RESEARCH ARTICLE

Social and Personal Information Use by Squirrel Monkeys in Assessing Predation Risk

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The threat of predation can significantly influence prey behaviors through altered perceptions of risk. Prey risk perception is constantly updated via collection of personal and social information about predators. Better understanding of the links between information availability, its use, and prey species’ perception of risk will aid in explaining how animals adapt to predation. The goal of this study was to determine the environmental and social cues—available to prey via personal and social information, respectively—that influence wild squirrel monkey (Saimiri sciureus) reactivity to potential predators, treated here as a proxy for risk perception. We followed squirrel monkey troops for 3 years in Suriname, South America, and accounted for environmental and social variables associated with potential predator encounters. We utilized logistic regression models applied to a robust and long-term data set to reveal relationships among factors affecting squirrel monkey anti-predator responses. Our analyses revealed that height, season, type of predator stimulus, and mixed-species associations with capuchin monkeys (Sapajus apella) were highly related to intensity of squirrel monkey anti-predator responses. Moreover, our analyses revealed that squirrel monkeys overestimate the immediate threat of predation when individuals have incomplete information regarding the potential predator. Am. J. Primatol.

Key words: personal information; social information; risk perception; mixed-species association; Saimiri sciureus

INTRODUCTION

Most species of primates fall prey to diverse predator species [Hart, 2007] and the constant threat of predation ensures that anti-predator activities (e.g., avoidance, inspection, and alarm) are major components of primate behavior [Boesch, 1991; Boinski & Chapman, 1995; Gursky & Nekaris, 2007; Hill & Dunbar, 1998; Stanford, 2002]. In general, anti-predator behaviors define the “non-lethal” (or non-consumptive) responses of prey animals to perception of risk and underlie a high proportion of prey decisions. Behavioral changes by primates and other taxa in the face of predation risk perception influence various aspects of inter-species interactions [e.g., mixed-species group formation, Bshary & Noe, 1997; Semeniuk & Dill, 2006; Terborgh, 1983], habitat use [e.g., avoidance of dangerous habitat, Cowlishaw, 1997; Schmitz, 2006; Stone, 2007b], and social systems [e.g., social group composition and formation, Beauchamp, 2004; van Schaik & Hörstermann, 1994]. Anti-predator behaviors are highly observable in primates (and other socially complex vertebrates) and can provide unique insights into understanding how critical information about ambient predation risks influences perception and, in turn, key decision-making processes with important fitness consequences [Enstam & Isbell, 2004; Lönnstedt et al., 2012; Schmidt et al., 2010; Sieving et al., 2010; Stone, 2007a].

Primates gather information about incident risks from two main sources; they use both socially derived information (indirect information from watching the decisions of other individuals) and personally collected information (from direct sensory detection of cues...
from an external individual’s environment) in decision-making to avoid predators [Danchin et al., 2008; Emerson et al., 2011; Enstam & Isbell, 2004; King & Cowlishaw, 2007; Shultz et al., 2003; Wolters & Zuberbühler, 2003]. In heterogeneous landscapes, the relative abundance and quality of personal and social information available within animal communities is highly variable [Fletcher & Sieving, 2010; Seppänen et al., 2007] and determined by complex changes in conditions. It is also clear that variations in anti-predator behaviors are dependent on variations in information availability, and that prey perceptions of incident risks and their associated reactions wax and wane along a continuum from subtle and un-noticeable to disproportionately heightened [Thaker et al., 2011; Willems & Hill, 2009]

Personal information, or cues gleaned directly from the environment by an individual, is used to update and modify threat perception and response [Danchin et al., 2008]. For example, habitat structure strongly influences how prey respond to potential predator encounters [Blumstein, 2006; Lima & Dill, 1990]. Habitat complexity is important because it influences an animal’s ability to detect predators and escape efficiently [Lima, 1993]. For instance, vervet (Cercopithecus aethiops) and patas monkey (Erythrocebus patas) responses to alarm calls depend on tree height and vegetation density [Enstam & Isbell, 2002]. As habitat becomes more open animals are, both, more at risk from attack but better able to detect predators [Boinski et al., 2003]; depending on different species’ escape and vigilance functions they may perceive either more or less risk as habitat density shifts [Lima, 1993; Sieving et al., 2004]. An animal’s ability to assess risk also depends on its physical location within a habitat. Arboreal primates close to the ground have higher perceptions of risk from terrestrial predators as the distance at which they can detect a terrestrial predator is reduced [Jaffe & Isbell, 2009]. Foliage density varies with habitat, as does food availability, thus animals must change their feeding behaviors depending on risk. Seasonal changes in food availability can force animals to forage in less-suitable, riskier habitats, or else to adapt their diet to avoid such habitats with high levels of predator exposure [Cowlishaw, 1997; Stone, 2007a]. In sum, habitat structure seems to influence the completeness of personal information available on the location, threat, and identity of a predator. Thus, incomplete information on risk may increase an individual’s perception of risk [Jaffe & Isbell, 2009; Whittingham et al., 2004].

