



Interspecific Interactions Between *Cebus capucinus* and other Species: Data from Three Costa Rican Sites

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*Capuchins exhibit considerable cross-site variation in domains such as foraging strategy, vocal communication and social interaction. We report interactions between white-faced capuchins (*Cebus capucinus*) and other species. We present comparative data for 11 groups from 3 sites in Costa Rica that are ecologically similar and geographically close, thus reducing the likelihood that differences are due solely to genetic or ecological differences. Our aim is to document both the range of variation and common elements across sites and situations. We also consider factors that contribute to the variation or consistency or both, including social learning, local ecology, and temperament. We consider 4 categories of allospecifics: (1) vertebrate prey, (2) potential predators, (3) feeding competitors, and (4) neutral species. Although we cannot rule out local differences in ecology, our data suggest that social learning may account for at least some cross-site differences in behavior toward allospecifics.*

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*Our strongest finding is that boldness, aggression and pugnacity are displayed consistently across sites, groups and circumstances, even in interactions with neutral species, which reflects a critical aspect of species-specific temperament in *Cebus capucinus* that has been evolutionarily developed and reinforced through highly opportunistic foraging, strong predator defense, and active hunting. We suggest directions for future research, particularly in regard to primate temperament as an evolved trait with consequences for fitness.*

KEY WORDS: *Cebus capucinus*; allospecifics; predator-prey interactions; social learning; temperament.

INTRODUCTION

An important aspect of the behavioral ecology of most wild primates is the presence of other animals in their environment—allospecifics—with which they interact. Of particular interest are species that are potential competitors, predators, or prey. Various researchers have considered competition between sympatric primate species (Chapman, 1988; Gautier-Hion *et al.*, 1983; Porter, 2001; Terborgh, 1983; Wahunga, 1998) or responses to predators (Boinski, 1987; Fichtel and Kappeler, 2002; Sauther, 1989; Seyfarth *et al.*, 1980; Stanford, 2002; Tutin *et al.*, 1981), and considerable attention also has been paid to primates as predators. By far the best-known predator-prey interactions are those between chimpanzees and red colobus (Boesch, 1994; Stanford, 1998; Watts and Mitani, 2002). However, systematic predation on relatively large vertebrates also is well documented in white-faced capuchins (Fedigan, 1990; Rose, 1997, 2001). Rose (1997) suggested that the pattern of aggressive behaviors exhibited by white-faced capuchins toward predators, prey, and other animals may be linked, but their interactions with allospecifics have not been systematically examined. In particular, no study had been have focused on the range of behaviors directed toward other species in terms of common elements, or variation among populations.

White-faced capuchins (*Cebus capucinus*) are medium-sized (males average 3.5 kg, females 2.5 kg), Neotropical monkeys. They are primarily arboreal, inhabit a wide range of forest types, and are highly flexible in terms of both diet and behavior (Fragaszy *et al.*, 1990). Wild white-faced capuchins are noteworthy for their inquisitiveness and general pugnacity, as well as their proficiency as hunters. Knowing that capuchins interact with a broad range of vertebrate species, we set out to do a systematic cross-site comparison of interaction patterns as part of a broader study on social traditions in wild capuchins (Perry *et al.*, in press). Considerable intersite variability exists in other behavioral domains, including vocal behavior (Boinski, 1996),

foraging behavior (Chapman and Fedigan, 1990; Janson and Boinski, 1992; Panger *et al.*, 2002), patterns of social interactions (Manson *et al.*, 1999), and social conventions (Perry *et al.*, 2003).

Social learning is one factor that may contribute to variation in responses to allospecifics, and thus help to explain variation among sites (Custance *et al.*, 2002; Fragaszy and Perry, in press). Ecological differences are also likely to contribute to intersite variation, especially responses toward feeding competitors, and predator-prey interactions. Temperament or personality (Clarke and Boinski, 1995; Gosling and John, 1999; Karli, 1989; Stevenson-Hinde and Zunz, 1978) may be another factor shaping responses to allospecifics. Species-specific temperament may help account for common elements in responses to allospecifics across sites and in different contexts, while the degree of malleability in those responses helps to determine the potential for variability. We know very little about the role of evolved psychology in nonhuman primates and the extent to which this may influence behavioral patterns, including responses to allospecifics. Documenting responses to interspecific encounters across a range of social groups and contexts is a crucial first step to identify the range of variation that exists and to make inferences about the possible causes.

METHODS

Study Sites

Our data are from long-term studies of white-faced capuchins at three sites in Guanacaste Province in Northwestern Costa Rica: Santa Rosa, Lomas Barbudal and Palo Verde (Figure 1). We limited our comparison to a single species at 3 nearby sites to minimize the likelihood that behavioral differences were due solely to major genetic or ecological differences. Ecologically, the 3 sites are broadly similar, consisting mainly of tropical dry forest with riverine and semi-evergreen patches (Janzen, 1983). Before extensive deforestation by humans within the past 50 years, they were almost certainly part of one continuous forest. Santa Rosa and Lomas are now *ca.* 50 km apart, while Palo Verde and Lomas Barbudal are still connected by a narrow corridor.

At Santa Rosa, average annual rainfall between 1990 and 1999 is 1365 mm (SD 511 mm; range 880–2261 mm), and at Palo Verde, annual rainfall between 1997 and 2000 is 1364 mm (SD 232 mm, range 713–2130 mm). We do not have detailed rainfall data for Lomas Barbudal, but Frankie *et al.* (1988) report a range from 1000–2200 mm. The 3 sites are subject to marked seasonality, with almost all rainfall occurring between mid-May and mid-November. Many trees lose their leaves during the dry season, and

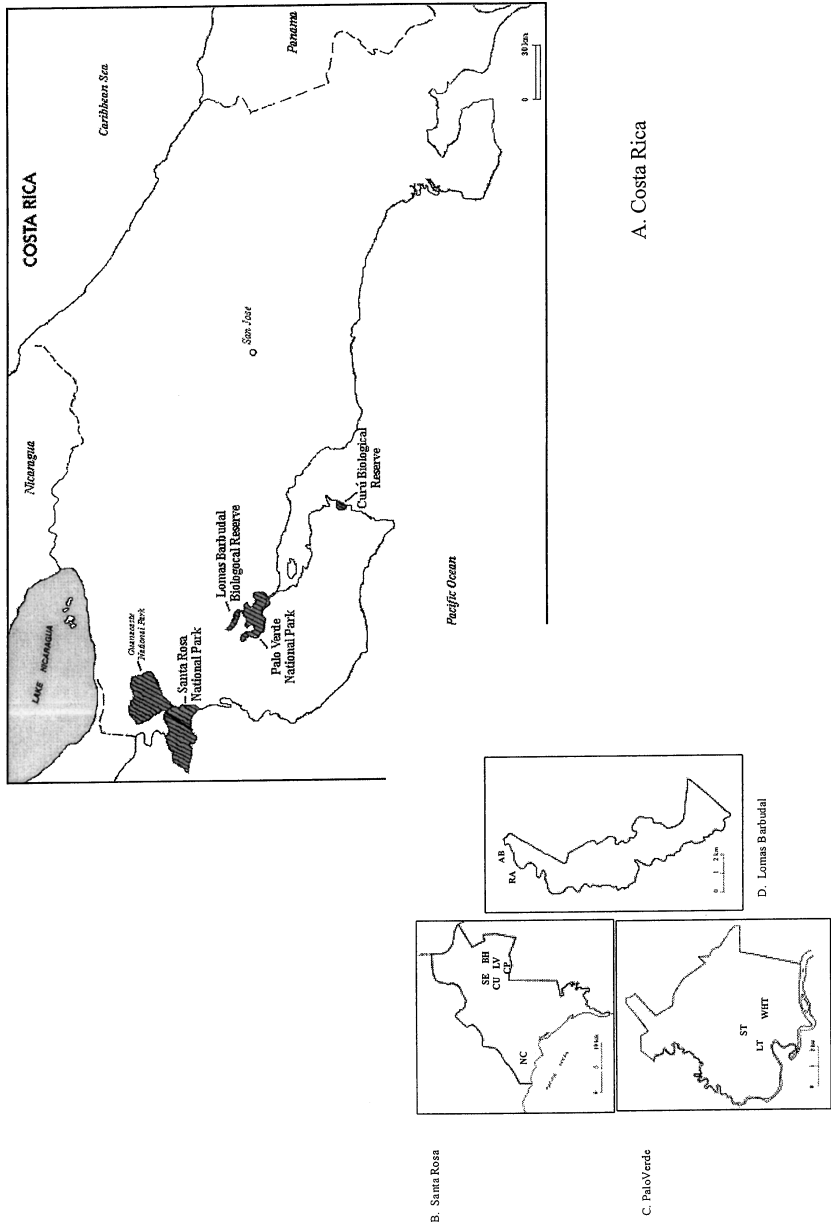


Fig. 1. Map of (A) Costa Rica showing locations of the 3 study sites and 11 study groups. (B) Santa Rosa, (C) Lomas Barbudal, (D) Palo Verde. Figure Legend: Santa Rosa. NC = Nancite group, SE = Sendero group, CU = Cuajiniquil group, LV = Los Valles group, BH = Bosque Humido group. Palo Verde: ST = Station troop, LT = Lagoon troop, WHT = Water Hole troop. Lomas Barbudal: AB = Abby's group; RA = Rambo's group.

in conjunction with the relatively low (<25 m) canopy in most areas, this allows for excellent observation conditions (Frankie *et al.*, 1974; Chapman, 1987; Chapman and Fedigan, 1990; Frankie *et al.*, 1988; Panger, 1997, 1998). In addition to white-faced capuchins, mantled howlers (*Alouatta palliata*) are present at all 3 sites, and black-handed spider monkeys (*Ateles geoffroyi*) are present at Santa Rosa and Palo Verde. Long-term studies of the 3 species have been conducted at Santa Rosa since 1983 (Fedigan *et al.*, 1996; Fedigan and Jack, 2001), and there are ongoing long-term studies of white-faced capuchins at Lomas Barbudal (Gros-Louis, 2002; Manson and Perry, 2000; Perry, 1998) and Palo Verde (Panger, 1998, 1999).

