

SQUIRREL MONKEY AERIAL ALARM CALLS AND PREDATOR AVERSION AS
PROXY MEASURES OF PERCEIVED RISK IN A HETEROGENEOUS SURINAME
FOREST

By

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To my parents, family and friends

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Multiple parameters contribute to risk perception by an animal. Similarly, an animal may respond to perceived risk through varying contextual dependant behavioral traits. Here we test the general hypothesis that perceived predation risk is context dependent using three continuous years of aerial alarm call data from wild squirrel monkey (*Saimiri sciureus*). A logistic regression analysis is used to model the likelihood of aerial alarm call and hide responses to potential predators as a function of ten ecological and social variables.

The analyses reveal that habitat and mixed species association with capuchins monkeys (*Cebus apella*) has significant affects on likelihood of aerial alarm call emission my squirrel monkeys. Season, troop dispersion and predator stimulus have significant effects on the likelihood of the monkeys to hide, an aversive anti-predator response. The particulars of the data set are site specific, but the general patterns and methodologies discussed can be broadly scaled to test predation risk perception in other taxa and milieu. The results reveal the utility of modeling predator-prey interactions using multivariate analyses.

CHAPTER 1 INTRODUCTION

Predation risk is a strong selective force that affects many aspects of animal behavior as well as having important repercussions on prey morphology and life history (Sih 1987; Lima & Dill 1990; Lima 1998; Stanford 2002). Predation is an intricate and multivariate event. Direct observation and description of predation events is further hindered because in the wild it is uncommon, especially in primates. Nevertheless, behavior of individuals in situations of perceived risk can be successfully modeled as a trade-off between the benefit of predator avoidance and risk associated with various activities (Abrams 1994; Janson & Goldsmith 1995; Cowlishaw 1997). To understand the behavioral impact of predation risk we can examine the anti-predator behavior that presumably evolved from predation events.

Alarm calls are commonly exploited as a proxy measure of perceived risk while also an indication of a strategy to protect self, kin and non-kin in association. Animals react to predator alarm calls in the same manner they react to a predator itself (Seyfarth & Cheney 1990; Seyfarth & Cheney 1997; Zuberbuhler et al. 1997). Therefore, reaction to alarm calls can provide insights into the decision making processes associated with predator-prey interactions. Other features of alarm calls offer access to test hypotheses on their ultimate function: 1) Alarm calls are an effective means to elicit anti-predator behavior from listeners (Boinski et al. 2000). 2) The acoustic structure of alarm calls can provide referential information on predator type, often distinguishing between terrestrial and aerial (Macedonia & Evans 1993). 3) Alarm calls can also function as a predator deterrent by alerting predators that rely on surprise that they have been discovered (Zuberbuhler et al. 1997; Zuberbuhler et al. 1999).

The underlying mechanism of alarm calls is that they are affect inducing vocalizations, the signaler uses the call to influence the listener affect and reactionary behavior (Bachorowski

& Owren 2003; Owren & Rendall 2001). The reaction to a given alarm call is a learned behavior that varies according to external context (Bachorowski & Owren 2003). The reactions are typical for various contexts and predators (Seyfarth & Cheney 2003; Zuberbuhler et al. 1996; Rendall et al. 1999). Consequently, we can understand and quantify the associated perceived risk based on those reactions.

It is important to study each predator-prey system at the local level. Specific anti-predator behaviors may have different functions at different locations due to different predators, life histories and ecological traits (Boinski et al. 2000; Boinski 2005). But patterns of anti-predator behavior observed in other taxa can create a framework for making predictions to test the general hypothesis that perceived predation risk varies as a function of context. This hypothesis is tested using 36 months of data on the biology of squirrel monkey (*Saimiri sciureus*) aerial alarm calls in Raleighvallen (RV), Suriname, using a logistic regression analysis. Logistic regressions are an underutilized multivariate method of modeling binary dependant variables. The regression model tested predictions of patterns of aerial alarm production by members of a squirrel monkey troop across various contexts. The squirrel monkey data set from RV is unique in its extrinsic ecological validity to test hypotheses on context specific perceived threat, allowing analysis of the environment to deconstruct what squirrel monkeys see as risky.

The objective is to identify the mechanisms that alter perceived risk for squirrel monkeys. This will allow us to identify tactics squirrel monkeys use to ameliorate predation risk. Based on experience and the available literature we can make several predictions concerning squirrel monkey reactivity to potential predator stimuli:

- 1) Perceived risk will vary as a function of habitat structure: habitat with higher vegetative density such as liana forest has less perceived risk because it can act as predator refuge.

2) Risk will increase during peak fruiting months: foraging on fruit reduces individual vigilance and increases exposure given fruit placement in more exposed portions of plants.

3) The absence of brown capuchin monkeys (*Cebus apella*) increases the squirrel monkeys' perceived risk: capuchins increase predator detection ability and deterrence of the group.

4) When squirrel monkeys are with capuchin monkeys their risk perception will vary as a function of troop overlap: the immediate spatial proximity to the capuchins reduces individual perception of risk.