Social information related to predation, usually in the form of alarm calls, is commonly observed in a variety of taxa [Danchin et al., 2008] and is a major benefit of forming conspecific and heterospecific social groups [Caro, 2005; Dall et al., 2005]. Squirrel monkeys, Saimiri sciureus, commonly form mixed-species associations with capuchin monkeys, Sapajus apella, for foraging and anti-predator benefits [Podolsky, 1990; Terborgh, 1983]. Terborgh [1983] argues that squirrel monkeys get anti-predator benefit from capuchins’ increased vigilance. This means that squirrel monkeys use the social information concerning predation broadcast by capuchins, both through observing their behavior and hearing their alarm calls. Alarm calls take different forms depending on their functions; to warn kin and mates [Clarke et al., 2006; Sherman, 1985; Wilson & Evans, 2008], elicit mobbing [Wheeler, 2008], or deter predators [Zuberbühler et al., 1997]. Social information availability and use is (like personal information) highly dependent on factors influencing its quality and detectability. As social signals become more distant in time or space [Fletcher & Sieving, 2010], as when a monkey troop’s cohesion declines and troop spread increases, signal relevance and the subsequent response intensity may decline [King & Cowlishaw, 2007]. However, anti-predator alarm calls in primates represent a highly observable set of social cues of known information content and are therefore very useful for understanding the complexity of information use in animal decision-making [Enstam & Isbell, 2002; Zuberbühler, 2000].

The objective of this study was to examine how information gleaned by wild squirrel monkeys, S. sciureus, from social and environmental contexts influenced anti-predator behavior. In particular, we were interested in establishing inference regarding prey behavior in cases where information is incomplete. Previous studies have shown that habitat structure and food availability have an extremely strong effect on squirrel monkey risk perception and anti-predator behavior [Boinski et al., 2003; Stone, 2007a]. In this study, however, our goal was to investigate what information squirrel monkeys use during a potential predator encounter to get a better understanding of how squirrel monkeys perceive risk and then decide to act. We employed a descriptive observation study design to quantify the social and environmental conditions that influence the probability of squirrel monkeys displaying anti-predator behavior associated with high-perceived risk (escape behavior) during a potential predation event.

Our major predictions were as follows: (1) The presence of capuchins and their anti-predator behaviors would increase the probability of squirrel monkeys exhibiting escape behavior, given the hypothesized anti-predator benefit of mixed-species association. (2) We predicted that squirrel monkeys would have increased probability of escape behavior in situations where monkeys had incomplete personal information on predation risk (i.e., habitat with thicker vegetation, at heights that put monkeys in close proximity to potential predators, and when predator identity was unknown). (3) When squirrel monkey troops were less cohesive (more spread out), we predicted that squirrel monkeys would be less
reactive because the social information being transmitted would be less reliable than the personal information about the immediate environment. Given that habitat and season may have influenced the height and spacing of the troops, we also tested for significant interactions between environmental variables.

METHODS

Site Description

All data are from three continuous years (1998–2001) of squirrel monkey observation collected at a study site in Raleighvallen, Suriname (4° 43' N, 56° 12' W). 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 [for detailed descriptions see Mittermeier & van Roosmalen, 1981]. (1) Liana/low forest: dense forest typified by numerous lianas and vines. The study site is comprised of approximately 40% liana forest. (2) High forest: “primary forest” with fewer lianas, taller trees, encompassing locations of most of the primate dietary fruit. High forest covers approximately 40% of the study site. (3) Swamp forest: similar structure to high forest, but with seasonal standing water and plants adapted for seasonal flooding (e.g., *Euterpe* sp.). Swamp forest covers approximately 10% of the study site. (4) Bamboo patches: continuous, dense, homogenous patches of bamboo (*Guadua latifolia*). Bamboo patches cover approximately 10% of the study site. The fruiting season in Raleighvallen begins in January and lasts through April. May marks the onset of the wet season, which continues through August. The dry season follows in September and continues through December.