We lack quantitative data on the composition of predator communities. However, most potential predators on white-faced capuchins are present at all 3 sites, though not all were encountered by our study groups. The major potential predators are boa constrictor (*Boa constrictor*), jaguar (*Panthera onca*), puma (*Felis concolor*), jaguarundi (*F. yaguaroundi*), tayra (*Eira barbara*), coyote (*Canis latrans*), caiman (*Caiman crocodilus*), and possibly ocelots (*Felis pardalis*) and margays (*F. weidii*). Among the many smaller raptors, the largest is the greater black hawk (*Buteogallis uribitinga*). The harpy eagle (*Harpia harpyia*), a major avian predator at many other Neotropical sites (Boinski, 1987; Sherman, 1991), is not at any of our sites.

Data Sources and Collection Methods

Our data are drawn from *ca.* 17,000 observation hours (time spent by ≥ 1 observer in visual contact with ≥ 1 member of a study group) and 11 study groups, (6 at Santa Rosa, 2 at Lomas Barbudal and 3 at Palo Verde) between 1991 and 2001. (Table I). Because none of our studies was designed specifically to investigate interspecific interactions, our data are limited by differences in research objectives, methodology and extraction *post hoc* from observations *ad libitum* recorded by different researchers. For broad questions such as with which species our study groups interacted and their general behavior, we used the entire data set; but for some more specific questions and quantitative analyses, we were able to use only subsets of our data.

All of our studies involved the intensive collection of focal samples on known and well-habituated individuals, most in the form of 10-min or 15-min continuous sessions recorded during the course of an average 12-h day. However, all observers also collected a large quantity of data *ad libitum*, particularly in respect to conspicuous events such as predation and predator encounters. At Santa Rosa in 1995–1996 and at Lomas Barbudal in 1991–93 were specifically collected occurrence data with respect to alarm calls and mobbing responses, (including the cause whenever possible), and recorded

Table 1. Data on interspecific interactions for 11 white-faced capuchin groups at 3 Costa Rican sites

Site and study group	Years	Observation hours ^a	Principal investigators	Data type ^b	Quantitative data used in analyses ^c
Santa Rosa (SR)					
Sendero (SE)	1992–1993	45	KM	A	
Cerco de Piedra (CP)	1991	285	LR	Q & A	VP
CP	1992–1993	270	KM	A	
CP	1995–1996	732	LR	Q & A	VP, P, H, C
CP	1998	290	KM	Q & A	Play
CP	1998–1999	267	KJ	Q & A	VP, C
Los Valles (LV)	1991	260	LR	Q & A	VP
LV	1992–1993	370	KM	A	
LV	1995–1996	997	LR	Q & A	VP, P, H, S, C
LV	1998	270	KM	Q & A	Play
LV	1998–1999	536	KJ	Q & A	VP, S, C
Nancite (NC)	1995–1996	408	LR	Q	VP, P, H, S, C
Cuajiniquil (CU)	1998	126	KJ	Q	H, S, C
Bosque Humido (BH)	1998–1999	436	KJ	Q	H, S, C
	SR total	5292			
Lomas Barbudal (LB)					
Abby's group (AB)	1990	337	SP	A	
AB	1991–1993	3703	SP	Q & A	VP, P, H, C
AB	1994–2001	3209	SP, JM, JGL	A	
Rambo's group (RA)	1997–2001	3235	SP, JM, JGL	A	
	LB total	10484			
Palo Verde (PV)					
Station Troop (ST)	1995–1996	888	MP	Q	VP, P
Water Hole Troop (WHT)	1995	84	MP	Q	VP, P
Lagoon Troop (LT)	1995	228	MP	Q	VP, P
	PV total	1200			

^aHours that >1 observer was in visual contact with ≥ 1 group member.

^bQ = Quantitative data (including hourly rates) available; A = source of descriptions and anecdotes only.

^cVP = Vertebrate Predation; P = encounters with predators; H = howlers, S = spider monkeys, C = coatis.

all encounters with mammalian allospecifics at Lomas during the latter period. The data presented here include focal observations and observations *ad libitum* during all group contact hours, including but not limited to focal sessions. All rates are per 100 h observation (occurrences/contact hours *100) unless otherwise stated.

Because many of the results are preliminary and descriptive, we include few statistical tests. However, in some cases, we examine relationships between variables using nonparametric correlation tests (Kendall's tau), and we performed a stepwise regression to further elucidate factors influencing squirrel hunting. We performed all statistical tests on SPSS (version 9.0), with significance set at $p \leq 0.05$.

INTERACTIONS WITH PREY SPECIES

Table II shows the range of prey taken at each of the 3 study sites. As not all prey could be identified specifically we use general categories rather than scientific nomenclature in some cases. Even so, it is evident that a similar range of prey is available to monkeys at each site. However, capuchin take a wider ranges of prey at Santa Rosa (19 of 20 categories common to all 3 sites, 1 attempted) and Lomas Barbudal (11 categories, 1 attempted) than at Palo Verde (6 categories, 1 attempted; Table II). Placing bird prey in 3 categories only (eggs, nestlings, adults) to allow for intersite

Table II. Vertebrate prey taken by white-faced capuchins at three Costa Rican sites

	Santa Rosa ^a	Lomas ^a	Palo Verde ^a
Mammals			
Squirrels (<i>Sciurus variegatoides</i>)			
... Nestlings	xxx	xxx	xx
... Adults and large immatures	xxx	xxx	0
Coatis (<i>Nasua narica</i>) – nestlings ^b	xxx	xxx	x
Anteater (<i>Tamandua mexicana</i>) – juvenile	0	x	0
Tree rats (<i>Nelomys</i> sp.?)	xx ^c	xx	0
Unidentified (small) rodents	xx ^c	xxx	0
Bats (various)	x ^d	x	attempted
Reptiles/Amphibians			
Ctenosaurs (<i>Ctenosaura similis</i>) – immatures	xx	0	0
Anolids and other small lizards	xxx	xxx	0
Frogs (various)	x	0	0
Birds			
Currassows (<i>Crax rubra</i>): eggs	x	x	0
Guans (<i>Penelope purpurascens</i>): nestlings and eggs	xxx	xxx	0
Magpie jays (<i>Cyanocorax formosa</i>): adults	x	0	0
Magpie jays: nestlings and eggs	xxx	x ? (eggs)	x ? (eggs)
Nightjars, tinamous, doves: eggs	x	x	0
Parrots: adults	attempted	0	0
Parrots: nestlings and eggs	xx	attempted	0
Trogon (nestling and eggs)	x	0	x ? (eggs)
Woodpeckers: nestlings and eggs	xxx	0	xxx (eggs)
Wrens: nestlings and eggs	xxx	xxx	xxx (eggs)
Herons: eggs	x	0	0
Wood ducks: (<i>Dendrocygna autumnalis</i>): eggs	n/a	n/a	xxx (eggs)

Note. xxx = common (>5 observations per group/year); xx = occasional (2–5 observations per group/year); x = rare (isolated occasions; only one group or year); ? (eggs) = thought to be taken but not positively identified; n/a = prey not available; 0 = prey known to be available but no predation episodes observed. Attempted = predation attempts but no successful captures observed.

^aBased on quantitative and qualitative data from all groups and observation periods.

^bLarger pups occasionally chased but no observation of successful capture.

^cEaten almost exclusively by juveniles.

^dReported by Fedigan (1990) at Santa Rosa but not observed in subsequent years.

Table III. Vertebrate predation by white-faced capuchins at 3 Costa Rican sites

Site	Mean group size	Observation hours	Predation events ^a	Adult squirrels	Squirrel nest raids	Coati nest raids	Bird/egg nest raids	Other events ^b
Santa Rosa ^c	15.4	2682	81	14	3	12	43	9
Lomas Barbudal ^d	20.0	3703	81	14	1	13	35	18
Palo Verde	18.5	1200	n/a	0	2	1	“many”	0
<i>Rate per 100 hrs of observation</i>								
Santa Rosa			3.02	0.52	0.11	0.45	1.60	0.34
Lomas			2.19	0.38	0.03	0.35	0.95	0.49
Palo Verde			n/a	0.00	0.17	0.08	n/a	0.00

^aSuccessful predation events resulting in the capture and consumption of ≥ 1 prey items.

^bPrimarily rodents, lizards, one bat at Lomas.

^cBased on quantitative data for LV and CP in 1991 and 1995–96, and NC 1996.

^dBased on quantitative data for group AB 1991–1993.

differences in specific identification reduces the contrast, but the pattern remains the same (Santa Rosa 12 prey categories, Lomas Barbudal 9, Palo Verde 3). The differences are further reduced if we allow for the shorter (one-year) sampling period at Palo Verde by considering only one year at Lomas Barbudal and single group/years at Santa Rosa. Then there are 7 prey categories at Lomas Barbudal and 6–9 categories per group/year at Santa Rosa versus 3 prey categories at Palo Verde.