5) Squirrel monkey troop dispersion will affect risk perception: less dispersed groups have more effective detection and deterrence for individuals.

In short, we are looking at and testing hypotheses on prey reactivity to perceived predation risk. How squirrel monkeys allocate time to these varied situations can reveal squirrel monkey's strategy to ameliorate perceived risk. Squirrel monkey anti-predator behavior can provide general patterns for better understanding how other vertebrate species adapt to predation risk. While other taxa are unlikely to perceive or respond to predation risk identically, the types of trade-offs and tactics found in other taxa can show general patterns that can be used to understand specific observed behaviors. Here we review the current primary literature pertaining to vertebrate anti-predator behavior.

Anti-Predator Behavior

Anti-predator behavior can be generally categorized as: detection and deterrence (Sih 1987; Boinski et al. 2000). Detection behavior consists of behaviors evolved to reduce predation risk through means that enhance predator detection (e.g., differential habitat use). Deterrence behavior decreases the likelihood of a predation attempt upon detection (e.g., large social group). Anti-predator behavior is a reflection of an animal's perceived risk. Individual animals assess their risk based on learned behavior and previous predator encounters associated with that

context. By examining the anti-predator behaviors associated with certain contexts we can better understand how animals perceive risk and their behavioral mechanisms for dealing with that risk.

Social Grouping

Animals living in social groups reduce predation risk through dilution, increase predator detection, increase predator deterrence and confusion (Williams 1966; Pulliman 1973; Roberts 1996; Boinski et al. 2000). Individuals in a group trade-off the cost of increased competition for the benefit of reducing predation risk. Individuals reduce intergroup competition by increasing their dispersal, but when predation pressure increases group dispersion tightens (Williams 1966; Janson 1990).

Some animals increase the anti-predation benefits of group living by forming mixed-species groups. Heterospecific grouping occurs in numerous species of bird, mammals and fish (reviewed in: (Morse 1977; Terborgh 1990; Stensland et al. 2003). There are two possibilities for the formation of mixed-species groups: groups that come together by chance (Waser 1982), and those that actively seek another species and the association persists regardless of the presence of any shared resource (Morse 1977). For the purposes here I will only discuss those associations that have a functional purpose and are not purely made by chance. Mixed-species associations are generally considered to be driven by predation pressure (Morse 1977; Terborgh 1990; Bshary & Noe 1997; Chapman & Chapman 2000; Stensland et al. 2003). Foraging benefits are also widely cited as an advantage to mixed-species groups. A larger group can flush more insects (e.g., bird citations in Morse 1977) and one species can act as ‘beaters’ by stirring up insects for the other (e.g., *Saguinus*, Peres 1992). Different species may have differing knowledge of the distribution of resources in the environment (Struhsaker 1981); by associating the species are able to increase their foraging success. This is especially true in primate groups

with differing home-ranges and when fruits are patchy and seasonal one species may 'guide' another to the food (Podolsky 1990).

Gautier-Hion et al. (1983) and Struhsaker (1981) assert that the benefits in predation avoidance and foraging are not mutually exclusive in mixed-species groups. Therefore it is difficult to determine the ultimate cause of mixed-species groups. Predator detection is enhanced in larger groups given that there are more vigilant individuals to detect a predator and communicate its presence to the group through a cue such as an alarm call (Terborgh 1990; Roberts 1996). This advantage is group size dependent, which is limited by resource and mating competition. Mixed-species grouping is a way to increase group size without severe intraspecific resource competition (Terborgh 1990).

Grouping has been documented to reduce predation. Roth, Lima et al. (2006) empirically documented that sharp-shinned hawks (*Accipiter striatus*) captured significantly more solitary than grouped prey. They also noted that several species of bird that formed mixed-species groups were avoided possibly due to the benefits of increased vigilance. Similarly, Harpy eagles (*Harpia harpyja*) have much more success hunting social arboreal species when the prey's vigilance is decreased by clouds and rain (Touchton et al. 2002). Beauchamp (2004) added to this by showing that birds reduced flocking, mono-and heterospecific, on islands with less predation pressure.

Often there is a differential ability between associated species to detect predators, which may in turn benefit one species more than the other (Stensland et al. 2003). In Tanzania, Grant's (*Gazella granti*) and Thompson's gazelles (*G. thomsoni*) form mixed species groups where one species gets more benefit from the association (Fitzgibbon 1990). Both species are able to reduce their predation risk while in association, but the Thompson's gazelles are able to take

advantage of the improved overall group vigilance since Grant's gazelles are taller and more vigilant (Fitzgibbon 1990). This differential detection ability is also evident in the resting behavior of some stingray species. Semeniuk and Dill (2006) found that cowtail stingrays (*Pastinachus sephen*) preferentially rest next to whiprays (*Himantura uarnak*) due to their enhanced ability to detect predators through their mechanoreceptors in their tails. In Kibale Forest, Uganda, Redtail monkeys (*Cercopithecus ascanius*) preferentially associate with the more vigilant red colobus monkeys (*Colobus badius*) (Struhsaker 1981; Cords 1990). Meanwhile, in Tai National Park, Ivory Coast red colobus, black-and-white colobus (*Colobus polykomos*), olive colobus (*Procolobus badius*), Campbells's monkey (*Cercopithecus campbelli*) and the lesser spot-nosed monkey (*C.petaurista*) all form mixed species groups with Diana monkeys (*C. diana*), the most vigilant species when in mixed groups (Bshary & Noe 1997).