The terrestrial predator community is intact at our research site, with the key predator species being boa constrictors (*Boa constrictor*), rainbow boas (*Epicrates cenchria*), bushmasters (*Lachesis muta*), pumas (*Puma concolor*), ocelots (*Leopardus pardalis*), jaguars (*Panthera onca*), and margays (*Leopardus wiedii*). Harpy eagles (*Harpia harpyja*) and Crested eagles (*Morphnis guianensis*) are two major aerial predators and are frequently observed in the study area and have been observed predating on adult squirrel monkeys.

Study Species

The South American common squirrel monkey, *S. sciureus*, lives in multi-male multi-female hierarchical groups ranging in size from 15 to 50 individuals with home ranges of 110–300 ha [Boinski et al., 2002, 2005; Stone, 2007b]. At our research site squirrel monkeys spent the majority of their time in liana/low rainforest (60% of observation time), followed by high forest (21%), bamboo (10%), and swamp (9%) [unpublished data]. The squirrel monkey diet consists mostly of insects (72%) supplemented by fruit and leaves [Boinski et al., 2002; Mittermeier & van Roosmalen, 1981]. Squirrel monkeys actively associate with brown capuchin monkeys (*S. apella*), spending an average of 52% of their time in a mixed-species group at our site [unpublished data]. Squirrel monkeys give birth synchronously usually around January–March (coinciding with the period of highest available fruit) and wean their young at 3–4 months of age [Boinski et al., 2005].

Our field observations are consistent with Newman’s [1985] categorization of squirrel monkey alarm calls as “peeps,” which are only given in response to a potential aerial predator, and “yaps” which are more variable than peeps but are considered a terrestrial predator alarm call and are often used to elicit mobbing. Squirrel and capuchin monkey [Wheeler, 2010] terrestrial and aerial alarm calls are acoustically distinctive vocalizations given in response to a perceived terrestrial or aerial predator and are distinguishable in the field.

Study Design

Predator alarm response data were collected from January 1998 through May 2001 (~2,600 hr of contact time) from two habituated troops whose numbers averaged 25 and 28 individuals. One group was followed more frequently; approximately 77% of the data used here was from the one group. Researchers (in teams ranging from 2 to 5 individuals) searched for squirrel monkeys daily over the course of the entire study, and groups were followed until researchers lost the group or the group settled for the night. Terrestrial and aerial alarm responses were documented *ad libitum*.

We concerned ourselves with the first two of the four possible potential predator-detection scenarios. These cases included (1) true positives, when monkeys detected an actual predator and reacted, and (2) false positives, when they reacted without any obvious predator stimulus or to non-threatening stimuli (e.g., a falling branch). (3) True negative responses (when monkeys were calm and there were no threats) are not informative as this condition is essentially the baseline. Finally (4) false negatives (when there is a real threat that goes undetected) were beyond our capabilities to quantify, as predators are cryptic. We recorded and classified all monkey alarm responses and all stimuli co-occurring with those responses that we could detect, such as observed predator species or alarm calls by capuchins and squirrel monkeys. Observers documented each event as the sum of the reactions of all visible individuals within a 30 sec span following the first detection of a potential predator by a monkey, directly (visually) or indirectly (social cue; see below).
The number of visible monkeys ranged from 0 to 17, with an average of 2.7 (2.3 SD) individuals visible at a given moment [data from instantaneous scans; Boinski et al., 2003]. We documented whether or not monkeys exhibited an escape behavior to any potential predator stimulus. In all cases, we tried to determine the stimulus that initiated the alarm response. If we could not detect and identify the predator or stimulus we classified the stimulus as unknown. Occasionally, observers detected the predator stimulus before or simultaneously with the primate response. For each alarm response the following variables were recorded: time, location, habitat, the height of the lowest and highest individual, predator response stimulus, group spread (troop length (m) × width (m)) and presence (<50 m away) and reaction of capuchin monkeys (S. apella) to the predator response stimulus.

