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Effect of Male Emigration on the Vigilance Behavior of Coresident Males in White-Faced Capuchins (*Cebus capucinus*)

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I examined the vigilance behavior of male Cebus capucinus *residing in four groups in Santa Rosa Park, Costa Rica. One male emigrated from each of three study groups, providing ideal experimental conditions for examining the effect of coresident males on male vigilance behavior (social and nonsocial). Following the predator and conspecific defense theories for the adaptive value of male vigilance behavior and the occurrence of multimale groups, I predicted that male nonsocial vigilance would increase after the emigration of a coresident male. My prediction was supported in only one of the three study groups. Males in two groups decreased their nonsocial vigilance after the emigration of a coresident male, which was probably influenced by seasonal changes and the peripherality of one group's coresident male before his emigration. The social vigilance hypothesis proposes that for species with rigid dominance hierarchies, social vigilance should increase with an increase in same sex competitors. Therefore, I predicted that male social vigilance would decrease after the emigration of a coresident male. The hypothesis is generally supported in my findings, as two of the three groups displayed a decrease in social vigilance after the emigration of a coresident male. Increased social vigilance in the third group is best explained by the change in the alpha male's social behavior after the emigration of his only coresident male.*

KEY WORDS: *Cebus capucinus*; vigilance; social monitoring; male emigration.

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INTRODUCTION

The Primates display an almost universal pattern of gregariousness, with the vast majority of species residing in stable groups containing multiple males and females (Smuts *et al.*, 1987). Attempts to explain the adaptive significance and evolution of group living and group composition are numerous (van Schaik, 1983; O'Brien, 1991; Rose, 1994; Treves and Chapman, 1996) and attention has recently turned to explaining the number of males in primate groups (Mitani *et al.*, 1996; van Schaik, 1996; Pereira, 1998; Nunn, 1999; Kappeler, 2000). Mitani *et al.* (1996) tested the two major competing hypotheses proposed to explain the evolution of the multimale social system in primates: (1) breeding seasonality (Ridley, 1986) and (2) female distribution (Emlen and Oring, 1977; Wrangham, 1980; Terborgh, 1983; Dunbar, 1988; Altmann, 1990).

The breeding-seasonality hypothesis proposes that for species characterized by female mating synchrony, multiple males will be common because male monopolization of mating access is difficult when females come into estrus synchronously and for relatively short periods (Mitani *et al.*, 1996). The female-distribution hypothesis for the evolution of multimale groups proposes that a male's ability to monopolize mating access is dependent upon the spatial distribution of females. Species with large female group size usually contain multiple males, while those with small female group size contain fewer males. Mitani *et al.* (1997) concluded that female group size and consequently male mating competition—female-distribution hypothesis—are the main factors influencing the number of males in primate groups.

There were several exceptions, however, in which counter to what is predicted by the above hypotheses, some species displaying small female group size nevertheless exhibited a multimale social system (Mitani *et al.*, 1996). White-faced capuchins (*Cebus capucinus*) are exceptional as they are not seasonal breeders (Fedigan *et al.*, 1997) and their average group composition is 5.5 adult males and 4 adult females (Mitani *et al.*, 1996 from Fedigan, 1993). Explaining the existence of the capuchin multimale-multifemale social system presents a particularly challenging problem. Mitani *et al.* (1996:326) suggested that group composition for species that cannot be explained by female defensibility and male mating competition may be attributed to "the benefits gained by males who tolerate others [males] in groups." The potential benefits that males may gain include: decreased predation risk, cooperation against extragroup conspecifics, and increased reproductive success of related coresident males (Mitani *et al.*, 1996).

White-faced capuchins reside in groups containing related females, their offspring, and probably unrelated immigrant males (Oppenheimer, 1968; Freese, 1978; Fedigan, 1993). Natal male white-faced capuchins emigrate

together or disperse into groups that older, familiar males have previously joined (pers. obs.; Fedigan pers. comm.). However, until we have concrete evidence on the genetic relationships of coresident males, we cannot be certain that an increase in the reproductive success of related coresidents is a benefit secured by male white-faced capuchins. Regardless of the presence or absence of kinship among capuchin males, the cooperation of group males during encounters with predators and extragroup conspecifics is crucial to protect the group and to retain residency (Rose and Fedigan, 1995; Perry, 1995, 1996). This added protection from the attacks of predators, conspecifics or both may be the main benefit that the presence of multiple coresident males provide to both female and male members of their group.

Since researchers are unlikely to observe predator-prey interactions and intergroup encounters often enough to allow tests of relevant hypotheses, investigators have used vigilance behavior to indicate the severity of threats (Baldellou and Henzi, 1992; van Schaik and Höstermann, 1994; Blumstein, 1996; Treves and Chapman, 1996; Treves, 1997, 1999). However, in addition to vigilance directed at detecting predators and conspecifics, group living individuals may also direct vigilance against members of their own group (social monitoring hypothesis: Kervene *et al.*, 1978; Caine and Marra, 1988). According to Caine and Marra (1988), in species with rigid dominance hierarchies, individuals will engage in high levels of social vigilance at a cost to vigilance directed at detecting threats external to the group (nonsocial vigilance). When this occurs, it is beneficial to increase group size, particularly in the sex that is most active in detecting and defending against predators and conspecifics, since the costs of social vigilance will decrease when there are more individuals to monitor the nonsocial environment.