Mixed-species groups may deter predators because predators may be less inclined to attack a larger group of animals (e.g., Fitzgibbon 1990). Some species associate with others that actively defend against predators and thus gain the protective deterrence by happenstance. For example, Bullock's orioles (*Icterus galbula bullockii*) preferentially nest in proximity to yellow-billed magpies (*Pica nuttalli*) over conspecifics (Richardson & Bolen 1999). The authors suggest this association is due to the predation protection that magpies provide by mobbing potential nest predators. A similar pattern can be seen in the aforementioned associations of olive colobus, Campbell's monkeys, lesser spot nosed monkeys and Diana monkeys with red and black-and-white colobus. Bshary and Noe (1997) report that the other species benefit from the red and black-and-white colobus' propensity to attack predatory eagles.

The formation of mixed-species groups statistically ‘dilutes’ the predation risk to an individual because of the increase in group size. The increase in group size also increases combined vigilance, which in turn can allow individuals more time to forage and conduct social behavior. The decreased perception of risk also allows species to expand their habitat use, taking advantage of different resources and areas that they may not normally use in a monospecific group. McGraw and Bshary (2002) argue that red colobus and Diana monkeys expand their habitat niche to include more terrestrial areas when associated with sooty mangabeys (*Cercocebus atys*) by acting as sentinels for ground predators. Similarly, Diana and Campbell’s monkeys expand their strata use when in association, focusing more on the riskier middle strata than when foraging in single species groups (Wolters & Zuberbuhler 2003).

Habitat Use

Most of the foraging trade-offs that animals must make under threat of predation are realized in their habitat use (Lima 1992; Isbell 1994; Lima 1998; Lima 1998; Boinski et al. 2000; Blumstein 2006). The threat of predation forces the avoidance of riskier habitats, often at the expense of optimal foraging. For example, baboons (*Papio cynocephalus ursinus*) make a trade-off by feeding in safer less optimal areas over the more dangerous areas with more available food (Cowlshaw 1997). Animals assess predation risk of an environment based on the ability to detect and escape a predator afforded by the environment (Lima & Dill 1990). Indian Ocean bottlenose dolphins (*Tursiops aduncus*) feed in safer suboptimal deep water and feed only at the edges of shallow optimal habitat to allow for easier escape when there is a high density of tiger sharks (*Galeocerdo cuvier*) in the shallows (Heithaus & Dill 2006). Animals avoiding predator detection may forage in areas with more overall protective cover, but Lima and Dill (1990) point out that cover may sometime impede predator detection. Lima and Dill (1990) argue that predation risk influences what, when and where to eat, which means that animal behavior is

closely tied to predator behavior as well as local ecology. Seasonal changes in food availability can force animals to forage in riskier locations, or adapt their diet to avoid certain areas (e.g. *S. sciureus*, Stone, 2007a; 2007b).

Escape

Escape occurs when the cost of staying put outweighs the cost of fleeing. The costs to escape can accrue as a function of energy expenditure and lost time for feeding and other behaviors (Ydenberg & Dill 1986). Escaping means different things in different contexts, for some animals it may mean taking refuge, while others may simply try to outpace the predator (Lima 1992). Escape strategies often vary as a function of differing habitat structure (e.g. Enstam & Isbell 2002). Sometimes escape is restricted or otherwise not useful, in these cases deterrent behavior is best suited. For example, red colobus monkeys in Gombe National Park, Tanzania aggressively attack predatory chimpanzees because their habitat does not allow an easy escape like their conspecifics in Tai National Park, Cote d'Ivoire (Stanford 1995; Bshary & Noe 1997).

CHAPTER 2 MATERIALS AND METHODS

Site Description

The data is from three continuous years of ad libitum and group scan data of squirrel monkeys (*Saimiri sciureus*), collected independently at a well established study site in Raleighvallen, Suriname. The site is part of the larger Central Suriname Nature Preserve, consisting of 1.6 million ha of primary tropical forest. We have classified the forest structure of our field site into four distinct habitats (Boinski et al. in prep):

1) liana forest: dense forest typified by numerous lianas and vines.

2) plateau forest: 'primary forest' with fewer lianas, taller trees, locations of most of the dietary fruit.

3) swamp forest: similar structure to plateau forest, but with different floristic content and seasonal standing water.

4) bamboo patches: continuous, dense, homogenous patches of bamboo (*Guadua latifolia*)

The fruiting season begins around February and lasts through April. May marks the onset of the wet season, lasting through June. The flower season follows in August and goes through October, overlapping with the breeding season.

The aerial predator suite is intact with the key predator species being Harpy eagle *Harpia harpyja*, and Crested eagle *Morphnus guianensis*.

