three times higher than anti-predatory vigilance bouts (social=27.2%, anti-predatory=8.2%). The average unknown bout length (1.74 s) was much closer to the average social bout length (1.77 s) than to the average anti-predatory bout length (1.44 s), suggesting that the unknown vigilance bouts more closely resemble social monitoring bouts in duration than anti-predatory bouts (Fig. 3).

As mentioned above, anti-predatory vigilance bouts were recorded when it was clear that the target of vigilance was directed towards a noise, conspecific alarm call, potential predator, or the observer. If the monkey perceived a threat during or before anti-predatory vigilance bouts, it might spend more time being vigilant, but have short bouts and look around for the predator. This behavior is different from the anti-predatory vigilance bouts recorded by Rose (1998). In that study, *C. capucinus* would clearly scan the environment looking for potential predators with no obvious immediate threat. Due to the subtle nature of *C. apella* vigilance behavior, it may be impossible or misleading to classify the target of vigilance in the Iguazu population (Rose, personal communication). Nevertheless, the overwhelming impact of social monitoring on the vigilance patterns found in this population (shown most clearly by the relationship between number of neighbors and percent of time spent
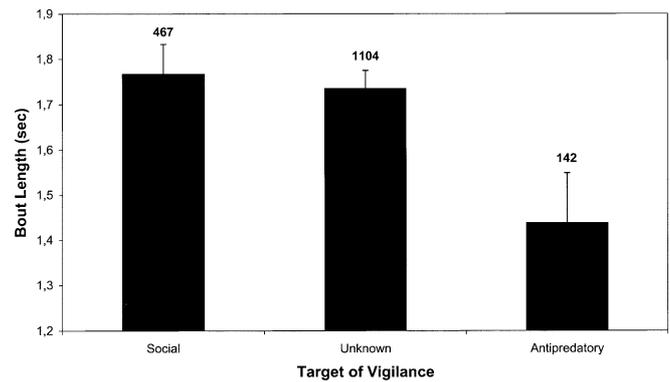

Fig. 3 Vigilance category effect on bout length, +/-SE. *n* Sample size

vigilant) is different from other published studies of mammalian vigilance behavior.

Height in canopy

In this study, height was negatively correlated with percent time spent vigilant showing that monkeys spent more time looking around when close to the ground. The relationship between height and vigilance is consistent with an anti-predatory function for vigilance, and inconsistent with a social monitoring function. The pattern that monkeys are more vigilant while lower in the canopy has been found by other authors (de Ruiter 1986; van Schaik and van Noordwijk 1989; Steenbeek et al. 1999). However, contrary to these studies, very low levels of vigilance were recorded high in the canopy. This would suggest that the threat of aerial predators is minimal at this site or has little affect on vigilance behavior in this population. The low levels of vigilance high in the canopy are similar to patterns found in wedge-capped capuchins (*Cebus olivaceus*) by de Ruiter (1986), who states that the threat of predation from raptors in his Venezuelan study area was low. The pattern in Iguazu differs from the high levels of vigilance found at the top of the canopy in Manu, which has a significant aerial predation threat (van Schaik and Janson, personal communication).

Alarm calls

The presence of alarm calls within 30 min of a vigilance sample had a significant effect on vigilance levels, with the percentage of time spent vigilant decreasing with time after the presence of an alarm call. This pattern leads to the conclusion that alarm calls elicit increased levels of vigilance, confirming results of earlier studies (Cheney and Seyfarth 1981; Baldellou and Henzi 1992).

An increase in vigilance following an alarm call should result in some level of time tradeoff with other fitness-enhancing behaviors. The average percent of time

C. apella in Iguazu spent being vigilant was 12.7% which is much less than the approximately 30% found in Manu (van Schaik and van Noordwijk 1989, Fig. 1a) which is consistent with lower levels of predation in Iguazu. This should allow monkeys in Iguazu to spend more time engaged in other activities. Since van Schaik and van Noordwijk (1989) excluded bouts of social monitoring from their measure of vigilance, actual differences in time spent vigilant between Iguazu and Manu may be even higher. Although it is not possible to quantify exactly how much less time *C. apella* spends engaged in anti-predator vigilance in Iguazu compared with Manu, it is clear that this number is a small fraction of the time spent vigilant in Manu. It is unknown how much time monkeys in Manu spent engaged in social monitoring. It is conceivable that both populations spend similar amounts of time monitoring conspecifics, but even if this is true, the fitness costs associated with vigilance behavior are markedly different between these two well-studied populations.