For every alarm response we categorized the reaction as including an escape response or not for this study because the behavior is associated with predation situations with the highest perceived personal risk [Coss & Ramakrishnan, 2000; pers. obs.]. We classified a response as an escape response when one or more individual was observed behaving in the following way. Escape responses of squirrel monkeys included any rapid changes of location following predator detection or alarm call. The typical escape response to terrestrial predator stimuli consisted of individuals climbing and/or jumping at least one meter higher from the ground than their original position. Individuals generally responded to aerial predator stimuli by running toward denser habitat cover and/or dropping down to a lower height.

We note that in defining alarm events, there were cases where we did not identify any stimulus ourselves but relied on the type of monkey alarm response to code the stimulus type in the data set. For example, in some cases only one responding monkey and an observer could see a predator stimulus. If three other monkeys responded during this event, but only to the alarm call of the first responding monkey (i.e., they could not have seen the predator) we would then record one event of a true positive. The classes “unknown ground; unknown aerial” were used for all cases when observers did not detect stimuli themselves, but the monkeys (squirrel or capuchin) indicated through their alarm call type what class of stimulus they had detected (aerial or ground predator).

To minimize the influence of potentially dominant individuals, observers made daily efforts to space themselves throughout the entire troop in order to get observations of as many different individuals as we could. We are confident that this approach was effective because on several occasions in each year of the study observers applied temporary black dye markings to track individuals [see Boinski et al., 2002]. From this the goal was that multiple different individuals’ behaviors were sampled daily, and not the same few individuals day to day. This approach did not provide unique identifications to the degree that would allow us to include individual ID as a factor in analysis. We do acknowledge that despite our efforts we cannot guarantee that all individuals’ responses are, to a sufficient degree, consistently represented in the data set.

Data Analysis

Terrestrial and aerial alarm responses were modeled separately using a logistic regression [JMP Pro, version 10, SAS Institute Inc., Cary, NC, 1989–2012] with two social variables (capuchin response, and group spread) and three environmental variables (habitat, season, predator stimulus), and the height of the lowest (terrestrial) or highest (aerial) individual entered into each model (Table I). For each terrestrial alarm response the stimulus was coded as one of the following categories: dangerous (e.g., any of the cats or large snakes), person (occasionally monkeys react to a person), harmless (stimulus identified as an animal that is harmless to the squirrel monkeys), and unknown. The stimulus for each aerial alarm response was coded as: large bird (stimulus was identified as a large bird, including large birds that were harmless, such as vultures), harmless (stimulus identified as harmless to the squirrel monkeys, e.g., falling leaf or tiny bird)

<table>
<thead>
<tr>
<th>Variables</th>
<th>Values</th>
<th>Information type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Capuchin response</td>
<td>Alarm call and escape; alarm call only; escape only; no response; capuchins not present</td>
<td>Social</td>
</tr>
<tr>
<td>Troop spread</td>
<td>Total area (m²) occupied by troop</td>
<td>Social</td>
</tr>
<tr>
<td>Predator stimulus</td>
<td>Aerial: large bird, harmless, unknown; terrestrial: harmless, unknown, human, dangerous</td>
<td>Personal</td>
</tr>
<tr>
<td>Season</td>
<td>Dry; fruit/birthing; wet</td>
<td>Personal</td>
</tr>
<tr>
<td>Habitat</td>
<td>Bamboo, high forest; liana forest; swamp forest</td>
<td>Personal</td>
</tr>
<tr>
<td>Height</td>
<td>Lowest or highest troop member distance (m) from ground</td>
<td>Personal</td>
</tr>
</tbody>
</table>

TABLE I. Independent Variables Entered Into the Logistic Regression Model and the Type of Information They Provide to the Receiver

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and unknown. Using Akaike Information Criterion (AIC) model comparison, we selected the model with the combination of parameters that best predicted the odds of squirrel monkeys exhibiting an escape response to a potential aerial and terrestrial predator. We also included potentially important interactions between dependent variables to test if they improved the fit of the models. We tested interactions between season and troop height, season and habitat, troop spread and season, troop spread and height, and troop spread and habitat. Additionally, the different habitats varied in canopy height and vegetation density, both of which could affect the heights at which squirrel monkeys travelled and the inter-individual spacing. To test this potential effect we entered a three-way interaction between height, troop spread, and habitat as a variable in our models. We also tested the effect of group ID to see if there was a difference in reactivity between the two groups.