In the four species of capuchins, males are significantly more vigilant than females (Robinson, 1988a, b; van Schaik and van Noordwijk, 1989; Fragaszy, 1990; Fedigan, 1993; Rose, 1994, Rose and Fedigan, 1995). In *Cebus capucinus*, *C. albifrons* and *C. apella*, the number of males in a group influences individual rates of nonsocial vigilance, rather than the total number of group members (van Schaik and van Noordwijk, 1989; Rose and Fedigan, 1995). That is to say, the more males in a group the less time individuals of both sexes spend being vigilant towards threats external to the group. This would allow members of groups containing more males to devote an increased amount of time to foraging, resting and engaging in social interactions. Rose and Fedigan (1995) suggest that because both sexes benefit from male nonsocial vigilance, the behavior may have been an important factor in the evolution of the multimale social system of *Cebus capucinus.* Nonsocial vigilance may then be a good indicator of the benefits males receive by tolerating the presence of coresident males: protection for

themselves, their mates, and their offspring from predator and conspecific attack (van Schaik and van Noordwijk, 1989).

I examined the social and nonsocial vigilance behavior of male white-faced capuchins residing in four social groups in Santa Rosa Park, Costa Rica. Several males emigrated from their social groups, providing ideal experimental conditions for testing the suggestion of Rose and Fedigan (1995) that male vigilance was an important factor influencing the evolution of the multimale social system in the species. I address this hypothesis by examining the effect that the emigration of a coresident male had on the vigilance behavior of the males remaining in the study groups. If males are benefiting from the presence of coresident males in terms of increased protection from predators or conspecifics or both via their vigilance behavior, I predicted that males remaining in their groups will increase their rates of nonsocial vigilance after the emigration of a coresident male. I tested Caine and Marra's (1988) suggestion that an increase in social monitoring is a cost of sociality for species with strict dominance hierarchies. If an increase in time spent in social vigilance is a consequence of multiple males within groups of white-faced capuchins, I predict that male social vigilance will decrease after the emigration of a coresident male.

METHODS

Study Site, Species and Subjects

I studied white-faced capuchins (*Cebus capucinus*) in the Santa Rosa Sector of the Area de Conservacion Guanacaste, Costa Rica. Santa Rosa (formerly known as Santa Rosa National Park) is 35 km northwest of Liberia, in the Guanacaste Province and encompasses approximately 10,800 ha of dry deciduous forest and reclaimed pasture. The area has two distinct seasons: dry season from December through May, and rainy season from June through November. Annual rainfall in the park averages between 900 and 2,500 mm (Glander *et al.*, 1991). Observational and demographic data have been collected on the white-faced capuchins in Santa Rosa by Fedigan and her students since 1983.

White-faced capuchins are female-bonded monkeys that range from Panama through Southeastern Belize (Rowe, 1996). They reside in multimale-multifemale social groups which comprise presumably related females, their offspring, and unrelated immigrant males (Oppenheimer, 1968; Freese, 1978; Fedigan, 1993). Average group size ranges from 11 to 18 individuals with sex ratios approximating 1:1 (Fedigan *et al.*, 1997). The home ranges of white-faced capuchins are approximately 1–2 km^2 (Fedigan *et al.*,

Table I. Composition of study groups for comparison period and date of coresident male emigration

Group	Adult males	Subadult males	Adult females	Immatures	Total	Date of coresident male emigration
Cerco de Piedra (CP)	2	0	3	3–5	8–10	No emigration; group included in analyses as a control group
Los Valles (LV)	2–3	0	4	6–8	12–15	Dec. 1999
Bosque Humedo (BH)	1	2–3	3	1	7–8	Nov. 1999
Cuajiniquil (CU)	1–2	0	1	3	5–6	May 1999

1997). On average, males are 25–35% larger than females, and they are individually dominant over them (Fedigan, 1993). White-faced capuchins are not seasonal breeders, but they display a birth peak between January and April (Fedigan *et al.*, 1997). As diurnal forest-dwelling primates, capuchins must anticipate three main types of predators: raptors, felids, constricting and venomous snakes (van Schaik and van Hooff, 1983; Terborgh, 1983). In addition to these three types of predators, the Santa Rosa capuchins must also contend with coyotes and tayras (Freese, 1983; Chapman, 1986).

I studied four groups of white-faced capuchins from Feb. 1998 through April 1999: Cerco de Piedra, Los Valles, Bosque Humedo and Cuajiniquil (Table I). The Cerco de Piedra group (CP) included two adult males and ranged from 8 to 10 members. CP was the only group that did not experience an emigration of a coresident male. They are included in the study as a control group. The Los Valles group (LV) contained three adult males and ranged from 12 to 15 members. An adult male and two immature group members, one 3-year-old and one 2-year-old, disappeared from LV in late Dec. 1998 or early Jan. 1999 over a 3-week period when the groups were not under observation. The Bosque Humedo group (BH) originally included 1 adult and 3 subadult males. They totaled 8 members before the emigration of a subadult male in October 1998. Later he joined a neighboring group. The Cuajiniquil group (CU) is the smallest of the study groups with 2 adult males and a total of 6 group members before the coresident young adult (~10 yr) male's emigration in June 1998. He also later joined a neighboring group.