The squirrel monkey troops were also often traveling in mixed-species groups with brown capuchin monkeys (*Cebus apella*).

Data Collection

The data used was collected from January 1998 through May 2001. The data is comprised of group-scan and aerial alarm call data taken from the observation of two habituated study

troops whose numbers average 25 and 28 individuals. Group-scan data was taken at 15 minute intervals, totaling 2981 h of observation documenting contextual intrinsic and extrinsic parameters. Group-scans were taken the entire time a monkey troop was followed. The scans documented the time, troop activity, location (which was later prescribed a habitat), troop dispersal (troop length and width), troop height range, observability index (number of individuals seen in a one minute scan), habitat cover (0-3 scale with 3 being fully covered and 0 being completely exposed), food eaten and presence of other animals within 50m. Aerial alarm call data was taken ad libitum as specific observations. Terrestrial and aerial alarm calls are acoustically distinctive vocalizations given in response to a perceived terrestrial or aerial predator. For this paper we focused only on aerial alarm calls. The aerial alarm call data was subsequently pooled into several categories.

Analysis

Aerial alarm calls were organized by their corresponding group scan data. For each alarm call the stimulus was coded: Harpy (interactions Harpy eagles), Big bird (stimuli was identified as a large bird, even if harmless), Harmless (stimulus identified as harmless to the squirrel monkeys) and Unknown. There were only 3 aerial alarm calls to Harpy eagles, those data were not used for the analysis. The species giving the alarm call was also noted, squirrel monkey or capuchin, and also whether or not there was a hide response. Capuchin presence was coded, as was if the troops were overlapped and if so their integration level (fully or partially integrated) was noted.

A stepwise logistic regression analysis of the categorized data was used to test the data. The regression was performed twice with two different dependent variables: 1) alarm call, 2) hide response. Both were modeled for the presence of dependent variable. Twelve independent variables were entered into the model, six ecological variables: predator stimulus, associated

habitat (liana, plateau, bamboo and swamp), season (wet, flower, fruit and transitional), habitat cover, and height (low and high). Six social variables were entered: capuchin presence, overlap and level of integration, troop speed (50x50m quad/15min), troop dispersion (m^2), and group movement (still or traveling).

The logistic regression analysis for this paper was generated using [SAS/STAT] software, Version [8] of the SAS System for Windows. Copyright [2001] SAS Institute Inc. SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc., Cary, NC, USA.

CHAPTER 3 RESULTS

Frequency of Squirrel Monkey Aerial Alarm Responses

A total of 1788 aerial alarm responses were given by squirrel monkeys during the 2981 h of observation, these included 1566 aerial alarm calls and 721 incidents of hiding as a response to a potential predator. Of the 1788 total responses all but 5 included an alarm call by either capuchins or squirrel monkeys.

Likelihood of Squirrel Monkey Alarm Call Response

Logistic regression results revealed the main factors affecting the likelihood of an aerial alarm call response (model Hosmer and Lemeshow goodness-of-fit $\chi^2 = .364, p = .985$) and hide response (model Hosmer and Lemeshow goodness-of-fit $\chi^2 = 7.404, p = .494$). The regression showed that habitat type and whether or not the squirrel monkey troop was overlapped with a capuchin troop are significant effects (Wald $\chi^2 = 9.816, 33.696$; $p = .020, <.0001$ respectively) in determining the likelihood of an aerial alarm call. Of the habitats, only plateau forest had a significant impact on likelihood of aerial alarm call response ($p = .002$). The probability of alarm calling in plateau habitat is almost double the probability of calling in the other three habitats (Table 3-1). Squirrel monkeys are much more likely to alarm call when not overlapped with capuchins (odds ratio = 2.872; Table 3-1).

The logistic regression for hide response yielded three significant effects: season, predator stimulus type, and troop spread (Wald $\chi^2 = 9.135, 94.346, 7.51$, $p = .028, <.0001, .006$ respectively). Only the flower season yielded a significant effect on hide response ($p = .0043$; Table 3-2). The odds ratio estimates indicate that the probability of squirrel monkeys hiding as a response to a potential predator is slightly less during the wet season than the other three seasons (Table 3-2). The type of predator stimulus has the strongest effect on the model with squirrel

monkeys being much more likely to hide in response to an unknown stimulus than a big bird ($m \pm SE = -.301 \pm .084$, odds ratio = .349; Table 3-2) and a harmless stimulus ($m \pm SE = -.450 \pm .122$, odds ratio = .301; Table 3-2). Troop spread has a slightly negative effect on hide response ($m \pm SE = -.0003 \pm .0001$; Table 3-2).

Model Variable Description

Squirrel monkeys were associated with capuchins 52.23% of the time observed. Of that, they were overlapped 72.32% of the time (Table 3-3). The squirrel monkeys alarm called to a potential predator 10% less frequently while overlapped with capuchins (Table 3-3).

Associations with capuchins varied by habitat with 67% of the time that squirrel monkeys were observed in both bamboo and swamp they were with capuchins (Table 3-4). While in plateau forest squirrel monkeys and capuchins were associated 56% of the time and in liana habitat only 47% of the time (Table 3-4). Alarm calls to a potential aerial predator were most frequent in plateau forest (90.3%), followed by liana (88.3%), bamboo (83.9%) and swamp (79.9%) (Table 3-4).