Our research methods complied with protocols approved by the University of Florida Institutional Animal Use and Care Committee, adhered to the laws of the Republic of Suriname, and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

RESULTS

A total of 1,790 squirrel monkey aerial alarm responses were observed. Squirrel monkeys were observed “escaping” in response to a predator stimulus in 727 of the 1,790 total incidents. The logistic regression model predicting the odds of squirrel monkeys giving an escape response to an aerial predator stimulus yielded several significant parameters (Table II): capuchin monkey response, predator stimulus identity, season, troop spread, troop height, the interaction between spread and season, and the interaction between troop spread, habitat, and troop height. The identity of the group did not have a significant influence on the odds of escaping a potential aerial predator \( (P = 0.63) \).

Squirrel monkeys gave 489 terrestrial predator alarm responses, 66 of those the squirrel monkeys exhibited escape behavior. The logistic regression model predicting the odds of squirrel monkeys giving an escape response to a terrestrial predator stimulus yielded two highly significant parameters (Table II): predator stimulus identity and troop height. Habitat had a nonsignificant effect on squirrel monkey behavior \( (P = 0.18) \), but removal of habitat as a model parameter worsened the fit of the model. Group identity did not have a significant effect on the odds of escaping \( (P = 0.41) \).

The response of capuchin monkeys to an aerial predator stimulus strongly influenced the reactivity of nearby squirrel monkeys to the aerial predator stimulus (Tables II and IIIa). When capuchin monkeys reacted more severely (escaping) squirrel monkeys were much more likely to react by escaping as well. Capuchins exhibiting escape behavior increased the probability of squirrel monkeys also escaping by 18–30% over when capuchins were absent (Table IIIa). Likewise, when capuchins did not escape during a predator event, squirrel monkeys were 17–38% less likely to escape than when capuchins were absent (Table IIIa).

Squirrel monkeys reacted less severely to aerial predators when the group was less cohesive, that is, spread out over a larger area. The effect of group spread varied significantly in a three-way interaction with habitat and troop height (Table II, Fig. 1). In high, swamp and liana forest, the general trend is that squirrel monkeys reduced reactivity as the troop height and spread increased. The exception was at 4 m in liana forests, where as a result of the interactive effects between the variables, there was a slight increase in the probability of an escape response as troop spread increased. The effect of group spread and troop height was strongest in the bamboo (Fig. 1d), where the increase in troop spread had dramatically different effects at heights greater than 4 m on the probability of squirrel monkeys giving an escape response. With very tight troop cohesion, monkeys closer to the ground were much more reactive to aerial alarm stimuli, but as the troop spread out reactivity dramatically drops at 4 m and increased for monkeys that were 15 and 27 m above the ground in the bamboo habitat (Fig. 1d).

The effect of season on squirrel monkey reaction to an aerial alarm stimulus was also dependent on troop spread (Fig. 2). During the fruiting/birthing and wet seasons, when squirrel monkeys were both eating more fruit and females are carrying dependent offspring, squirrel monkeys were less likely to give

### TABLE II. Parameters in the Best-Fit Models Obtained Via AIC Model Comparison, Predicting the Odds of an Escape Response to Aerial and Terrestrial Predator Stimuli