All members of the four study groups were habituated to the presence of researchers, and my assistants and I were able to make observations from 5–10 m. We could individually recognize all individuals according to their size, facial characteristics, and brow shape.

Data Collection and Analysis

Three research assistants and I collected data from late Feb. 1998 through April 1999. Before commencing data collection, we practiced together in the field to ensure interobserver reliability. We collected 1198.25 hours of focal data on all adult males (≥10 years) and subadult males (7–10 years) residing in the four study groups. We collected data in 15-minute focal-animal continuous-time samples (Altmann, 1974). During sampling we entered all behaviors of the focal male and identifications of interactants directly into a handheld PSION computer using the FOCOBS data entry program designed by Dr. Joan Silk at the University of California, Los Angeles. We collected 10 h of focal observations on all subject males in a group before observating the next group. However, due to the inherent difficulty of locating free-ranging primates, a strict sampling schedule could not be followed. We tried to sample all individuals for the 10-h round before moving on to the next study group and to collect ≤2 back-to-back samples on any individual within the study group. We kept records of focal sessions to ensure that each individual was observed equally and at varying times throughout the day. We discarded a focal session if the subject was out of sight for ≥2 min during the 15-min session.

Although the topic of vigilance and its effect on primate grouping patterns has been widely investigated, there is great variation in how the behavior has been defined. For example, Rose and Fedigan (1995:65) defined vigilance as "intently staring beyond immediate vegetation with a stationary, alert posture," while Treves (1998) defined vigilance as scanning beyond arms reach. Cowlishaw (1998) recorded a subject as being vigilant when "its eyes were open and its head up," while Steenbeek *et al.* (1999) defined it as a head movement of ≥45°. Although this variation no doubt reflects differences among subject species and conditions under which observations are made, it makes comparisons between study groups and species extremely difficult.

I used two measures of vigilance behavior: social and nonsocial vigilance. Social vigilance is directed at events within the group; that is, activities and locations of group members and other nonthreatening events in the group's immediate environment, e.g., deer foraging nearby. Nonsocial vigilance is directed against targets outside of the group, predators and extragroup conspecifics. Although it is difficult to distinguish the exact target of vigilance, e.g., predator vs. conspecific, it is possible, even in a field situation, to distinguish between vigilance directed external to and within the group.

Following Rose and Fedigan (1995), we recorded a focal subject as engaged in nonsocial vigilance when he ceased an activity and stared beyond the immediate vegetation in an alert, stationary posture. Male nonsocial

vigilance was most commonly recorded before and after the focal male, group member or another animal species, e.g., agouti, deer, magpie-jay, emitted an alarm call, when sudden loud noises were heard, e.g., branches falling, human shouting, when directing or receiving lost-calls, before and during foraging on the ground, and before and during drinking from terrestrial waterholes. Accordingly, this measure of vigilance, represents the monitoring of events external to the social group and is primarily directed at locating potential predators or extragroup conspecifics or both (Rose and Fedigan, 1995).

We recorded a focal subject as engaged in social vigilance when he interrupted an activity, e.g., foraging, resting, grooming, and scanned beyond the immediate vegetation, being watchful of group members or events occurring at close range. The behavior was not accompanied by a distinctive posture, as in nonsocial vigilance, and was directed around the immediate area occupied by the focal male. Although the behavior was most often directed towards the activities and locations of fellow group members, it was occasionally directed at other nonthreatening animals nearby. This measure of vigilance represents an individual's monitoring of the immediate environment, both social and otherwise. An individual could only be recorded as engaged in one of these behaviors, social or nonsocial vigilance, at any one time. By separating these two measures of vigilance, the results of this study will be more broadly comparable with other studies.

I excluded from analyses focal sessions in which predators or extragroup conspecifics were encountered as they resulted in increased levels of vigilance and there was no way to ensure that all males were equally sampled under these conditions. I also excluded focal sessions during which males were separated from their social group, as they displayed heightened vigilance levels, particularly while calling and trying to locate the group. In order to keep group composition consistent, I also excluded samples that were taken on focal subjects within the group when ≥ 1 coresident males were absent. Following Rose and Fedigan (1995) and Gould *et al.* (1997), I expressed social and nonsocial vigilance as the percentage of time each focal male was observed.

Data Analysis

I compared data separately for each of the three emigration events. First, I compared the vigilance behavior—(social and nonsocial)—for the two subject males remaining in the Los Valles group between the two rounds of data collected before and the two rounds of data collected after the emigration of their coresident male (approximately 20 h before and 20 h after). To account

for factors other than the emigration of a coresident male that may influence male vigilance behavior, e.g., seasonal or ecological changes or both, I used the subject males residing in CP (n = 2) and BH (n = 3) as a control group. I also compared their social and nonsocial vigilance for the two rounds of data collected before and after the emigration of the LV coresident male. I did not use the remaining CU male in the control group as he was in the process of changing groups during the period after the LV male's emigration, which may have influenced his vigilance rates. I used the CP and BH subject males as a control group because they experienced no change in their group compositions during the LV comparison periods. Significant changes in male vigilance behaviors between the before and after periods were not, therefore, the result of an emigration event and may help to identify extraneous influences on vigilance behavior.