Conclusion

The data presented here support the notion that social monitoring is the primary function of vigilance in this population. The degree to which social monitoring influences vigilance behavior in this population is more pronounced than in previous studies. It is likely that low predation pressure found in this study population is the cause of the unique results herein. I predict that these patterns will be found in other sites with low predation pressure. If these patterns are typical in such populations, this study raises the question of how vigilance impacts group size and composition in other populations. In populations such as the one at Iguazu, vigilance due to social monitoring may be a cost to grouping. This pattern is in marked contrast to previous studies and present social theory (Pulliam 1973; Caraco 1979; McNamara and Houston 1992). It is beyond the scope of this study to distinguish precisely the multiple purposes social monitoring serves in this study population.

Although not significant in the final multiple regression model, dominant monkeys spent more time vigilant than subordinates, which is consistent with the hypothesis that dominant individuals may be looking at surrounding group members for opportunities to scrounge or steal food items (Robinette and Ha 2000; Coolen et al. 2001; DiBitetti and Janson 2001), rather than the alternate hypothesis that subordinate individuals are monitoring dominant conspecifics to be forewarned of impending aggression (Nikolei and Borries 1997). The higher vigilance levels in the alpha male and female could also be a result of their central spatial position in the group, which is associated with an increase in neighbor density. In order to clearly distinguish between these two hypotheses, more detailed studies of vigilance in conjunction with dominance relations and kleptoparasitism (producer-scrounger relationships) are needed.

The non-significant relationship between sex and vigilance is interesting, given that sex differences are reported for this species elsewhere (van Schaik and van Noordwijk 1989) and in many other primate species (de Ruiter 1986; Baldellou and Henzi 1992; Rose and Fedigan 1995). The effect of sex on vigilance levels in this population is minor compared to individual behavior, group speed, height, and number of neighbors. The vigilance patterns in this population could add support to the hypothesis that male capuchins in other populations are vigilant in order to defend females and related offspring from predators (van Schaik and van Noordwijk 1989; Rose 1998). If predation avoidance causes increased male vigilance in populations with frequent predation, the low predation risk in this population may allow males to decrease their vigilance levels, resulting in less between-sex differences in this population. Rose (1998) found that differences in social monitoring levels between males and females were less than sex differences in anti-predatory vigilance. This may indicate that the sex differences found in previous studies were mostly the result of anti-predatory vigilance, and the amount of social monitoring does not differ as greatly between males and females.

It has been noted that individuals engaged in social monitoring are likely to detect predators as well (Treves 2000). Some indirect support for this theory has been provided by Lima and Bednekoff (1999), who have found that even non-vigilant individuals are able to detect predators. What is not clear from empirical studies of vigilance behavior is to what degree individuals engaged in social monitoring can detect predators, and to what degree anti-predatory vigilance serves to monitor conspecifics. A reasonable presumption is that an individual who is monitoring conspecifics cannot detect predators as effectively as an individual who is specifically scanning the environment for predators. I believe that answers to these questions will only be resolved through careful experimental studies. The vigilance patterns in Iguazu show that the dominant function of vigilance in this population is social monitoring. Even if social monitoring can function to detect predators, the overall levels of vigilance, and hence the tradeoff costs of being vigilant, are clearly driven by social monitoring. These results indicate that the opportunity costs of vigilance in low predation populations are highest among individuals who have more neighbors, and not among peripheral individuals.

To further assess the degree of opportunity costs experienced by individuals engaged in social monitoring, it is important to conduct further, more detailed studies of vigilance. Because most studies either do not define, or poorly state the definition of vigilance, comparing vigilance levels across studies is difficult. This problem is particularly relevant in studies of primate vigilance because determining what constitutes a vigilance bout is typically more ambiguous compared to avian studies. Primates also vary widely in the manner of vigilance behavior exhibited (for two opposite extremes of primate

vigilance methods, see Rose 1998; Treves 1998). Another problem in comparing vigilance studies is that most authors do not control for a variety of social, ecological, and spatial correlates of vigilance. One method of investigating the relative opportunity costs of anti-predator vigilance and social monitoring is to conduct experiments in the field that would manipulate predation threat in a population. The resultant data would shed light on how anti-predator vigilance responds to increasing predation threat, as well as record how various rank, age, and sex classes adjust vigilance levels accordingly. Using methods similar to ones reported here in conjunction with predation manipulation experiments could more accurately determine how the two functions of vigilance respond to changes in social and ecological variables.