Comparative predation rates suggest that white-faced capuchins are somewhat more predatory at Santa Rosa than at Lomas Barbudal, and that both are more predatory than those at Palo Verde (Table III). Bird nest raiding may be equally common at Palo Verde, but in the absence of a precise count, we could not calculate rates for it or for total predation events. However, there was only one coati nest raid and no squirrel hunt, excluding nest raids, during >1200 observation hours at Palo Verde. Lomas Barbudal and Santa Rosa share a common pattern of bird, squirrel and coati predation rates in descending order, with somewhat lower rates at Lomas Barbudal in each case. Only the rate of other prey captures is higher at Lomas Barbudal than at Santa Rosa. These are mainly small rodents and lizards that are taken quietly by single individuals, and at Santa Rosa, mainly by juveniles (which were not focal subjects during our study), so sampling bias cannot be ruled out as a source of error. However, adults took about half of the rodents and lizards at Lomas Barbudal, so the possibility that they are more systematically targeted by the monkeys there warrants further investigation.

Squirrel Hunting

We lack independent data regarding comparative squirrel densities at our sites, but we systematically recorded the rate at which the monkeys encountered squirrels (*Sciurus variegatoides*) at Santa Rosa in 1995–96 and at Lomas Barbudal in 1991–93. Accordingly, we have at least a rough proxy measure of prey availability. Based on general observation and encounter rates (Table IV), squirrels appear to be more abundant at Santa Rosa than at Lomas Barbudal. At Santa Rosa, squirrels seem to be more abundant in the home ranges of groups LV and CP than in that of group NC. On average, capuchins at Santa Rosa encounter non-nestling squirrels about 7 times more often than at Lomas Barbudal, and squirrel hunts are 4 times more common (Table IV). There is considerable variation across groups and years, but squirrel encounter rates are consistently higher at Santa Rosa than at Lomas Barbudal, and hunting rates are higher in all cases except for group NC. However, Lomas Barbudal capuchins are twice as likely to hunt squirrels when they encounter them. Over 90% of squirrel encounters at Lomas Barbudal led to hunts in both periods versus 49% (range 13%–60%) at Santa Rosa. Squirrel hunting success was also higher at Lomas Barbudal: 64% overall (91% in 1991–92; 44% in 1992–93). In short, capuchins at Lomas Barbudal encounter fewer squirrels, but are more likely to hunt, and to kill them.

Hunting Frequency

At Santa Rosa, the frequency of squirrel hunting seems mainly determined by squirrel abundance, at least to the extent that abundance is reflected by encounter rates. Across 5 group/years, the rate of squirrel hunting, squirrel kills, and proportion of squirrels chased are all positively correlated with encounter rates (Kendall's $\tau = 1.0$, $p < 0.001$, $n = 5$). The correlation between encounter and hunting rates remains significant when the Lomas Barbudal data are added ($\tau = 0.81$, $p = 0.011$, $n = 7$ group/periods), but not those between encounter and kill rates ($\tau = 0.52$, $p = 0.099$) or encounter rates and proportion chased ($\tau = 0.048$, $p = 0.881$).

Group composition has little effect on the frequency of squirrel hunting. Neither group size nor the number of adult males in a group are significantly correlated with squirrel encounter rates, hunting rates, kill rates, or the proportion of encounters that lead to hunts at either Santa Rosa or in the combined data set (τ all ≤ 0.06 , all $p > 0.15$). A stepwise regression confirms that the only significant predictors of the proportion of encounters that lead to hunts are site and encounter rate. Site accounts for 71% of the

Table IV. Squirrel hunting by white-faced capuchins at Santa Rosa and Lomas Barbudal

Site/group	Mean grpsize	Adult males	Obs. hrs.	Squirrel encounter	Squirrels chased	Squirrels caught ^a	Encounter rate ^b	Chase rate ^b	Catch rate ^b	% Squirrels chased	Hunting success ^c	
Santa Rosa												
LV 1995	22	4.8	656	47	28	6	7.17	4.27	0.92	60	21	
LV 1996	18	2.8	341	15	7	2	4.40	2.05	0.59	47	29	
CP 1995	13	4.0	405	16	7	2	3.95	1.73	0.49	44	29	
CP 1996	9	3.7	327	8	3	1	2.45	0.92	0.31	38	33	
NC 1996	15	3.0	408	8	1	0	1.96	0.25	0.00	13	0	
<i>Total</i>			2137	94	46	11	4.40	2.15	0.51	49	24	
Lomas Barbudal												
1991-92	20	4.0	1317	12	11	10	0.91	0.84	0.76	92	91	
1992-93	20	4.0	2386	10	9	4	0.42	0.38	0.17	90	44	
<i>Total</i>			3703	22	20	14	0.59	0.54	0.38	91	70	

^aExcludes nestling squirrels.^bRate per 100 observation hours.^cPercentage of squirrel chases that ended in kills.

variance in proportion of encounters that lead to hunts; site and encounter rate together account for 91%.

Hunting Success

The greater hunting success of Lomas Barbudal capuchins does not seem to derive from differences in group composition or squirrel abundance. There is no significant correlation between squirrel hunting success and group size, number of adult male group members, encounter rates, hunting rates, or percentage of encounters that lead to hunts in either the Santa Rosa data set or in the combined data set (all $\tau < 0.50$, all $p > 0.13$). A stepwise regression indicated only site as a significant predictor of hunting success, accounting for 54% of the total variance.

Previous analyses of squirrel hunting at Santa Rosa showed that the number of males involved in a hunt had no obvious effect on squirrel hunting success (Rose, 1997). However, group hunts that included at least one adult male, especially the alpha male, were more successful than group hunts in which no adult male participated (Rose, 1997). At least one female participated in about half of the squirrel hunts, but males were predominant in successful hunts and prey capture. In 1995–96, adult males made 10 (77%) of the 13 non-nestling squirrel kills for which the captor was identified, and alpha males made 6 of them. A female caught one squirrel, and 2 (15%) were caught by juvenile males. By contrast, adult males at Lomas Barbudal caught 5/14 (36%) of non-nestling squirrels, adult females caught 36%, and juvenile males caught 28%.

Why do juvenile and female capuchins at Lomas Barbudal kill more squirrels than their counterparts at Santa Rosa do? We suggest 3 hypotheses, all of which warrant more systematic investigation than we provide:

1. Females and juveniles at Lomas Barbudal are less inhibited from making kills due to strong alliances or other social behaviors that help to counter male dominance and potential food theft;
2. Females and juveniles at Santa Rosa obtain a greater share of meat through food-sharing or secondary carcass acquisition, and thus have less need to make kills for themselves;
3. There are circumstances that make squirrels easier for females and juveniles to capture at Lomas Barbudal than at Santa Rosa.

Hypothesis 1: Fear of Theft Inhibits Female and Juvenile Hunting at Santa Rosa

Females at Lomas Barbudal have strong alliances compared with those at Santa Rosa (Manson *et al.*, 1999). However, there is no evidence that meat theft is less common at Lomas Barbudal (Table V). At Santa Rosa, there was only one case in which a male attempted (unsuccessfully) to steal meat from a female. Most of the 10 attempted thefts at Lomas Barbudal involved juveniles attempting to steal from females or from one another, not adult males attempting to steal from them. It thus seems unlikely that potential theft is a major factor inhibiting females or juveniles from killing squirrels.

Hypothesis 2: Juveniles and Females Obtain More Shared Meat at Santa Rosa

Adult squirrels are shared somewhat more often at Santa Rosa than at Lomas Barbudal (Table V). However, most of the sharing at Santa Rosa

Table V. Meat-sharing and theft by white-faced capuchins at Santa Rosa and Lomas Barbudal

	Carcasses	Mean # owners	Sharing incidents ^a	Attempted theft ^b	Actual theft ^c	Rate of sharing	Rate of theft
Adult/large immature squirrels							
Santa Rosa	14	2.8	11	0	0	0.79	0.00
Lomas	12	3.0	6	10	3	0.50	0.25
Nestling squirrels							
Santa Rosa	8	1	2	1	1	0.25	0.13
Lomas	3	3.0	2	0	0	0.67	0.00
Nestling coatis							
Santa Rosa	31	1	9	1	3	0.29	0.10
Lomas	36	2.9	50	64	11	1.39	0.31
Total							
Santa Rosa	53	1.60	22	2	4	0.42	0.08
Lomas	51	2.97	58	74	14	1.14	0.27

Note. Data for Santa Rosa based on 2682 observation h, 1991, 1995, 1996; for Lomas, 3703 observation h 1991–93.

^aIncludes tolerated scrounging, food offering, co feeding; excludes retrieving dropped pieces and secondary ownership.

^bIncludes aggressively chasing carcass owner and/or trying to pull carcass away; excludes persistent begging and pestering.

^cAll or part of a carcass is taken from the previous owner, which responds aggressively or flees as a result of aggression received. At Lomas, squirrel thefts include 1 observed theft of a carcass, 1 strongly suspected theft, and 1 squirrel torn in half during a fight over it. At Santa Rosa, there was 1 strongly suspected theft of all or part of a nestling squirrel, 2 strongly suspected cases of whole coati pup theft, and 1 case in which a piece of meat was stolen.

involves infants obtaining scraps from adults or juveniles or juveniles sharing with one another (Rose, 1997). There were only two cases of adult males sharing with females and two cases of adult males sharing with juvenile males, and all involved very small amounts of meat. The pattern at Lomas Barbudal is similar: frequent sharing with infants and between juveniles, but only one case of an adult male sharing with a female and one case of an adult male sharing with a juvenile. The pattern of secondary adult squirrel ownership also appears to be similar at the two sites. Based on our small sample of complete eating sequences, Santa Rosa juveniles gained secondary access to 5 carcasses and females to one. At Lomas Barbudal, juveniles were secondary carcass owners ≥ 3 times and a female once. Overall, there is no good evidence that females gain greater access to squirrel meat through sharing or secondary carcass acquisition at Santa Rosa than at Lomas Barbudal.