I also controlled comparisons for the BH and CU emigration events. The control group for the comparison periods before and after the emigration of the BH coresident male comprises the 6 males residing in the 3 remaining study groups (LV n = 3, CP n = 2; and CU n = 1). The control group for the CU male's emigration comprises 9 males residing in the three remaining study groups (LV n = 3; CP n = 2; BH n = 4).

I used a 2-tailed Wilcoxon paired-sample test (Zar, 1999) to compare the social and nonsocial vigilance of the control groups before and after the emigration of their test group's coresident male. I then descriptively compared the changes in the vigilance of test groups with their control groups. Test group sample sizes are too small to allow for further statistical comparisons.

RESULTS

Los Valles Emigration

Table II is a summary of the changes in vigilance behavior for the control group and the two remaining LV males before and after the emigration of their coresident males. The nonsocial vigilance of the LV males both decreased after the emigration of their coresident male ($\bar{x}$ before = 1.37%; $\bar{x}$ after = 0.81%). The change in nonsocial vigilance for the control group is not significant ($Z = -0.135$; $p = .89$), with the mean decreasing from 0.73% to 0.72% after the LV emigration event. Both LV males displayed a decrease in social vigilance after their coresidents disappeared, with the mean percentage of time they engaged in social vigilance falling from 10.59% to 7.75%. All of the control males (n = 5) displayed an increase in social vigilance during the comparison period and the group's mean percentage of

Table II. Male social and nonsocial vigilance before and after the emigration of the Los Valles coresident male (expressed as % of time spent in each activity)

Group	Social before	Social after	Nonsocial before	Nonsocial after
Test Group:				
Diablo (LV; ad; α)	9.53	7.79	1.37	1.15
Side (LV; ad)	11.64	7.70	1.36	0.46
Mean	10.59	7.75	1.37	0.81
Control Group:				
Nose (CP; ad; α)	7.46	11.53	0.61	1.65
Trickle (CP; ad)	4.07	5.91	0.22	0.66
Leo (BH; ad; α)	5.01	10.17	1.98	0.81
Regis (BH; sa)	3.06	6.03	0.37	0.24
Casey (BH; sa)	3.58	5.30	0.42	0.27
Mean	4.64	7.79	0.73	0.72
Wilcoxon paired sample test (2 tailed)	$Z = -2.023^a$	$p = .043^*$	$Z = -0.135^b$	$p = .893$

LV = Los Valles; BH = Bosque Humedo; CP = Cerco de Piedra.
ad = adult male; sa = subadult male; α = alpha male.
[a]based on positive ranks.
[b]based on negative ranks.
*significance set at $\alpha < .05$.

time engaged in social vigilance increased significantly from 4.64% to 7.79% ($Z = -2.023$; $p = .043$).

Bosque Humedo Emigration

The nonsocial vigilance of the three remaining BH males increased from 0.55% to 1.0% after the emigration of their coresident males (Table III). The control males ($n = 6$) also displayed an increase in nonsocial vigilance during this time, from 0.84% to 0.86%, but this change is not significant ($Z = -0.943$; $p = .345$). The remaining BH males displayed a decrease in the percentage of time devoted to social vigilance after the emigration of a coresident subadult male, with their mean falling from 5.94% to 3.68%. The control males also displayed an overall decrease in social vigilance during this time period, however, the decrease from 7.81% to 6.35% is not significant ($Z = -0.943$; $p = .345$).

Cuajiniquil Emigration

The sole remaining male in the CU group displayed a decrease in nonsocial vigilance, from 4.14% to 1.89%, after the emigration of his coresident

Table III. Male social and nonsocial vigilance before and after the emigration of the Bosque Humedo coresident male (expressed as % of time spent in each activity)

Group	Social before	Social after	Nonsocial before	Nonsocial after
Test Group:				
Leo (BH; ad; α)	8.72	4.58	0.92	2.17
Regis (BH; sa)	5.31	3.10	0.39	0.42
Casey (BH; sa)	3.79	3.37	0.35	0.42
Mean	5.94	3.68	0.55	1.00
Control Group:				
Diablo(LV; ad; α)	6.97	8.11	1.28	1.26
Side (LV; ad)	11.60	11.61	1.13	1.38
Pirate (LV; ad)	8.41	4.93	0.56	1.02
Nose (CP; ad; α)	6.10	6.98	0.57	0.76
Trickle (CP; ad)	4.79	3.38	0.22	0.30
Spike (CP; ad; α)	9.00	3.09	1.26	0.41
Mean	7.81	6.35	0.84	0.86
Wilcoxon paired sample test (2 tailed)	$Z = -0.943^a$	$p = .345$	$Z = -0.943^a$	$p = .345$

LV = Los Valles; BH = Bosque Humedo; CP = Cerco de Piedra; CU = Cuajiniquil.
ad = adult male; sa = subadult male; α = alpha male.
[a] based on positive ranks.

male (Table IV). All of the control males also exhibited a decrease in nonsocial vigilance between the comparison periods, with the mean falling from 6.49% to 1.02%; this decrease is significant ($Z = -2.666$; $p = .008$). The CU male displayed an increase in social vigilance, from 7.37% to 11.38%, after the emigration of his only coresident male. The control males ($n = 9$) displayed an overall decrease in mean social vigilance during the period after the emigration of the CU male ($\bar{x}$ before = 8.45%; $\bar{x}$ after = 6.79%). This decrease is not significant ($Z = -1.599$; $p = .11$), and 3 of the 9 control males increased their social vigilance during this period.