During the fruit season squirrel monkeys hid in response to 45.95% of the stimuli, the transitional season followed with 44.5%, then wet and flower with 39.8% and 32.8% respectively (Table 3-5). Squirrel monkeys hide much more frequently in response to an unknown potential predator (57.3%) than to a big bird or a harmless stimulus (Table 3-5).

Table 3-1. Maximum likelihood and odds ratio estimates of the model parameters testing the likelihood of an aerial alarm call response.

Parameter	Estimate	SE	Wald ChiSq	Pr > ChiSq
Habitat			9.8160	0.0202
Bamboo	-0.298	0.230	1.6830	0.1950
Plateau	0.570	0.183	9.6510	0.0020
Liana	-0.002	0.135	0.0003	0.9860
Swamp	-0.269	0.194	1.9300	0.1650
No capuchin overlap	0.527	0.091	33.6960	<.0001
	Odds ratio estimate	95% Wald CI		
Habitat effects				
Plateau vs Bamboo	2.38	1.19, 4.78		
Plateau vs Liana	1.77	1.12, 2.82		
Plateau vs Swamp	2.31	1.27, 4.24		
Capuchin overlap				
No vs Yes	2.87	2.01, 4.10		

Table 3-2. Maximum likelihood and odds ratio estimates of the model parameters testing the likelihood of a hide response.

Parameter	Estimate	SE	Wald ChiSq	Pr > ChiSq
Aerial alarm stimulus			94.346	<.0001
Big Bird	-0.3010	0.0840	12.758	0.0004
Harmless	-0.4500	0.1220	13.623	0.0002
Spread	-0.0003	0.0001	7.510	0.0061
Season			9.135	0.0280
Flower	-0.2830	0.0990	8.151	0.0043
Fruit	0.1160	0.0920	1.591	0.2072
Transition	0.1710	0.1040	2.691	0.1009
Wet	-0.0030	0.0930	0.001	0.9709
	Odds ratio estimate	95% Wald CI		
Seasonal effect				
Flower vs Wet	0.756	.557, 1.025		
Flower vs Transition	0.635	.455, .886		
Flower vs Fruit	0.671	.495, .909		
Stimulus effect				
Big Bird vs Unknown	0.349	.278, .439		
Harmless vs Unknown	0.301	.206, .439		

Table 3-3. Frequency of squirrel monkey association with capuchins during 15-minute scans and associated frequency of an alarm call response to a potential predator stimulus.

	Frequency (total number of observations)	Alarm call frequency (total number of observations)
Capuchins Present	52.23% (6383)	85.62% (1092)
Overlapped	72.32% (4616)	83.52% (807)
No overlap	27.68% (1749)	93.76% (977)

Table 3-4. Frequency of squirrel monkey habitat use with and without capuchin associations, and frequency of alarm call responses in different habitats.

Habitat	Frequency of Use (total observations)	Frequency of Use w/ Capuchin Association (total observations)	Alarm Call Frequency
Liana	59.12%(7225)	47.46%(3429)	88.28%(949)
Plateau	20.79%(2541)	56.16%(1427)	90.30%(363)
Swamp	8.35%(1020)	67.06%(684)	79.89%(139)
Bamboo	9.51%(1162)	67.47%(784)	83.94%(115)

Table 3-5. Frequency of hide as a response to a potential predator in during each season.
 Frequency of hide as a response to different predator stimuli.

	Frequency of Hide Response (total observations)
Season	
Flower	32.81%(147)
Fruit	45.95%(221)
Transition	44.48%(157)
Wet	39.76%(202)
Predator Stimulus	
Big Bird	29.51%(260)
Harmless	29.29%(58)
Unknown	57.34%(406)

CHAPTER 4 DISCUSSION

Mixed-Species Associations as an Anti-Predation Strategy

This analysis suggests that squirrel monkeys consider themselves less at risk from predation when associated with capuchins. Squirrel monkeys are almost 3 times more likely to give an aerial alarm call when not associated with a capuchin troop (Table 3-1). These findings add empirical data in support of Terborgh's (1983) observations concerning the anti-predator function of squirrel monkey (*S.boliviensis*) and capuchin (*C.apella*) mixed-species groups. Terborgh (1983) and Boinski and Mitchell (1992) note that squirrel monkeys actively associate with capuchins, but the inverse is not true. Terborgh also observes that squirrel monkeys are more reactive to aerial alarm calls from the more vigilant capuchins than their own.