Hypothesis 3: It is Easier for Females and Juveniles to Catch Squirrels at Lomas Barbudal

There is no obvious difference between Lomas Barbudal and Santa Rosa squirrels in terms of body size, agility, or other behaviors affecting difficulty of capture, though we lack the data to exclude these possibilities entirely. However, there were more hunts involving multiple squirrels at Lomas Barbudal than at Santa Rosa, and females and juveniles were very successful in these cases. There was only one multiple squirrel hunt at Santa Rosa, in which a female and a juvenile each caught large juvenile squirrels. At Lomas Barbudal, there were 3 multiple squirrel hunts, 2 involving 2 squirrels and one involving 3. The 3 hunts account for all of the 5 squirrels caught by females and one of the squirrels caught by a juvenile male. Only one squirrel was killed by an adult male during the 3 multiple hunts. All of the squirrels were large immatures or adults. It is possible that hunts involving multiple squirrels allow more opportunities for females and juveniles than hunts involving single squirrels, either because adult males are unable to monopolize more than one target or because multiple prey allow different hunting tactics to be practiced. It may also be that multiple squirrel hunts allow females and juveniles more chances to observe, to learn and to practice successful hunting techniques.

Squirrel Hunting and Coati Nest Raiding Techniques

At Santa Rosa, there is one hunting technique (active search) definitely not observed at Lomas Barbudal, and 4 techniques that have not been specifically noted (Table VI). The techniques of chasing on intersecting trajectories,

Table VI. Squirrel hunting and handling techniques at Santa Rosa and Lomas Barbudal

	LV ^a	CP ^a	Lomas ^a
Hunting techniques			
<i>Active Search</i>			
In areas of high squirrel abundance or sites of recent kills, ≥1 monkeys stalk purposefully and quietly through trees, very vigilant, not engaging in other foraging, apparently searching for squirrels	YES ^b	NO	NO
<i>Flush into open</i>			
≥1 monkeys flush squirrel from dense undergrowth or concealed position into the open.	YES	YES	YES
<i>Relay chase</i>			
If initial chasers fall behind or lose squirrel, others overtake or join in and continue the hunt.	YES	YES	YES
<i>Intersect and trap</i>			
≥2 monkeys run on parallel or intersecting trajectories, trapping the squirrel between them.	YES	YES	? No
<i>Block</i>			
≥2 monkeys run to block the route of a squirrel attempting to escape other monkeys chasing it	YES	YES	? No
<i>Surround</i>			
Trapping squirrel on large tree trunk or isolated tree and surrounding it.	YES	YES	? No
<i>Rearguard intercept</i>			
≥1 monkeys at the rear or periphery of a chase intercept a squirrel that has doubled back or swerved abruptly and escaped the leading hunters.	YES	NO	? No
Handling techniques			
<i>Grab and flail</i>			
Grab squirrel and vigorously shake it, or bang it against a nearby tree or branch.	YES ^a	NO	YES
<i>Neck bite</i>			
Kill squirrel by biting on the back of the neck.	NO	YES ^d	YES ^d
<i>Bite and drop</i>			
Captor is unable to kill squirrel immediately (e.g. hands needed to maintain position on branch), but bites it so that it falls to the ground; then initial captor or another completes the kill	YES ^d	NO	?No
<i>Launch and pin with body</i>			
Captor launches onto squirrel from above, pinning it against a tree and using body weight to crush it.	NO	YES ^e	NO

^aBased on quantitative and qualitative data from all observation periods

^bOnly alpha male, accompanied by 2–3 others, seen to engage in this behavior and only in 1995.

^cOccasionally seen in group CP only at Santa Rosa, one similar instance at Lomas.

^dIn CP only the alpha male, only one occasion (in conjunction with “Launch and pin”) versus habitually seen at Lomas

^eOnly the CP alpha male seen to do this on one occasion (in conjunction with neck bite)

blocking, and surrounding occurred during *ca.* 40% of group hunts at Santa Rosa. Typically, these techniques are used by adult males, and are very successful if the target squirrel can be kept from escaping into the undergrowth. The rearguard intercept behavior occurred only once and may not have been a deliberate strategy. The active search pattern of group LV in the dry season of 1995 is a marked departure from the monkeys' usual opportunistic style of hunting. It was almost certainly instigated by then alpha male, Butch, and has not been seen in other groups.

We found no unique capture techniques at Lomas Barbudal that might account for greater hunting success, but we noted a striking difference between Lomas Barbudal and Santa Rosa capuchins in terms of kill techniques. On the 6 occasions that kill techniques were observed at Lomas Barbudal, all individuals (females and juveniles as well as adult males) killed the squirrels by biting them on the neck or head before consuming them. By contrast, Santa Rosa capuchins begin eating smaller squirrels while they are alive, and attempt to kill or to subdue larger squirrels through a variety of rather inefficient techniques that include flailing or banging, biting and dropping, and landing on the squirrel from above. A variant of flailing was only observed once at Lomas Barbudal, and the case involved a juvenile male beating a squirrel that he had already killed by neck biting. At Santa Rosa, there was only one observed instance of a monkey killing a squirrel by biting its neck, and it was not clear that the placement of the bite was deliberate. The technique of consistently killing squirrels by biting their necks or heads may help to account for the greater hunting success (and also the greater propensity to hunt squirrels when encountered) at Lomas Barbudal versus Santa Rosa.

Coati Nest Raiding

Predation on nestling coatis (*Nasua narica*) is highly seasonal, the majority occurring during the first month of the coati birth season in April or early May. Coati predation rates are similar at Santa Rosa and Lomas Barbudal, and considerably lower at Palo Verde (Table III). The rate for Santa Rosa would undoubtedly have been higher if the coati females in the home ranges of all 3 groups had not moved to other areas during the birth season in 1995 (J. Saenz, pers. comm.), and if data were available for groups LV and CP in 1996. However, the Santa Rosa data include 2 groups (LV and CP) for 1991 and one group (NC) for 1996, and are therefore roughly equivalent to the 3 raiding seasons in 1991, 1992 and 1993 in the Lomas Barbudal data set for one capuchin group.

Coati nest raiding involving very young pups shows little or no variation in techniques between sites or groups (Table VII). When adult coatis were

Table VII. Coati nest raiding techniques at Santa Rosa and Lomas Barbudal

	LV ^a	CP ^a	Lomas ^a
<i>Active Search</i>			
• Carefully inspect potential sites for coati nests, without engaging in other foraging behavior.	YES	YES	YES
• Visually and/or manually investigate all coati nests encountered, whether occupied or not.	YES	YES	YES
<i>Try again</i>			
Return to a coati nest where a previous raid had been unsuccessful, or not all pups had been taken, and try to raid it again.	YES	YES	YES
<i>Take pups from undefended nests</i>			
Take pups from a nest where no female is present. This is the most commonly successful form of nest raiding, and no particular skill or strategy is required once the nest is found.	YES	YES	YES
<i>Surround defended nest and attempt to take pups</i>			
Many monkeys (typically females and juveniles as well as adult males) surround a nest that is occupied by an adult female coati. Any monkey may try to get under her guard and grab a pup or pups as opportunity allows. This is rarely successful as mother remains on nest.	YES	YES	YES
<i>Bait mother from nest and try to grab pups.</i>			
≥1 monkeys bait mother to edge of or off nest by repeated threats and lunges, then attempt to rush in and grab pups. Rarely successful as window of opportunity is small.	YES	YES	YES
<i>Division of effort: some bait while others grab pups.</i>			
As above, but while some (often juveniles and females) distract the female coati, others (usually one or more adult males) quietly enter nest from the other side and grab pups.	NO	YES	YES
<i>Grab additional pups while mother tries to rescue one or more already taken</i>			
≥1 monkeys have succeeded in getting ≥1 pups. The female coati leaves the nest in an attempted rescue, and other monkeys grab the remaining pups.	YES	YES	YES
<i>Cause female to move pups to another nest</i>			
After an attempted nest raid, female begins to move surviving pups to another nest; monkeys chase and try to take pups from her and/or take any pups remaining (undefended) in first nest.	NO	NO	YES
<i>Force pups from nest and take them on the ground</i>			
During nest raids, pups are (perhaps accidentally?) forced or dropped from the nest. ≥1 monkeys then move to the ground and take them.	NO	YES ^b	YES
<i>Exhaust by attempted drowning (larger pups)</i>			
Repeatedly harass pups in a river, fish them and drop them back in again, preventing them from reaching either shore, until pups are exhausted.	NO	NO	YES

^aBased on quantitative and qualitative data from all observation periods^bObserved twice in CP group but no pup captured.

not present, the capuchins at both sites simply raced in, grabbed the pups, and retired to nearby trees to eat them. In the case of guarded nests, the strategy of dividing forces between those baiting the adult female from the nest and those attempting to take pups (Rose, 1997, 2001) occurred at both sites. However, there was a remarkable strategy displayed at Lomas Barbudal in respect to older, i.e., independently locomoting, pups. During two separate nest raids (1993 and 2001), the monkeys forced or dropped several pups into the nearby river. They then harassed the pups by slapping them and pulling their tails as they were swimming toward the opposite bank of the river. Each time it appeared that a pup was about to reach the riverbank, a monkey would grab it by the tail, haul it out of the river, and then drop it back mid-stream. This appeared to be a deliberate strategy aimed at wearing the pups out (and almost drowning them) so that eventually they could be caught and eaten. It is noteworthy that at Santa Rosa, where the study groups had no dry-season river, the few attempts to capture independently locomoting coati pups were unsuccessful.