DISCUSSION

Effect of Male Emigration on Coresident Male Nonsocial Vigilance

Traditional investigations of predation and vigilance indicate that individual nonsocial vigilance levels should increase with decreasing group size (Hamilton, 1971; Bertram, 1980; Yaber and Herrera, 1994) and with fewer numbers of males (van Schaik and van Noordwijk, 1989; Rose and Fedigan, 1995). Based on these findings, I predicted that male nonsocial vigilance

would increase after the emigration of a coresident male. However, of the 3 test groups only the Bosque Humedo males behaved as predicted. The mean level of nonsocial vigilance for BH nearly doubled—from 0.55% to 1.0%—after the departure of the coresident male, and though the control group also displayed a slight increase over the comparison period, it is not significant. This indicates that the more substantial increase observed for BH was the result of the emigration event rather than general ecological changes.

It is particularly interesting to note the substantial increase in the nonsocial vigilance of the BH alpha male, Leo. Alpha male white-faced capuchins often search for missing coresident males (Perry 1998a, b), and it is possible that Leo's increased vigilance was aimed at locating his missing coresident. However, the after period of comparison commenced 20 days postemigration, and with no lost calling or searching noted during data collection, this is an unlikely explanation for Leo's heightened vigilance. It is also important to consider the fact that Leo was the only adult male in BH. His two remaining coresident males were subadults; they contributed relatively little in the way of nonsocial vigilance, and their mean proportion of

Table IV. Male social and nonsocial vigilance before and after the emigration of the Cuajiniquil coresident male (expressed as % of time spent in each activity)

Group	Social before	Social after	Nonsocial before	Nonsocial after
Test Group:				
Spike (CU; ad; α)	7.37	11.38	4.14	1.89
Control Groups:				
Diablo (LV; ad; α)				
Side (LV; ad)	10.18	6.68	5.79	0.36
Pirate (LV; ad)	11.62	8.44	5.97	1.88
	7.86	8.80	7.88	1.01
Nose (CP; ad; α)				
Trickle (CP; ad)	6.00	7.88	12.80	1.68
	4.10	5.26	6.70	1.05
Leo (BH; ad; α)				
Regis (BH; sa)	8.52	9.14	8.28	1.14
Casey (BH; sa)	7.70	5.90	1.17	0.68
George (BH; sa)	6.60	4.26	4.68	0.93
	13.45	4.72	5.15	0.44
Mean	8.45	6.79	6.49	1.02
Wilcoxon paired sample test (2 tailed)	$Z = -1.599^a$	$p = .110$	$Z = -2.666^a$	$p = .008^*$

LV = Los Valles; BH = Bosque Humedo; CP = Cerco de Piedra; CU = Cuajiniquil.
ad = adult male; sa = subadult male; α = alpha male.
[a] based on positive ranks.
*significance set at $\alpha < .05$.

time spent in nonsocial vigilance (0.42%) is well below that of Leo and the mean for the control males.

For the two remaining emigration events, LV and CU, the test groups responded counter to my prediction. After the LV male's disappearance, his coresident males decreased rather than increased nonsocial vigilance. Similarly, the CU alpha male also displayed a decrease in nonsocial vigilance after the emigration of his only coresident male. Nonsocial vigilance represents an individual's perception of risk, predation or otherwise, so why would these males decrease nonsocial vigilance after the emigration of a coresident male?

The substantial decrease in nonsocial vigilance of the CU alpha male, Spike, is best explained by seasonal changes. Due to the timing of the CU coresident male's (Garth) emigration (May 1998), I compared data for CU between the dry and wet seasons. My finding that the control group displayed a significant decrease in nonsocial vigilance at this time indicates that the change in season had an overall effect on male vigilance levels. A decrease in male vigilance during the wet season is expected as Santa Rosa white-faced capuchins cease using terrestrial waterholes. Burger and Gochfeld (1992) note that waterholes are areas of high predation risk, and Rose and Fedigan (1995) found that male vigilance increased there. Rose (1988) noted that low levels of rainfall can lead not only to decreased food availability but also to increased vertebrate predation, decreased tree coverage, and increased use of terrestrial waterholes, all of which influences male vigilance.

Despite these seasonal effects on male nonsocial vigilance, Spike's level after the emigration of his only coresident male is still higher (1.89%) than the mean for the control group (1.02%). The greater time Spike devoted to nonsocial vigilance versus that of the control group also is not the result of his searching and lost-calling for his missing coresident (Perry, 1998a, b) because the after-period occurred almost 5 weeks following the last observation of Garth in CU. It is possible, however, that Spike was still monitoring the location of Garth, who emigrated to the neighboring Cafetal group with a range that substantially overlapped that of CU. This explanation is strengthened by the fact that Spike entered the Cafetal group on several occasions and eventually tookover as the group's alpha male. Another possible explanation for Spike's high level of nonsocial vigilance versus that of the control group is that after Garth's emigration, CU became a unimale group, the only one in this study. Spike's above average nonsocial vigilance may reflect that coresident males are taking up some of the burden of watching for predators and extragroup conspecifics, as I had predicted.