Terborgh (1990) argues that the high costs of primate heterospecific associations are due to competition over patchy plant resources. There are fewer foraging costs in the Saimiri -Cebus association because capuchins can process a larger variety of fruits and plant materials while squirrel monkeys forage more on insects and smaller, softer plant parts (Mittermeier & van Roosmalen 1981). There are also fewer foraging disadvantages for the larger capuchins because they actively displace squirrel monkeys for access to food, but this is mediated by the fact that the capuchins drop a large quantity of partially processed foods while foraging thus giving squirrel monkeys access to foods they may not be capable of processing. The fact that squirrel monkeys tolerate the limited access to foods while in association indicates that the anti-predator benefits of association are high enough to maintain this association. The frequency of association may be regulated by overall food availability despite the high predation risk (Podolsky 1990; Chapman & Chapman 2000), but that is a reflection of the high costs of

heterospecific association. Despite the costs squirrel monkeys clearly feel less at risk while associated with capuchins.

Squirrel monkey- capuchin associations have anti-predator benefits similar to several other species of animals. By associating with capuchins they are effectively doubling the number of individuals looking out for predators which in turn allows an individual to be less vigilant (Roberts 1996). The increase in group size also statistically reduces its risk through dilution in a larger group. Squirrel monkeys may also benefit from the predator deterrence of capuchins' aggressive mobbing behavior. *C. apella* troops routinely mob potential predators by virtually swarming the predator, giving threat and alarm vocalizations while often dropping sticks and branches. This mobbing behavior is especially effective in deterring the attacks of ambush predators such as harpy eagles (personal observation).

Habitat Use

Habitat has a less significant effect on perceived risk than the overlap with capuchins. The analysis shows that squirrel monkeys are significantly more likely to give aerial alarm calls in plateau forest habitat versus swamp, bamboo and liana habitats (Table 3-1). The most important difference in perceived risk is between the two most prevalent habitats in the research site liana and plateau forest. The overwhelming preference for liana habitat by squirrel monkeys (60% of observed time) appears to be driven (at least partially) by the habitat acting as a refuge from predators. This supports the argument put forth by Boinski et al. (2003) that preemptive vigilance is reduced in liana habitat due to its closed and dense understory. The authors show that raptor predators require open areas in the forest for successful attacks, liana forests are often too dense for the large raptors to fly into without risking serious injury. Plateau forest habitats have fewer lianas and a more open understory (Mittermeier & van Roosmalen 1981), giving aerial predators ample space to maneuver (Boinski et al. 2003). The open understory of plateau

forests can give a raptor waiting in the over-story a clear path to squirrel monkeys foraging at the edge of liana habitat. The disparity in aerial cover and escape refuge (Lima 1992) give squirrel monkeys a higher perception of predation risk while in plateau forests. Mixed-species association patterns support this notion as well with squirrel monkeys forming mixed-species groups with capuchins 10% more frequently in plateau forest than in liana (Table 3-4). More frequent association with capuchins in plateau forest may also reflect a strategy to offset the higher predation threat taken on when foraging for fruit not available in liana forest.

Predator Stimulus

One of the more interesting results of this analysis concerns the different probabilities of hiding in response to different stimuli. The odds ratio estimates reveal that the squirrel monkeys in RV are almost 3 times more likely to hide when the alarm stimulus is unknown (Table 3-2). By classifying this stimulus as unknown, I am not assuming to be able to assess whether or not the monkeys indeed do know the identity of the potential predator. Given these assessments were made by fieldworkers who were in identical circumstances as the squirrel monkey troop, it is safe to say that for the majority of the observations if the human observer can not see the stimulus then most of the monkeys cannot either (Boinski personal communication). These data shed light on the issue of animal risk estimation. If the squirrel monkeys are unable to assess the overall risk to of the stimulus it appears that they are more likely to take the most extreme measures to avoid predation. The cost of hiding can be high. At a minimum it may include loss of foraging opportunity and energy expenditure, but it may also involve risking injury by dropping several meters. Animals react differently towards different predators (e.g. Zuberbuhler et al. 1997). These data suggest that animals are more likely to estimate the highest level of risk when predator specific risk is unable to be assessed.

Season

The only season with a significant effect on hiding behavior is the flowering season (August –October) (Table 3-2). The odds ratio estimates show a slight, yet significant, decrease in the probability of hiding as a response to a potential predator during the flowering season (Table 3-2). Squirrel monkeys in RV do not have considerable seasonal differences in habitat usage given the differing fruit availability (Boinski unpublished data). The flower season has the lowest levels of available fruit and the highest levels new foliage in RV (Boinski et al. in prep). During the flower season squirrel monkeys in RV are likely reducing their fruit intake, which mean foraging less on exposed branches. *S. sciureus* in northern Brazil have similar foraging trends, focusing more on insect foraging in the non-fruiting months (Stone 2007). The change in microhabitat use coupled with more cover from the new foliage in the flower season may give squirrel monkeys in RV enough protective cover that they are less likely to hide when encountering a potential aerial predator. Another possible explanation of these results could be due to behavior associated with the mating season, occurring in August and September (Boinski 1987). Squirrel monkeys may reduce hiding behavior due to the costly possibility of losing dominance positions and mating opportunities as a result of hiding. This would explain why squirrel monkeys are less likely to hide given their conspicuous breeding behavior likely increases their predation risk (Lima & Dill 1990). If this is the case then squirrel monkeys seem to make a trade-off between predation risk and breeding behavior.