Although nestling coatis (and at Lomas Barbudal, older pups) are prey for the capuchins, adult coatis are much larger than the monkeys and have powerful jaws and claws. When adult coatis are guarding their nests or arrive during predation attempts (*ca.* 40% of cases), the monkeys do risk being injured. Capuchins are extremely agile and fast moving, and usually manage to evade the slashing and biting aimed toward them. However, occasionally they are scratched on the face or body. Most such injuries were superficial, but one juvenile male was quite deeply gashed across the shoulder and hand while attempting to reach into a guarded nest (M. Dohrn, pers. comm.). Nonetheless, even females carrying young infants participate in coati nest raids, and females and juveniles are often predominant in attempting to bait an adult coati from the nest.

INTERACTIONS WITH POTENTIAL PREDATORS

Predators on capuchins include boa constrictors (*Boa constrictor*, Chapman, 1986), domestic or feral dogs (Rosales family, pers. comm.), and humans (Hill *et al.*, 1985; Redford and Robinson, 1991). Predation attempts by caiman (*Caiman crocodilus*) have been seen by Perry (pers. obs.). Jaguars (*Panthera onca*) take howlers and miquis at other sites (Olmos, 1994; Peetz *et al.*, 1992), and tayras (*Eira barbara*) prey on smaller monkeys and possibly the larger cebids (Galef *et al.*, 1978). It is reasonable to infer that the following animals are also potential predators on at least young capuchins, given the consistently strong antipredator response to them: venomous snakes (particularly rattlesnakes, *Crotalus durissus*), pumas (*Felis*

concolor), ocelots (*F. pardalis*) and margays (*F. wiedii*), coyotes (*Canis latrans*), crocodiles (*Crocodylus acutus*) and some of the larger raptors such as greater black hawks (*Buteogallus uribitinga*). For capuchins, behavioral defenses against predators include vigilance, warning alarm calls, moving to less exposed areas, and conspicuously aggressive mobbing or chasing (Boinski, 1988; Chapman, 1986; Jack, 2001; Oppenheimer, 1982; Rose, 1994a, 1998; Rose and Fedigan, 1995).

At all 3 sites, researchers were easily able to distinguish raptor alarms from terrestrial predator alarms aurally, the latter being lower pitched, shorter barking vocalizations of greater intensity (Perry, 1995; Rose, 1998). There may be finer differentiation of alarm calls, but this will require detailed acoustic study. Capuchins at the 3 sites react differently to raptor and terrestrial alarm calls, respectively looking up, and sometimes diving down to a lower level in the canopy, versus looking down, or if on the ground, moving rapidly into the trees and scanning. Raptors usually evoke little further reaction unless they are perched near the group, though LV group at Santa Rosa routinely mobbed a large spectacled owl (*Pulsatrix perspicillata*) in their home range in 1997, and NC group often alarm-called at caracaras (*Caracara cheriway*). Mobbing is typically reserved for large and/or concealed snakes, especially boa constrictors or rattlesnakes, felids, tayras, coyotes, and crocodiles or caimans. In some cases, a predator probably poses little real threat, but they are included here because they evoked a strong alarm call or mobbing response.

Predator Encounters and Alarm Responses

The rate of observed predator encounters is similar at Santa Rosa and Lomas Barbudal, though somewhat differently distributed across types of predators (Table VIII). Capuchins at Santa Rosa encounter more felids, mostly jaguaroundis, tayras, crocodiles or caimans (the latter by NC only), while those at Lomas Barbudal encounter more canids, mostly domestic or feral dogs, and raptors. However, the striking difference is the low rate of predator encounters at Palo Verde; <50% that at Lomas Barbudal and Santa Rosa.

It is important to note that our respective records of predator encounters rely heavily on responses by the monkeys themselves. In the case of raptors and concealed or cryptic snakes in particular, observers would generally not be aware of their presence if the monkeys did not alarm call. In the absence of data regarding predator populations for the 3 sites, it is thus difficult to determine whether the monkeys at Palo Verde encounter fewer predators than those at Santa Rosa or Lomas Barbudal, or whether they

Table VIII. Encounters between white-faced capuchins and potential predators at 3 Costa Rican Sites

	Santa Rosa ^a		Lomas Barbudal ^b		Palo Verde ^c	
	Observed encounters	Rate per 100 hrs	Observed encounters	Rate per 100 hrs	Observed encounters	Rate per 100 hrs
Felids, tayras	20	0.94	6	0.16	1	0.08
Dogs, coyotes	10	0.47	33	0.89	5	0.42
Snakes	61	2.85	77	2.08	17	1.42
Raptors	26	1.22	78	2.11	8	0.67
Crocodiles/ caimans	17	0.80	8	0.22	1	0.08
Total predator encounters	134	6.27	202	5.46	32	2.67

^aBased on quantitative data for LV and CP 1995–1996, and NC 1996, total 2137 observation h.

^bBased on quantitative data for group AB 1991–1993, total 3730 observation h.

^cBased on quantitative data for ST 1995–96, WHT and LT 1995, Total 1200 observation h.

consider fewer animals to be dangerous predators. However, there is some qualitative evidence to suggest that capuchins at Palo Verde consider fewer snakes dangerous than capuchins at Santa Rosa or Lomas Barbudal. Palo Verde capuchins did not alarm call or mob boa constrictors <1 m in length or non-venomous snakes. By contrast, even small boas routinely evoked a response (albeit often brief or only by juveniles) at both Lomas Barbudal and Santa Rosa, and juveniles at Santa Rosa mobbed several vine snakes. Indigo snakes (*Drymarchon corais*) are present at all 3 sites. At Santa Rosa in 1991, LV encountered one of these large (>2 m) non-venomous snakes several times near a waterhole, and CP encountered one near a large fig tree. In each case, the snake evoked alarm calls, vigilance, and mobbings that involved all age/sex classes. At Lomas Barbudal, capuchins mobbed indigo snakes on 6 of 10 encounters, but only juveniles participated. At Palo Verde, the monkeys do not mob indigo snakes; in fact, an adult female capuchin drank from a waterhole while touching a large indigo snake that was also drinking. The monkeys of Water Hole Troop (in which this incident occurred) regularly visited the waterhole in the early morning during the dry season, and often spent a considerable time in the area. Other animals, including ≥ 2 large (*ca.* 2-m long) indigo snakes, were also regular visitors at the waterhole, and presumably the monkeys became accustomed to their presence. The waterhole had steep sides except for one small ramp-like area where the monkeys typically drank, a few at a time. Once an indigo snake was drinking there when the adult female capuchin went to drink, side by side with the snake.

Table IX is a comparison of species that evoke alarm and mobbing or harassment responses from capuchins at each site. The pattern is quite

Table IX. Mammals evoking alarm responses from white-faced capuchins

	Santa Rosa ^a	Lomas Barbudal ^a	Palo Verde ^a
<i>Carnivora</i>			
<i>Felidae</i>			
Jaguar (<i>Panthera onca</i>)	—	—	—
Puma (<i>Felis concolor</i>)	A, H	—	—
Ocelot (<i>Felis pardalis</i>)	A, H	UA, H	—
Margay (<i>Felis wiedii</i>)	—	UA, H	UA
Jaguaroundi (<i>Felis yaguaroundi</i>)	UA, H	UA	—
Feral house cat (<i>Felis domesticus</i>)	—	—	UA
<i>Canidae</i>			
Dog (<i>Canis familiaris</i>)	A	UA, H	—
Coyote (<i>Canis latrans</i>)	UA, H	UA, H	UA
<i>Mustelidae</i>			
Tayra (<i>Eira barbara</i>)	UA, H	SA, H	—
Skunk (<i>Conepatus semistriatus</i>)	—	UA, H	—
Otter (<i>Lutra longicaudus</i>)	—	UA, H	—
<i>Procyonidae</i>			
Kinkajou (<i>Potos flavus</i>)	H	RA, H	—
Coati (<i>Nasua narica</i>)	RA, H	RA (83% juvs), H	H
Raccoon (<i>Procyon lotor</i>)	SA, H	?	—
<i>Artiodactyla</i>			
Deer (<i>Odocoileus virginianus</i>)	RA	RA	H
Cow (<i>Bos indicus</i>)	—	SA, H	H
Peccary (<i>Tayassu tajacu</i>)	UA	SA, H	H
<i>Primates</i>			
Human (<i>Homo sapiens</i>)	SA, H	UA (campesinos) H (tourists)	RA, H
<i>Rodentia</i>			
Agouti (<i>Dasyprocta punctata</i>)	RA, JA	JA, H(4%)	— (or ignored)
Porcupine (<i>Coendou mexicanum</i>)	—	SA, H	—
<i>Edentata</i>			
Anteater (<i>Tamandua mexicana</i>)	H	JA, H	H
<i>Perissodactyla</i>			
Tapir (<i>Tapirus bairdii</i>)	UA, H	—	—

Note. UA = usually alarm (>75% of encounters); SA = sometimes alarm (25–75% of encounters); RA = rarely alarm (<25% of encounters); JA = only juveniles alarm; H = alarming sometimes accompanied by harassment; A = only one encounter observed but alarm occurred — = this animal never encountered by the monkeys or not present at the site.