The decrease in LV males' nonsocial vigilance is more problematic. The control group did not significantly alter their nonsocial vigilance over the comparison period, making a seasonal effect an unlikely explanation

for the change among the test males. The LV males displayed a higher mean rate of nonsocial vigilance (1.37%) than the control group (0.73%) before the emigration of their coresident male (Pirate). After his disappearance from the group, the LV males decreased nonsocial vigilance to a level more comparable to that of the control group (LV $\bar{x} = 0.81\%$; control group $\bar{x} = 0.72\%$). The emigrated LV male spent a large proportion of time on the periphery of the group, and the heightened vigilance of the LV males before Pirate's departure may have been an attempt to monitor his movement and keep him in, or out, of the group. This explanation is nonetheless counter to the prediction and indicates that some coresident males may be imposing a cost in terms of the amount of time males must devote to nonsocial vigilance.

Effect of Male Emigration on Coresident Male Social Vigilance

According to the social-monitoring hypothesis, species with strict dominance hierarchies should devote an increasing amount of time to social vigilance with an increasing number of competitors within the group (Caine and Marra, 1988). Following this hypothesis, I predicted that male social vigilance would decrease after the emigration of a coresident male because the number of competitors within the group had declined. Two of the three test groups, LV and BH, responded according to the prediction. Only the CU male, Spike, displayed an increase in social vigilance after the departure of his sole coresident male. Spike's social vigilance increased considerably from 7.37% to 11.38%, in contrast with the mean decrease displayed by the control group over the comparison periods ($\bar{x}$ before = 8.45%, $\bar{x}$ after = 6.79%).

Seasonality had a significant effect on male nonsocial vigilance. However, given that the control group did not exhibit a significant change in social vigilance and their mean rate actually decreased over the comparison periods, the increase in Spike's social vigilance probably is not exclusively due to seasonal influences. Spike's increased social vigilance may better be explained by the alteration in behavior that he underwent after the emigration of his only coresident male, Garth. Before Garth's emigration, Spike spent 26.4% of his time in contact with group members and 8.02% in proximity ($\leq$1 m) to them, for a total of 34.26%, of which time, approximately two thirds were in contact or proximity (22.5%) with Garth. After Garth's emigration, Spike spent only 0.64% of his time in contact and 0.77% in proximity with fellow group members (total = 1.41%). Following Garth's departure, Spike spent the vast majority of time alone on the periphery and often became separated from the group. Spike's increased social vigilance may, then, reflect an attempt to monitor the locations of his fellow

group members (females and immatures) and decrease the probability that he would become separated from them. It is unclear why Spike withdrew from the group, but it is interesting to note that he visited Garth's new group on several occasions and eventually joined them as alpha male in Feb. 1999 with Garth as the beta male. Although it is possible that seasonality may have influenced Spike's social behavior in some way, i.e., his withdrawal from the group, I noted no such seasonal change in sociality in the other three groups.

As predicted by the social monitoring hypothesis, the remaining two test groups, LV and BH, decreased their levels of social vigilance after the emigration of a coresident male. The LV males decreased the mean proportion of time spent in social vigilance from 10.59% to 7.75%. This effect is strengthened by the finding that the control group displayed a significant increase in the proportion of time they devoted to social vigilance—from 4.64% to 7.79%—over the same period. The similarity in the social vigilance levels of the LV males and the control group after the emigration event further illustrates the effect that the extra coresident male had on their social vigilance. After Pirate's emigration, the composition of LV more closely approximated the two control groups in terms of the number of coresident males. LV contained two adult males in the after period of comparison, as did CP; BH had one adult and two subadult males.

The BH males also decreased their social vigilance after the emigration of a subadult coresident male ($\bar{x}$ before = 5.94%, $\bar{x}$ after = 3.68%), though the group's levels for both the before and after periods a substantially lower than those of the control group ($\bar{x}$ before = 7.81%, $\bar{x}$ after = 6.35%). These lower levels of social vigilance during both the before and after periods of comparison may again have been the product of only one adult male and two subadult males residing in BH. The smaller size of subadult males, the limited support they receive from group females, and their generally lower competitive abilities all indicate that they are a lesser threat to adult coresident males. This may explain the lower levels of social vigilance within this group.

However, the alpha male of BH, Leo, displayed a substantial decrease in social vigilance after emigration of his subadult coresident male, George ($\bar{x}$ before = 8.72%, $\bar{x}$ after = 4.58%). George was 9 years old before his emigration, making him the oldest of the subadult males and approaching adulthood. Before his emigration, George began to display heightened levels of aggression. He engaged in frequent chases, lunges and general threats to all group members, with the exception of the alpha male. It is possible that the heightened social vigilance of the BH alpha male before George's emigration was the result of this increased aggression and that Leo was perceiving

George as a threat to his dominance within the group. George was becoming a competitor nearly the size and strength of the alpha male.

Are Male White-faced Capuchins Benefiting by Tolerating the Presence of Coresident Males?