References

Baldellou M, Henzi SP (1992) Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. Anim Behav 43:451–461

Brown AD, Zunino GE (1990) Dietary variability in *Cebus apella* in extreme habitats: evidence for adaptability. Folia Primatol 54:187–195

Caine NG, Marra SL (1988) Vigilance and social -organization in 2 species of primates. Anim Behav 36:897–904

Caraco, T (1979) Time budgeting and group size: a theory. Ecology 60: 611–617

Catterall CP, Elgar MA, Kikkawa J (1992) Vigilance does not covary with group-size in an island population of silvereyes (*Zosterops-lateralis*). Behav Ecol 3:207–210

Cheney DL, Seyfarth RM (1981) Selective forces affecting the predator alarm calls of vervet monkeys. Behaviour 76:25–61

Coolen I, Giraldeau LA, Lavoie M (2001) Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. Anim Behav 61:895–903

Cords M. (1990) Vigilance and mixed-species association of some East-African forest monkeys. Behav Ecol Sociobiol 26:297–300

Cowlishaw G (1998) The role of vigilance in the survival and reproductive strategies of desert baboons. Behaviour 135:431–452

Di Bitetti MS (2001) Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. J Zool (Lond) 253:33–45

Di Bitetti MS, Janson CH (2001) Social Foraging and the Finder's Share in Capuchin Monkeys, *Cebus apella*. Anim Behav 62: 47–56

Elgar MA (1989) Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. Biol Rev 64:13–33

Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295–311

Janson CH (1996) Towards an experimental socioecology of primates: examples for Argentine brown capuchin monkeys (*Cebus apella nigrivitus*). In: Norconk M, Rosenberger AL, and Gerber PA (eds) Adaptive radiation of neotropical primates. Plenum Press, pp 309–325

Janson CH (1998) Testing the predation hypothesis for vertebrate sociality: prospects and pitfalls. Behaviour 135:389–410

Janson CH, Di Bitetti MS (1997) Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. Behav Ecol Sociobiol 41:17–24

Jones ME (1998) The function of vigilance in sympatric marsupial carnivores: the eastern quoll and the Tasmanian devil. Anim Behav 56:1279–1284

Knight SK, Knight RL (1986) Vigilance patterns of bald eagles feeding in groups. Auk 103:263–272

Lima SL (1995) Back to the basics of antipredatory vigilance – the group size effect. Anim Behav 49:11–20

Lima SL, Bednekoff PA (1999) Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack. Anim Behav 58:537–543

Martin PR, Bateson P (1996) Measuring behaviour, 2nd edn. Cambridge University Press, Cambridge

McNamara JM, Houston AI (1992) Evolutionarily stable levels of group selection as a function of group-size. Anim Behav 43: 641–658

Nikolei J, Borries C (1997) Sex differential behavior of immature hanuman langurs (*Presbytis entellus*) in Ramnagar, South Nepal. Int J Primatol 18:415–437

Poysa H (1994) Group foraging, distance to cover and vigilance in the teal, *Anas crecca*. Anim Behav 48:921–928

Pulliam HR (1973) On the advantages of flocking. J Theor Biol 38: 419–422

Quenette PY (1990) Functions of vigilance behavior in mammals – a review. Acta Oecol 11:801–818

Roberts G (1996) Why individual vigilance declines as group size increases. Anim Behav 51:1077–1086

Robinette RL, Ha JC (2000) Social and ecological factors influencing vigilance by northwestern crows, *Corvus caurinus*. Anim Behav 62:447–452

Robinson JG (1981) Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus*. Anim Behav 29:1036–1056

Rolando A, Caldoni R, De Sanctis A, Laiolo P (2001) Vigilance and neighbor distance in foraging flocks of red-billed choughs, *Pyrrhocorax pyrrhocorax*. J Zool (Lond) 253:225–232

Rose LM (1998) Behavioral ecology of white-faced capuchins (*Cebus capucinus*) in Costa Rica. PhD thesis, Washington University, St. Louis, Miss.

Rose LM, Fedigan LM (1995) Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. Anim Behav 49:63–70

Ruiter JR de (1986) The influence of group-size on predator scanning and foraging behavior of wedgecapped capuchin monkeys (*Cebus olivaceus*). Behaviour 98:240–258

SAS Institute (1997) JMP statistics and graphics guide, version 3.3.2. SAS Institute, Cary, N.C.

Schaik CP van, van Noordwijk MA (1989) The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. Behav Ecol Sociobiol 24:265–276

Schoener TW (1981) An empirically based estimate of home range. Theor Popul Biol 20:281–325

Sokal R, Rohlf F (1997) Biometry, 3rd edn. Freeman, New York

Steenbeek R, Piek RC, van Buul M, van Hooff J (1999) Vigilance in wild Thomas's langurs (*Presbytis thomasi*): the importance of infanticide risk. Behav Ecol Sociobiol 45:137–150

Treves A (1998) The influence of group size and neighbors on vigilance in two species of arboreal monkeys. Behaviour 135: 453–481

Treves A (1999) Vigilance and spatial cohesion among blue monkeys. Folia Primatol 70: 291–294

Treves A (2000) Theory and method in studies of vigilance and aggregation. Anim Behav 60:711–722

Treves A (2001) Vigilance and aggregation in black howler monkeys (*Alouatta pigra*). Behav Ecol Sociobiol 50:90–95