Troop Dispersion

The maximum likelihood estimate for troop dispersion indicates that the likelihood of a hide response decreases very slightly as the troop becomes more dispersed (Table 3-2). This is consistent with the notion that group living animals are less dispersed when perceived predation risk is high (Boinski 1987; Boinski et al. 2000). Logically one could conclude that a greater

dispersion meant lower perception of imminent risk. But Janson (1990) argues that as individuals in a group distance themselves from each other their risk of predation increases. As the nearest neighbor distance increases an individual may perceive a high level of risk as a function of feeling disassociated from the group. Thus, individuals in a more dispersed group may be less likely to hide for fear the behavior may be too conspicuous when not done in a more cohesive group. This behavior is congruent with the cryptic predator avoidance behavior observed of social animals traveling alone (reviewed in Boinski et al. 2000).

Conclusions

The data appear to support the hypothesis that squirrel monkeys perceive risk based on their context. The importance of both social and ecological factors in risk perception is evident from the analysis. An interesting distinction appears between alarm call reactivity and hide response. While both are valid reflections of perceived risk, hiding is a better indicator of perceived individual risk. Hiding reflects an individual assessment that the risk of predation in that particular context is greater than the risk of injury or lost social and foraging opportunities. The probability of aerial alarm calling decreases in situations where the troop as a whole perceives less risk: denser habitats and overlapping with capuchin monkeys. Alarm calls are given as warnings for the good of the group. On the other hand, hiding behavior indicates an imperative of individual fitness. This indicates that perception of predation risk works on multiple scales, at the individual and the group. When discussing how animals behave under the risk of predation it is useful to take a multivariate approach to perception that also differentiates between the individual and the group.

LIST OF REFERENCES

- Abrams, P.** 1994. Should Prey Overestimate the Risk of Predation? *The American Naturalist*, **144**, 317-328.
- Bachorowski, J. & Owren, M.** 2003. Sounds of Emotion Production and Perception of Affect-Related Vocal Acoustics. *Annals of the New York Academy of Sciences*, **1000**, 244-265.
- Beauchamp, G.** 2004. Reduced flocking by birds on islands with relaxed predation. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 1039-1042.
- Blumstein, D.** 2006. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*, **71**, 389-399.
- Boinski, S.** 1987. Birth synchrony in squirrel monkeys (*Saimiri oerstedii*). *Behavioral Ecology and Sociobiology*, **21**, 393-400.
- Boinski, S.** 1987. Mating patterns in squirrel monkeys (*Saimiri oerstedii*). *Behavioral Ecology and Sociobiology*, **21**, 13-21.
- Boinski, S.** 2005. Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*): III Cognition. *Behaviour*, **142**, 679-699.
- Boinski, S. & Mitchell, C.** 1992. The ecological and social factors affecting adult female squirrel monkey vocal behavior. *Ethology*, **92**, 316-330.
- Boinski, S., Kauffman, L., Ehmke, E., Schet, S. & Vreedzaam, A.** 2003. Are Vigilance, Risk from Avian Predators and Group Size Consequences of Habitat Structure? A Comparison of Three Species of Squirrel Monkey (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*). *Behaviour* **140**, 1421-1467.
- Boinski, S., Treves, A., & Chapman, C.** 2000. A critical evaluation of the influence of predators on primates: effects on group travel. In: *On the move: How and why animals travel in groups* (Ed. by S. Boinski and P. Garber), pp. 43-72, Chicago, Illinois, University of Chicago Press.
- Bshary, R. & Noe, R.** 1997. Anti-predator behaviour of red colobus monkeys in the presence of chimpanzees. *Behavioral Ecology and Sociobiology*, **41**, 321-333.
- Bshary, R. & Noe, R.** 1997. Red colobus and Diana monkeys provide mutual protection against predators. *Animal Behaviour*, **54**, 1461-1474.
- Chapman, C. & Chapman, L.** 2000. Interdemic variation in mixed-species association patterns: common diurnal primates of Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, **47**, 129-139.

- Cords, M.** 1990. Mixed-species association of East African Guenons: General Patterns or Specific Examples? *American Journal of Primatology*, **21**, 101-114.
- Cowlishaw, G.** 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour*, **53**, 667-686.
- Enstam, K. & Isbell, L.** 2002. Comparison of responses to alarm calls by patas (*Erythrocebus patas*) and vervet (*Cercopithecus aethiops*) monkeys in relation to habitat structure. *American Journal of Physical Anthropology*, **119**, 3-11.
- Fitzgibbon, C.** 1990. Mixed-species grouping in Thompson's and Grant's gazelles: the antipredator benefits. *Animal Behaviour*, **39**, 1116-1126.
- Heithaus, M. & Dill, L.** 2006. Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos*, **114**: 257-264.
- Isbell, L.** 1994. Predation on Primates: Ecological Patterns and Evolutionary Consequences. *Evolutionary Anthropology*, **3**, 61-71.
- Janson, C.** 1990. Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, **40**, 922-934.
- Janson, C. & Goldsmith, M.** 1995. Predicting group size in primates: foraging costs and predation risks. *Behavioral Ecology*, **6**, 326-336.
- Lima, S.** 1992. Strong preferences for apparently dangerous habitats? A consequence of differential escape from predators. *Oikos*, **64**, 597-600.
- Lima, S.** 1998. Nonlethal effects in the ecology of predator-prey interactions. *BioScience*, **48**, 25-34.
- Lima, S.** 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* **27**, 215-290.
- Lima, S. & Dill, L.** (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619-640.
- Macedonia, J. & Evans, C.** 1993. Variation among mammalian alarm call systems and the problem of meaning in animal systems. *Ethology*, **93**, 177-197.
- McGraw, W. S. & Bshary, R.** 2002. Association of terrestrial mangabeys (*Cercrocebus atys*) with arboreal monkeys: experimental evidence for the effects of reduced ground predator pressure on habitat use. *International Journal of Primatology*, **23**, 311-325.