Mitani *et al.* (1996) suggested that for species whose multimale structure cannot be explained by female breeding synchrony and female group size, males must benefit from the presence of coresident males in some other way. I addressed this suggestion by testing whether coresident males provide a service to one another in terms of reducing the amount of time they devote to nonsocial vigilance. This service would lead to increased protection from both predators and conspecifics in exchange for membership in a social group. I predicted that if males benefit from the presence of coresident males in this way, they should increase the time devoted to nonsocial vigilance after the emigration of a coresident male. Although this prediction was not uniformly supported, the results from BH, and perhaps CU, indicate that some coresident males provide a positive service via nonsocial vigilance behavior.

Data on the effects of male emigration on the social vigilance of coresident males is somewhat more conclusive. Two of the study groups displayed a clear decrease in social vigilance after the departure of a coresident male. The increase in social vigilance displayed by the one male remaining in the third study group (CU) is attributable to the change in behavior that he underwent after the departure of his only coresident male. Accordingly, the presence of multiple coresident males, appears to have a cost: males need to spend more time engaged in social vigilance with an increasing number of coresident males. It also appears that social vigilance levels are affected by the threat that coresident males pose to one another, and that subadult males are less threatening than adult males are.

However, the Santa Rosa results most clearly illustrate the variability in male vigilance behavior in white-faced capuchins and the numerous factors that can influence it. Over the three emigrations (a period of 15 months), the range of time that individual males engaged in both social and nonsocial vigilance was quite dramatic. Male vigilance behavior may be influenced by seasonality (CU), the cohesion of the group (LV and CU), and even the age of coresident males (BH). This variability in the data makes it difficult, and unwarranted, to draw generalizations. Nevertheless, it appears that some males are more costly to have as coresidents than others. For example, subadult males contribute less to nonsocial vigilance than adult males do,

and they still require social monitoring as evidenced by the BH adult males' high levels of social vigilance throughout the three emigration events. The results from LV indicate that more peripheral males, i.e., ones that do not fully integrate within the group, may be particularly costly to tolerate. The two males remaining in LV decreased the amount of time they engaged in both social and nonsocial vigilance, indicating that they were investing a larger percentage of time monitoring the location and behavior of the peripheral coresident male.

Regardless of the costs that males impose on one another, the very presence of multiple coresident males appears to provide an important benefit to both females and males. Male takeovers in white-faced capuchins have resulted in the eviction of resident males, infanticide, and the deaths or disappearances of males and females (Rose and Fedigan, 1995). An increased number of males residing within a heterosexual group appears to reduce the chance, or at least the success, of male takeovers (Perry 1998a, b). From this cumulative evidence, Rose and Fedigan (1995) suggest that females may benefit from a reduction in the possible harm they and their kin might incur if they live in groups with multiple males. This may also be the main benefit to males. Long-term data from Santa Rosa demonstrates that once an alpha male loses the support of subordinates due to emigration, he is no longer able to defend the group from the immigration attempts of extragroup males. It may not be that males necessarily want to reside in groups with multiple males but instead that they need to. Male white-faced capuchins have great difficulty not only joining, but also remaining in a social group without the support and cooperation of other males.

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REFERENCES

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour* 49: 227–266.

Altmann, J. (1990). Primate males go where the females are. *Anim. Behav.* 39: 193–195.

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

Bertram, B. C. R. (1980). Vigilance and group size in ostriches. *Anim. Behav.* 28: 278–286.

Blumstein, D. T. (1996). How much does group size influence golden marmot vigilance? *Behaviour* 133: 1133–1151.

Burger, J., and Gochfeld, M. (1992). Effect of group size on vigilance while drinking in the coati, *Nasua narica,* in Costa Rica. *Anim. Behav.* 44: 1053–1057.

Caine, N. G., and Marra, S. L. (1988). Vigilance and social organization in two species of primates. *Anim. Behav.* 36: 897–904.

Chapman, C. A. (1986). Boa constrictor predation and group response in white-faced Cebus monkeys. *Biotropica* 18: 171–172.

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

Dunbar, R. I. M. (1988). *Primate Social Systems.* Comstock Publishing Associates, New York.

Emlen, S. T., and Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215–223.

Fedigan, L. M. (1993). Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *Int. J. Primatol.* 14: 853–877.

Fedigan, L. M., Rose, L. M., and Avila, R. M. (1997). See how they grow: Tracking capuchin monkey populations in a regenerating Costa Rican dry forest. In *Adaptive radiations of Neotropical Primates,* Norconk, M., Rosenberger, A., and Grabber, P. (eds.), Plenum Press, New York and London.

Fragaszy, D. M. (1990). Age and sex differences in the organization of behavior in wedge-capped capuchins (*Cebus olivaceus*). *Behav. Ecol.* 1: 81–94.

Freese, C. H. (1978). The behavior of white-faced capuchins (*Cebus capucinus*) at a dry-season waterhole. *Primates* 19: 275–286.

Freese, C. H. (1983). Cebus capucinus (Mono cara blanca, white-faced capuchin). In Janzen, D.H. (ed.), *Costa rica natural history,* University of Chicago Press, Chicago, pp. 458–460.

Glander, E. G., Fedigan, L. M., Fedigan, L., and Chapman, C. (1991). Field methods for capture and measurement of three monkey species in Costa Rica. *Folia Primatol.* 57: 70–82.