^aBased on quantitative and qualitative data from all groups and observation periods

consistent with that suggested by their respective responses to snakes: Santa Rosa capuchins are the most likely to consider nonpredatory animals as potentially dangerous, Palo Verde are the least likely to do so: and, Lomas Barbudal capuchins are intermediate.

Despite the cross-site variation in predators encounter rates and apparently differing perceptions of dangerous predator, an important commonality is the manner in which capuchins confront large terrestrial predators. Capuchins, particularly adult males, consistently display immense bravado (Costa Ricans often refer to them as *monos bravos*), even toward animals

that are many times their size. When a felid, tayra or coyote is detected, adult males immediately race toward it, furiously alarm barking, and are often followed by the entire group. Generally the predator leaves, and may be followed or chased for up to half an hour. However, sometimes the predator stands its ground, or is blocked by the capuchins, and an aggressive confrontation results. On one occasion, a group of LV males had been chasing a large jaguarondi for about half a mile when it leaped onto a small tree stump in the middle of a narrow *quebrada* (dry stream bed). Five adult males and several large juvenile males surrounded the jaguarondi, threatening it and repeatedly lunging forward as if to attack. The jaguarondi snapped at the monkeys and slashed at them with its claws, but they persisted. One young male even attempted to grab its tail. After *ca.* 5 min, the jaguarondi broke through and fled, with the capuchins in pursuit. A similar confrontation occurred at Lomas Barbudal, when the monkeys surrounded a treed ocelot and lunged at it from a range of about 1.5 body lengths. They continued harassing it until almost sundown, perhaps an unwise behavior in view of the need to find sleeping trees nearby. The group spent a very disturbed night, and the males spent several hours the next morning clearly searching for the ocelot.

Other noteworthy confrontations with large terrestrial predators include surrounding and baiting a small puma in a thicket, chasing and pulling the tails of a pair of tayras, stalking a large coyote, and mobbing a 1.8 m long crocodile on the banks of an estuary. Confrontations with dangerous snakes are generally less dramatic, but on one occasion at Lomas Barbudal, a 2-m boa constrictor coiled around a juvenile male capuchin and began squeezing. The juvenile's mother rushed over and attacked the snake, grabbing its tail and repeatedly pulling and biting it. The group's alpha male joined the attack, repeatedly hitting and biting the boa's head. During their combined assault, a second juvenile reached among the snake's coils and yanked the victim out unharmed.

Capuchins often break off and drop branches toward large snakes. Boinski (1988) observed capuchins kill a venomous snake (*Bothrops*) with a branch, but at our sites, the branches dropped were too light or too poorly aimed or both to cause a snake injury. The branch-dropping behavior may be derived from branch shaking—shaking small branches that are attached to a tree or shrub in the direction of the target—a common component of capuchin threat displays in conspecific as well as allospecific contexts. Juvenile capuchins in NC have developed another variant of branch dropping in respect to the small caimans. They are common in an estuary by which the monkeys often forage, rest, cool off by dipping their hands or tails in the water, and even occasionally drink. Lacking large branches, the capuchins break off pieces of mangrove and drop them over a submerged caiman until

it surfaces. They then alarm bark, bounce and display vigorously until the caiman submerges again. Although this seems to be primarily a game for the young monkeys, it undoubtedly serves to reveal the location of a hidden predator.

INTERACTIONS WITH POTENTIAL COMPETITORS

White-faced capuchins at all three of our sites share the forest with *Alouatta palliata*, and those at Palo Verde and most groups at Santa Rosa overlap with *Ateles geoffroyi*. Howlers spend <30% of their day eating fruit; the bulk of their diet consists of leaves and flowers. The average dietary overlap between howlers and capuchins at Santa Rosa is only 5% (Chapman, 1987). However, because of strong seasonality and variability in fruit availability, the overlap reaches 30% in some months. Fruit of *Ficus*, a highly preferred food for both species, is probably the most frequently contested resource. The estimated density of howlers at Santa Rosa is 7.9 individuals per km² in 1992 and 8.7 per km² in 1999 (Fedigan *et al.*, 1998; Fedigan and Jack, 2001). The most recent censuses available for Lomas Barbudal and Palo Verde give howler densities of 8.5 per km² and 69 per km², respectively (Chapman *et al.*, 1989; Massey, 1987). However, Massey calculated the density for Palo Verde from a strip census along 7 trails (totaling 18.7 km), while the Lomas Barbudal and Santa Rosa densities are based on thorough park-wide censuses, so the data probably are not strictly comparable. Although the estimates for Lomas Barbudal and Santa Rosa are very similar, the density of howlers at Lomas Barbudal is considerably higher in the area used by the capuchins than that estimated for the park as a whole.

Spider monkeys are ripe fruit specialists, and average dietary overlap with capuchins is *ca.* 24%, reaching 43% in some months (Chapman, 1987). The density of spider monkeys in the region of the Santa Rosa study sites is 16.8 individuals per km² (Chapman, 1989; Chapman *et al.*, 1995), while the overall density of spider monkeys at Palo Verde is 0.6 individuals per km² (Massey, 1987). Again, the difference in census methods are noteworthy. No spider monkey is present at Lomas Barbudal. In general, capuchins are able to displace howlers from feeding trees even though howlers are twice their size, but a group of >3–4 spider monkeys will usually supplant a group of capuchins.

Coatis (*Nasua narica*) are another potential competitor for capuchins at the sites. No datum on dietary overlap is available, but capuchins and coatis are generalized omnivores, and there is undoubtedly some competition for foods such as figs and other soft fruits that require little or no processing (Saenz, unpublished data). In addition to the potential for feeding

competition, capuchins also feed on nestling coatis during the birth season, so we might expect tense relationships between them. We do not have recent data for coati abundance at any of our sites, but the home ranges of each of our study groups overlapped with those ≥ 1 coati group ($X \approx 15$ individuals) and contained ≥ 1 solitary male or pairs of males.

Interactions Between Capuchins and Howlers

Capuchins at Lomas Barbudal interact with howlers *ca.* 3 times more often than capuchins at Santa Rosa do (Table X). On average, interactions between capuchins and howlers occur once per 1.5 days at Lomas Barbudal, about every 4.5 days at Santa Rosa, and an estimated once a week at Palo Verde. Across groups at Santa Rosa, interaction rates range from 0.79 per 100 h for SK, which had only one encounter with howlers in *ca.* 3 weeks of observation time, to 4.17 per 100 h (*ca.* every 2 days) for NC.

At Santa Rosa, 54% of all interactions between capuchins and howlers were aggressive, and 5% involved mixed affiliation and aggression. Almost all of the aggression was directed by capuchins toward howlers. In 11% of cases, the capuchins watched the howlers; in 26% they ignored them or fed peacefully in the same tree. Only 5% of interactions were affiliative, involving play without aggression, though 5% involved both affiliation and aggression. At Lomas Barbudal, interactions between capuchins and howlers were much more likely to be aggressive (80% of cases) and there was only one case (0.5%) of affiliation. As at Santa Rosa, the majority (93%) of aggression was directed by capuchins toward howlers. Aggression was mutual in 5% of cases, and on 3 occasions, howlers were aggressive toward capuchins. We do not have quantitative data for Palo Verde, but interactions seemed equally divided between aggression and ignore, with occasional co-feeding and no affiliation.

At first glance, it seems likely that the higher proportion of aggression between capuchins and howlers at Lomas Barbudal reflects the higher rate of encounters and reflects greater feeding competition. At Santa Rosa, NC had by far the highest encounter rate, and the highest proportion of aggressive encounters. However, when all groups were included, we found no correlation between encounter rates and the proportion of encounters that were aggressive ($\tau = 0.07$, $p = 0.851$, $n = 6$ groups). Nor did we find significant correlations between encounter rates and proportions of aggressive interactions or other types of interaction when we broke the Santa Rosa data down by year as well as group, or excluded the Lomas Barbudal data (all values of $\tau < 0.45$, all p values > 0.26). Thus, the patterning of interactions between capuchins and howlers does not appear to be determined solely

Table X. Interactions between white-faced capuchins and howlers at Santa Rosa and Lomas Barbudal

Site	Observation hrs	Encounters	Encounters per 100 hrs	% Aggressive	% Affiliative	% Mixed aggres/afil	% Watch	% Ignore	% Co-feed ^a
Santa Rosa	3066	54	1.76	54	5	5	11	15	11
Lomas Barbudal	3703	205	5.54	80	0.5	0	0.5	16	3
Santa Rosa									
CP group (1995-99)	999	19	1.90	47	11	16	11	11	5
LV group (1995-99)	1533	17	1.11	53	6	0	24	12	6
NC group (1996)	408	17	4.17	65	0	0	0	6	29
CU group (1998)	126	1	0.79	100	0	0	0	0	0
BH group (1998-99)	436	11	2.52	45	0	0	9	45	0

^aCapuchins and howlers feed in the same tree without aggression.

by encounter rates. Also, much of the aggression initiated by capuchins toward howlers occurred outside of feeding trees, and did not seem to have an obvious cause beyond the fact that howlers were present. However, an examination of contexts of aggression and proximity to relevant resources may prove helpful in the future.