- Mittermeier, R. & van Roosmalen, M.** 1981. Preliminary observations on habitat utilization and diet in eight Suriname monkeys. *Folia Primatologica*, **36**, 1-39.
- Morse, D.** 1977. Feeding behavior and predator avoidance in heterospecific groups. *BioScience*, **27**, 332-339.
- Podolsky, R. D.** 1990. Effects of mixed-species associations on resource use by *Saimiri sciureus* and *Cebus apella*. *American Journal of Primatology*, **21**, 147-158.
- Pulliman, H. R.** 1973. On the advantages of flocking. *Journal of Theoretical Biology*, **38**, 419-422.
- Richardson, D. & Bolen, G.** 1999. A nesting association between semi-colonial Bullock's orioles and yellow-billed magpies: evidence for the predator protection hypothesis. *Behavioral Ecology and Sociobiology*, **46**: 373-380.
- Roberts, G.** 1996. Why individual vigilance declines as group size increases. *Animal Behaviour*, **51**, 1077-1086.
- Roth, T., Lima, S. & Vetter, W.** 2006. Determinants of predation risk in small wintering birds: the hawk's perspective. *Behavioral Ecology and Sociobiology*, **60**, 195-204.
- Semeniuk, C. & Dill, L.** 2006. Anti-predator benefits of mixed-species groups of cowtail stingrays (*Pastinachus sephen*) and whiprays (*Himantura uarnak*) at rest. *Ethology*, **112**, 33-43.
- Seyfarth, R. & Cheney, D.** 1990. The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behaviour*, **40**, 754-764.
- Seyfarth, R. & Cheney, D.** 1997. Behavioral mechanisms underlying vocal communication in nonhuman primates. *Animal Learning and Behavior*, **25**, 249-267.
- Sih, A.** 1987. Predators and prey lifestyles: An evolutionary and ecological overview In: *Predation: Direct and indirect impacts on aquatic communities* (Ed. by W. C. Kerfoot and A. Sih) pp. 203-224. Hanover, NH, University Press of New England.
- Stanford, C.** 1995. The influence of chimpanzee predation on group size and anti-predator behavior in red colobus. *Animal Behaviour*, **49**, 577-587.
- Stanford, C.** 2002. Avoiding predators: Expectations and evidence in primate antipredator behavior. *International Journal of Primatology*, **23**, 741-757.
- Stensland, E., Angerbjorn, A. & Berggren, P.** 2003. Mixed species groups in mammals. *Mammal Review*, **33**, 205-223.

- Stone, A.** 2007. Responses of squirrel monkeys to seasonal changes in food availability in an eastern Amazonian forest. *American Journal of Primatology*, **69**, 142-157.
- Struhsaker, T.** 1981. Polyspecific associations among tropical rain-forest primates. *Z. Tierpsychol*, **57**, 268-304.
- Terborgh, J.** 1990. Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. *American Journal of Primatology*, **21**, 87-100.
- Touchton, J., Hsu, Y.-C. & Palleroni, A.** 2002. Foraging ecology of reintroduced captive-bred subadult harpy eagles (*Harpia harpyja*) on Barro Colorado Island, Panama. *Ornitologia Neotropical*, **13**, 365-379.
- Waser, P. M.** 1982. Primate polyspecific associations, do they occur by chance? *Animal Behaviour*, **30**, 1-8.
- Williams, G. C.** 1966. *Adaptation and Natural Selection*. Princeton, NJ, Princeton University Press.
- Wolters, S. & Zuberbuhler, K.** 2003. Mixed-species associations of Diana and Campbell's monkeys: The costs and benefits of a forest phenomenon. *Behaviour*, **140**, 371-385.
- Ydenberg, R. C. & Dill, L.** 1986. The economics of fleeing from predators. *Advances in the Study of Behavior*, **16**, 229-249.
- Zuberbuhler, K., Jenny, D. & Bshary, R.** 1999. The predator deterrence function of primate alarm calls. *Ethology*, **105**, 447-490.
- Zuberbuhler, K., Noe, R. & Seyfarth, R.** 1997. Diana monkey long-distance calls: messages for conspecifics and predators. *Animal Behaviour*, **53**, 589-604.

BIOGRAPHICAL SKETCH

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