Gould, L., Fedigan, L. M., and Rose, L. M. (1997). Why be vigilant? The case of the alpha male. *Intl. J. Primatol.* 18(3): 401–414.

Hamilton, W. D. (1971). Geometry for the selfish herd. *J. of Theor. Biol.* 31: 295–311.

Kappeler, P. M. (ed.) (2000). *Primate males: causes and consequences of variation in group composition.* Cambridge University Press, Cambridge, UK.

Kerverne, E. B., Leonard, R. A., Scruton, D. M., and Young, S. K. (1978). Visual monitoring in social groups of talapoin monkeys (*Miopthecus talapoin*). *Anim. Behav.* 26: 933–944.

Mitani, J. C., Gros-Louis, J., and Manson, J. H. (1996). Number of males in primate groups: comparative tests of competing hypotheses. *Am. J. Primatol.* 38: 315–332.

Nunn, C. L. (1999). The number of males in primate social groups: a comparative test of the socioecological model. *Behav. Ecol. Sociobiol.* 46: 1–13.

O'Brien, T. C. (1991). Female-male social interactions in wedge-capped capuchin monkeys: benefits and costs of group living. *Anim. Behav.* 41: 555–567.

Oppenheimer, J. R. (1968). Behavior and Ecology of the White-faced Monkey, Cebus capucinus on Barro Colorado Island, Canal Zone. Ph.D. dissertation, University of Illinois, Urbana.
Pereira, M. E. (1998). One male, two males, three males, more. *Evol. Anthrop.* 7: 39–45.
Perry, S. E. (1995). Social relationships in wild white-faced capuchin monkeys (*Cebus capucinus*). Ph.D. dissertation, University of Michigan.
Perry, S. E. (1996). Intergroup encounters in wild white-faced capuchin monkeys. *Cebus capucinus. Primates* 35: 409–415.
Perry, S. E. (1998a). Male-male social relationships in wild white-faced capuchins, *Cebus capucinus. Behaviour* 135: 139–172.
Perry, S. E. (1998b). A case report of a male rank reversal in wild white-faced capuchins (*Cebus capucinus*). *Primates* 39: 477–510.
Ridley, M. (1986). The number of males in a primate troop. *Anim. Behav.* 34: 1848–1858.
Robinson, J. G. (1988a). Demography and group structure in wedge-capped capuchin monkeys, *Cebus olivaceus. Behaviour* 104: 202–232.
Robinson, J. G. (1988b). Group size in wedge-capped capuchin monkeys *Cebus olivaceus* and the reproductive success of males and females. *Behav. Ecol. Sociobiol.* 23: 187–197.
Rose, L. M. (1994). Benefits and costs of resident males to females in white-faced capuchins (*Cebus capucinus*). *Am. J. Primatol.* 32: 235–248.
Rose, L. M. (1998). Behavioral ecology of white-faced capuchins (*Cebus capucinus*) in Costa Rica. Ph.D. dissertation, University of St. Louis.
Rose, L. M., and Fedigan, L. M. (1995). Vigilance in white-faced capuchins, Cebus capucinus, in Costa Rica. *Anim. Behav.* 49: 63–70.
Rowe, N. (1996). *The Pictorial Guide to the Primates.* Pogonias Press, New York.
van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour* 87: 120–144.
van Schaik, C. P. (1996). Social evolution in primates: The role of ecological factors and male behaviour. *Proc. Br. Acad.* 88: 9–31.
van Schaik, C. P., and van Hooff, J. A. R. A. M. (1983). On the ultimate causes of primate social systems. *Behaviour* 85: 91–117.
van Schaik, C. P., and Höstermann, M. (1994). Predation risk and the number of adult males in a primate group: a comparative test. *Behav. Ecol. Sociobiol.* 3: 261–272.
van Schaik, C. P., and van Noordwijk, M. A. (1989). The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. *Behav. Ecol. Sociobiol.* 24: 265–276.
Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.) (1987). *Primate Societies.* Chicago University Press, Chicago.
Steenbeek, R., Ruben, C. P., van Buul, M., and van Hooff, J. A. R. A. M. (1999). Vigilance in wild Thomas's langurs (*Presbytis thomasi*): the importance of infanticide risk. *Behav. Ecol. Sociobiol.* 45: 137–150.
Terborgh, J. W. (1983). *Five New World Primates: A Study in Comparative Ecology.* Princeton University Press, Princeton, New Jersey.
Treves, A., and Chapman, C. A. (1996). Conspecific threat, predation avoidance, and resource defense: implications for grouping in langurs. *Behav. Ecol. Sociobiol.* 39: 43–53.
Treves, A. (1997). Vigilance and the use of micro-habitat in solitary rainforest mammals. *Mammalia* 61: 511–525.
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). Has predation shaped the social systems of arboreal primates? *Int. J. Primatol.* 20: 35–67.
Wrangham, R. (1980). An ecological model of female-bonded primate groups. *Behaviour* 75: 262–299.
Yaber, M. C., and Herrera, E. A. (1994). Vigilance, group size and social status in capybaras. *Anim. Behav.* 48: 1301–1307.
Zar, J. H. (1999). *Biostatistical Analysis.* Fourth Ed. Prentice-Hall Inc., New York.