The most common aggression between capuchins and howlers at the 3 sites involves capuchins chasing or threatening howlers, or pushing, biting, hitting or lunging at them. Pulling or dragging infant or juvenile howlers by a foot or tail also occurs at the sites, in addition to occasional hair pulling. Physical contact aggression seems to be most severe at Lomas Barbudal, where capuchins sometimes inflicted quite severe wounds on howlers. At Santa Rosa, threats and chases are far more common than physical aggression, and physical aggression rarely leads to wounding. Play between juvenile capuchins and howlers seems more common at Santa Rosa than at Lomas Barbudal, though it is still relatively rare in LV and CP. The 3 affiliative interactions each involved juvenile play, and a further 3 interactions began as play but degenerated into aggression, in one case when an adult male howler intervened and aggressed against a juvenile capuchin. Juvenile capuchins of both sexes participated in play. The single case of affiliation observed at Lomas Barbudal involved play between an infant capuchin and an infant howler, and there was no case of interspecific play at Palo Verde. The sample size is too small to warrant conclusions at this stage, but the lower incidence of aggression and greater incidence of play between howlers and capuchins at Santa Rosa warrants further investigation.

Interactions Between Capuchins and Spider Monkeys

Table XI shows rates and patterns of interaction with spider monkeys for 4 study groups of capuchins at Santa Rosa. CP had no range overlap with spider monkey, and no spider monkey lives at Lomas Barbudal. There were very few encounters between capuchins and spider monkeys at Palo Verde (average *ca.* 1 per 2 mo), and they primarily involved aggression or co-feeding. Encounter rates for 3 of the 4 groups at Santa Rosa that overlap with spider monkeys are higher than howler encounter rates, but the proportion of aggressive encounters are somewhat lower (Table X, Table XI). By contrast, NC encountered spider monkeys and howlers at much the same rate (about every other day), but had a slightly higher proportion of aggressive encounters with spider monkeys (75% versus 65% aggression with howlers). Overall, our limited data show no obvious connection between encounter rates and aggression.

In contrast to capuchin-howler interactions, where aggression is overwhelmingly directed by capuchins toward howlers and often includes physical

Table XI. Interactions between white-faced capuchins and spider monkeys at Santa Rosa

Group	Observation hrs	Encounters	Encounters per 100 hrs	% Aggressive	% Affiliative	% Mixed aggress/afil	% Vigilance	% Ignore	% Co-feed ^a
LV 1995-1999	1533	48	3.13	44	17	13	10	10	6
NC 1996	408	16	3.92	75	6	0	0	0	19
CU 1998	126	5	3.97	20	0	0	0	80	20
BH 1998-99	436	22	5.05	27	14	18	5	27	5
Total	2503	91	3.64	44	13	11	7	16	9

^aCapuchins and spider monkeys feed in the same tree without aggression.

aggression (at least at Lomas Barbudal), aggression between capuchins and spider monkeys is often reciprocal, and is usually restricted to threats and chases. Most confrontations arise over heavily contested resources such as fig trees. A group of ≥ 5 spider monkeys can usually displace capuchins from a feeding site, which howlers almost never do. But capuchins do not give up easily, and a large capuchin group can displace a smaller group of spiders. On several occasions a fig tree was so large and laden with fruit that capuchins and spider monkeys both fed with minimal aggressive interactions, ignoring one another.

Another contrast with capuchin-howler encounters is that a significant proportion (24%) of capuchin-spider encounters are affiliative or involve a mix of affiliation and aggression. At Santa Rosa, 9 of the 22 affiliative or mixed affiliative/aggressive interactions involved capuchins grooming spider monkeys. The remainder consisted of juvenile play, and one case of an adult male resting in contact with a spider monkey. On one occasion, the alpha male of NC briefly groomed an adult female spider monkey and her infant. All of the other occasions involved ≥ 1 individual from LV or BH grooming spider monkeys, mainly juveniles temporarily traveling with the capuchin group, for periods ranging from 5 to >30 min. One case involved ≥ 4 individuals grooming an injured juvenile spider monkey. All 10 of the capuchins that groomed spider monkeys (3 adult females, 2 subadult females, 2 adult males and 3 juveniles) were, or had at some point been, members of LV. MacKinnon reports 4 members of LV (1 adult female, 2 large juvenile males and 1 small juvenile female) grooming spider monkeys in 1999. The reason for allospecific grooming, particularly the benefits for capuchins, are unknown. The reasons for the almost exclusive restriction of this behavior to past or present members of a single group at one site are also obscure, but it might be a socially transmitted behavior (Perry *et al.*, 2003).

Non-predatory Interactions Between Capuchins and Coatis

Table XII is a comparison of patterns of interaction between capuchins and coatis (*Nasua narica*) at Santa Rosa and Lomas Barbudal, excluding those associated with coati nest raiding. Quantitative data are not available for Palo Verde, but interactions there are almost exclusively aggressive on the part of the capuchins. Encounter rates and the pattern of encounters at Lomas Barbudal and Santa Rosa are similar. Capuchins at Lomas Barbudal are more likely to alarm call at coatis, but the calls are mostly given by juveniles (Table VIII). About two-thirds of non-predatory interactions with coatis at both Santa Rosa and Lomas Barbudal involve aggression. There

Table XII. Encounters^a between white-faced capuchins and coatis at Santa Rosa and Lomas Barbudal

Site	Observation hrs	Encounters	Encounters per 100 hrs	% Aggression	% Alarm	% Ignore
Santa Rosa	3502	40	1.14	68	10	23
Lomas Barbudal	3703	52	1.40	63	19	17
Santa Rosa						
CP group (1995–99)	999	13	1.30	69	15	15
LV group (1995–99)	1533	13	0.85	38	15	46
NC group (1996)	408	11	2.70	91	0	9
CU group (1998)	126	2	1.59	100	0	0
BH group (1998–99)	436	1	0.23	100	0	0

^aExcludes nest raids and other predation attempts by white-faced capuchins.

is no clear relationship between encounter rates and aggression, though for the 3 Santa Rosa groups that encounter coatis most often (NC, CP and LV), the proportion of aggressive encounters increases with encounter rate.

During aggressive encounters between capuchins and coatis at Lomas Barbudal, it is always capuchins that direct non-predatory aggression toward coatis, usually in feeding contexts. The pattern is similar at Santa Rosa and Palo Verde, but coatis there occasionally respond with mild aggression (lunges, attempts to chase) toward capuchins. Capuchins at Palo Verde and Lomas Barbudal direct more physical aggression toward coatis than those at Santa Rosa. They frequently hit and bite or attempt to bite coatis, and pull their tails. At Santa Rosa, aggression by capuchins toward coatis typically takes the form of threats or chasing, and contact aggression is rare.

INTERACTIONS WITH NEUTRAL SPECIES

One striking behavior that researchers often discuss is the manner in which capuchins harass many animals that are clearly no threat to them and are too large to be considered potential prey. In the majority of cases, the animals are directing no behavior toward the capuchins, but the monkeys seem to go out of their way to provoke them. For white-faced capuchins, howlers seem to be the most popular targets, but they also harass animals ranging in size from frogs to cows and horses. Forms of harassment include making threat faces, double threats—overlords—branch-shaking and bouncing at, chasing, poking, hitting, biting, leg or tail-pulling (a favorite for juveniles), hair-pulling, and for smaller victims, picking up, shaking and dropping, dragging by the leg or tail, and knocking over.

Harassment of Neutral Species

Table XIII is a list of neutral animals that white-faced capuchins harassed at ≥ 1 of our sites. There are few striking contrasts, in part because many of the species harassed at Santa Rosa or Lomas Barbudal or both were not encountered by the monkeys at Palo Verde. Lomas Barbudal and Palo Verde capuchins frequently harass peccaries (*Tayassu tajacu*), while Santa Rosa capuchins typically respond to them by alarm barking, and capuchins at Palo Verde are more likely to harass unfamiliar humans than capuchins at the other two sites. Our impression is that the monkeys are more likely to harass neutral animals that they do not often encounter than those they encounter regularly, but we lack sufficiently detailed data to verify this. In addition, responses to unfamiliar animals are not necessarily consistent across

Table XIII. Neutral species harassed by white-faced capuchins at 3 Costa Rican sites^a

	Santa Rosa ^a	Lomas Barbudal ^a	Palo Verde ^a
Mammals			
agouti (<i>Dasyprocta punctata</i>)	RH	RH	RH (ignore)
anteater (<i>Tamandua mexicana</i>)	UH	UH	UH
Armadillo (<i>Dasypus novemcinctus</i>)	H	alarm response	—
Bats (various)	RH	UH	H (attempt to eat)
Cows (<i>Bos indicus</i>)	—	UH	SH
Daschound (<i>Canis familiaris</i>)	—	H	—
Deer (<i>Odocoileus virginianus</i>)	RH	SH (dead deer)	RH
Horse (<i>Equus caballus</i>)	SH	SH	SH
Human - unfamiliar (<i>Homo sapiens</i>)	SH	SH	UH
Kinkajou (<i>Potos flavus</i>)	UH	UH	—
Opossum (<i>Didelphis marsupialis</i>)	UH	UH	—
Otter (<i>Lutra longicaudus</i>)	—	H	—
Peccaries (<i>Tayassu tajacu</i>)	alarm response	SH	SH
Pig (<i>Sus domesticus</i>)	—	SH	—
Porcupine (<i>Coendou mexicanum</i>)	—	UH	—
Raccoon (<i>Procyon lotor</i>)	SH	?	—
Skunks (<i>Conepatus semistriatus</i>)	—	H (cautiously)	—
Sloth (<i>Bradypus variegatus</i>)	UH	—	—
Tapir (<i>Tapirus bairdii</i>)	SH	—	—
Other			
Basilisk lizard (<i>Basiliscus basiliscus</i>)	RH	UH	—
Box turtle (<i>Rhinoclemmys annulata</i>)	UH	—	—
Frogs (various)	RH	UH	—
Ctenosaur - large (<i>Ctenosaura similis</i>)	RH	UH	—
Toad (<i>Bufo sp.</i>)	SH	SH	—

Note. UH = usually harass (>75% of encounters); SH = sometimes harass (25–75% of encounters); RA = rarely harass (<25% of encounters); H = only one encounter, but harassment occurred; — = this animal never encountered by the monkeys or not present at the site.

^aBased on quantitative and qualitative data from all groups and observation periods.

sites. For example, at Santa Rosa capuchins harassed an armadillo, while Lomas Barbudal capuchins gave an alarm response. The comparative severity of aggression at the 3 sites is difficult to assess, but interactions with neutral species tend to mirror those with potential competitors: capuchins at Lomas Barbudal and Palo Verde are more likely to engage in direct physical aggression than those at Santa Rosa.

Why do white-faced capuchins expend time and energy harassing allospecifics that are no threat to them? There seems to be no benefit (and at least some cost) to such behavior, and it thus seems inexplicable in evolutionary terms. However, we suggest 3 possible, inter-related explanations as a direction for future research: (1) practice and learning; (2) testing unfamiliar allospecifics and (3) a generalized trait of pugnacity that reflects underlying temperament.

Hypothesis 1: Practice and Learning

At all three sites, juvenile males are the age/sex class most likely to harass clearly harmless, familiar or relatively small allospecifics, and most likely to persist in prolonged harassment. This may be a form of play in which young monkeys practice the techniques they will use as adults, and in cases of real danger. Play serves several important functions, including development of motor skills and practicing adult behaviors (Dolhinow, 1999; Dolhinow and Bishop, 1970; Jolly, 1985; Smith, 1978). Rambunctious play is an important part of the behavioral repertoire for young capuchins (MacKinnon, 2002). At Santa Rosa, two categories of play, play-chase, and play-wrestle account for an average 12.4% of the time budget for juvenile males ($r = 9\text{--}21\%$, $n = 8$) and 6% for juvenile females ($r = 4\text{--}10\%$, $n = 4$; MacKinnon, 2002). In white-faced capuchins, adult males play the leading role in defense against both predators and competitors, including conspecific groups (Fedigan, 1993; Jack, 2001; Perry, 1996a; Rose, 1994a, 1998). Fragaszy (1990) suggested that male wedge-capped capuchins (*Cebus olivaceus*) have a less heightened perception of danger than females do. Based on sex differences in response to potential predators, this also appears to be true of *Cebus capucinus* (Rose, 1998). It is thus consistent that juvenile males would be most likely to engage in play/practice aggression involving a range of allospecifics, harmless or otherwise, to prepare for more serious encounters.

We might also extend this explanation to adults harassing harmless allospecifics such as kinkajous, cows, horses and primatologists. It may allow capuchins to practice and to refine tactics used in situations of true danger

or contest, especially the coordination of coalitionary aggression (Perry, in press). In addition, younger individuals have opportunities to learn through observation, an important component of social learning and transmission (Perry *et al.*, 2003). Finally, coalitions against harmless animals (and even inanimate objects) may serve additional social functions such as communicating information about relationships among participants, and distracting dominant monkeys in order to avoid displacement at feeding sites (Perry, 2003).

Hypothesis 2: Testing Unfamiliar Allospecifics

Bold curiosity is the typical capuchin response to any unique or rare situation. The harassment of unfamiliar allospecifics, or encounters with allospecifics in unusual situations, may be a means to test their responses and help to determine whether they are a threat to the monkeys.

Hypothesis 3: A Generalized Trait of Pugnacity that Reflects Underlying Temperament

Behaviors involving bold, aggressive confrontation are widespread among capuchins and pervasive across our study sites and groups in a range of different situations. This probably reflects an important aspect of white-faced capuchin temperament. Comparing congener *Cebus apella* with crab-eating macaques (*Macaca fascicularis*), Vitale *et al.* (1991:285) suggested that capuchins have “a greater readiness to react to, or act on, a novel/frightening feature of the environment in ways that might allow its exploitation.” Clarke and Boinski (1995) refer to *Cebus apella* as bold and instrumental, related to their omnivorous diet and active defense against predators. In *Cebus capucinus*, boldness and pugnacity are apparent in everyday foraging behavior; capuchins are constantly ripping off bark and breaking off branches in search of food, dealing with noxious, biting and stinging invertebrates and opening spiny, difficult to process fruits (Janson and Boinski, 1992; Rose, 1994b). Boldness and aggression are also consistent components of intragroup social relationships, intergroup encounters, and especially male competition (Fedigan, 1993; Fedigan *et al.*, 1996; Jack, 2001; Perry, 1996a, b, 1997, 1998; Rose, 1994a). Our study reveals the pervasiveness of this trait in dealing with potential predators, competitors, and in successful hunting. The traits of boldness, aggression and pugnacity that serve capuchins so well in other domains probably simply carry over into interactions with neutral species.

SUMMARY AND CONCLUSION

Our primary goal was to document the range of behaviors directed toward other species, especially in terms of variation among populations, across different contexts. There are several intriguing differences. In regard to squirrel hunting, Lomas Barbudal capuchins encounter squirrels less often than those at Santa Rosa, but are more likely to hunt and to kill them. Their greater success in squirrel hunting may be at least partly due to a technique not found at Santa Rosa: deliberate killing by biting the squirrel's head or neck. This may be an example of a socially learned or transmitted behavior or both (Perry *et al.*, 2003), and clearly indicates flexibility in white-faced capuchin hunting techniques. Females and juveniles are more successful hunters at Lomas Barbudal, we tentatively attributed this to hunting multiple squirrels simultaneously, which may reflect some aspect of local squirrel ecology. Increased hunting opportunities and the ability to learn by observation may be factors here.

In respect to predator responses, our main finding was a difference in the apparent perception of danger across sites. This may reflect ecological variation in terms of predator abundance or habitat use that determines encounter rates or past experience with predators, but flexibility in response and a possible role for social learning are indicated. Similarly, in terms of interactions with competitors, the greater tendency for capuchins at Lomas Barbudal and Palo Verde to respond with physical aggression may reflect underlying ecological conditions not apparent vis encounter rates, but cross-site differences also indicate malleability in response and a possible role for social learning. However, the most intriguing puzzle raised by our data is the frequency with which capuchins from one particular group spend time and energy grooming spider monkeys. Finally, a comparison of interactions with neutral allospecifics reinforces the impression of increased physical aggression at Lomas Barbudal and Palo Verde, but highlights the important similarity in capuchin behavior across sites and contexts.

A related goal was to consider various factors that may contribute to both variation and consistency in the responses of capuchins to allospecifics across sites and contexts. The variation among sites (and in a few cases, among groups) is an important indication of malleability in white-faced capuchin responses to allospecifics. In a highly intelligent, long-lived generalist species such as *Cebus capucinus*, we would expect to find such malleability, and at least the potential for social learning to play a role (Panger *et al.*, 2002; Perry *et al.*, 2003). However, ecological differences and social learning likely contribute to the variation in behavior, and we are unable to confirm or to determine their relative importance. We stress, however, the importance of consistent elements—boldness, aggression and pugnacity—that

were revealed across sites and across contexts. The best explanation for this would seem to lie in the temperament of *Cebus capucinus*, evolutionarily developed and constantly reinforced by a highly opportunistic foraging strategy, and situations such as strong predator defense and active hunting. Whatever underlying factors determine whether an individual adopts aggression as a strategy in a given situation (Karli, 1989), it is clear that in many contexts of capuchin life, boldness, aggression and pugnacity contribute to survival, and ultimately to increased reproductive success. This suggests continuity between the concept of primate temperament as an evolved trait and the well-established theory of an evolutionarily stable strategy (Taylor and Jonker, 1978).

Suggestions for Future Research

In respect to inter site variation in interspecific interactions, 3 key areas for future research stand out. One is the importance of accurate ecological data, particularly in regard to the abundance or availability of the target species. For example, having at least a proxy measure of squirrel abundance allowed us to determine that it is an important determinant of hunting rates, but encounter rate is a poor substitute for accurate squirrel census data. We also would benefit from data with respect to overall food availability, especially in regard to predator-prey and competitive interactions, and the feeding, ranging, and behavioral characteristics of other animals with which primates interact. These data would make it easier to determine whether group or populational differences in primate behavior are simply due to differences in local ecology. Finally, inter-site comparisons would be greatly facilitated if all encounters with other animals, including ones during which nothing occurs were routinely recorded.

Secondly future research should focus not only on variation in responses to allospecifics by the study species across as many populations as possible but also on acquisition of responses by young monkeys and the transmission of behaviors to others (Perry *et al.*, 2003). This would greatly aid us to separate ecologically based variation from social learning. Such work is an extremely challenging prospect that requires intensive, long-term study of well-known individuals. However, it is also an area wherein experimental studies conducted in captive situations (Cook and Mineka, 1990; Custance *et al.*, 1999; Frigaszy and Visalberghi, 1990; Visalberghi and Addessi, 2000) can help to identify indicators of social learning and protocols for establishing the social transmission of behavior. Field experiments could also be designed to test the responses of individual monkeys to model predators in varying social contexts.

Finally, we would encourage further research on species specific and individual temperament in primates, and their relationship with behavioral ecology and evolved, adaptive strategies that enhance reproductive success. In an (inter specific) review of animal personality studies, Gosling and John (1999) noted that research is widely dispersed among multiple disciplines, with no unifying framework or consistent methodology. Clarke and Boinski (1995) and Boinski (1999) also stressed the need for comparative, hypothesis-driven research on temperament, and noted the advantage of focusing on closely related species in order to reduce the confounding effects of phylogenetic distance and to better identify ecological or demographic variation.

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