<table>
<thead>
<tr>
<th>Parameter</th>
<th>DF</th>
<th>Chi-square</th>
<th>Pr (&gt;Chi)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aerial predator</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capuchin response</td>
<td>4</td>
<td>93.70</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Predator stimulus</td>
<td>2</td>
<td>90.77</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Spread × habitat × height</td>
<td>3</td>
<td>13.21</td>
<td>0.004</td>
</tr>
<tr>
<td>Season × spread</td>
<td>2</td>
<td>7.25</td>
<td>0.027</td>
</tr>
<tr>
<td>Spread</td>
<td>1</td>
<td>4.69</td>
<td>0.030</td>
</tr>
<tr>
<td>Season</td>
<td>2</td>
<td>4.49</td>
<td>0.101</td>
</tr>
<tr>
<td>Highest height (m)</td>
<td>1</td>
<td>3.54</td>
<td>0.060</td>
</tr>
<tr>
<td>Habitat</td>
<td>3</td>
<td>0.73</td>
<td>0.867</td>
</tr>
<tr>
<td>Terrestrial</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lowest height (m)</td>
<td>1</td>
<td>26.77</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Predator stimulus</td>
<td>3</td>
<td>22.06</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Habitat</td>
<td>3</td>
<td>4.85</td>
<td>0.180</td>
</tr>
</tbody>
</table>
TABLE III. Logistic Model Parameter Estimates From the Best-Fit Model With (Last Column) Probabilities of Squirrel Monkeys Giving an Escape Response to, Either, an Aerial Predator Stimulus (Panel a) or Terrestrial Predator Stimulus (Panel b)

<table>
<thead>
<tr>
<th></th>
<th>Estimate ($\beta_i$)</th>
<th>Standard error</th>
<th>Chi-square</th>
<th>P-value</th>
<th>Pr[Escape]</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aerial Predator Stimulus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept ($a$)</td>
<td>0.54</td>
<td>0.22</td>
<td>0.35</td>
<td>&lt;0.001</td>
<td>—</td>
</tr>
<tr>
<td>Capuchin response</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alarm call and escape</td>
<td>1.98</td>
<td>0.39</td>
<td>46.03</td>
<td>&lt;0.001</td>
<td>0.93</td>
</tr>
<tr>
<td>Alarm call only</td>
<td>−1.63</td>
<td>0.23</td>
<td>68.07</td>
<td>&lt;0.001</td>
<td>0.25</td>
</tr>
<tr>
<td>Escape only</td>
<td>0.91</td>
<td>0.32</td>
<td>8.50</td>
<td>0.004</td>
<td>0.81</td>
</tr>
<tr>
<td>No response</td>
<td>−0.70</td>
<td>0.14</td>
<td>29.54</td>
<td>&lt;0.001</td>
<td>0.46</td>
</tr>
<tr>
<td>Not present</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.63</td>
</tr>
<tr>
<td><strong>Terrestrial Predator Stimulus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predator stimulus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Large bird</td>
<td>−0.31</td>
<td>0.09</td>
<td>16.14</td>
<td>&lt;0.001</td>
<td>0.56</td>
</tr>
<tr>
<td>Harmless</td>
<td>−0.45</td>
<td>0.12</td>
<td>12.45</td>
<td>&lt;0.001</td>
<td>0.52</td>
</tr>
<tr>
<td>Unknown</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.63</td>
</tr>
<tr>
<td><strong>Habitat</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bamboo</td>
<td>0.77</td>
<td>0.39</td>
<td>3.76</td>
<td>0.052</td>
<td>0.36</td>
</tr>
<tr>
<td>High forest</td>
<td>−0.50</td>
<td>0.37</td>
<td>1.99</td>
<td>0.158</td>
<td>0.14</td>
</tr>
<tr>
<td>Liana forest</td>
<td>0.08</td>
<td>0.26</td>
<td>0.09</td>
<td>0.76</td>
<td>0.22</td>
</tr>
<tr>
<td>Swamp</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.21</td>
</tr>
<tr>
<td>Lowest height</td>
<td>−0.31</td>
<td>0.07</td>
<td>26.77</td>
<td>&lt;0.001</td>
<td>—</td>
</tr>
</tbody>
</table>

P-values represent a test of the parameter estimate being different from the baseline category (which is 0). The probability of escape was calculated:

$$Pr[\text{Escape}] = \frac{\exp(a + \beta_i \times x)}{1 + \exp(a + \beta_i \times x)}.$$
social factors based on a comprehensive data set designed specifically for this purpose.

**Role of Predator Type and Social Information**

It is not surprising that aerial predators generated the highest perception of threat to self, causing squirrel monkeys to produce more severe aerial predator responses (both numerically and proportionally) than terrestrial anti-predator responses (Fig. 1). Aerial predators are widely considered to pose one of the greatest predation threats to bird [Lima, 1993] and primate communities [Hart, 2007] around the world. In examining the factors most closely associated with the highest-risk responses in our study (i.e., escape behavior), it is also obvious that squirrel monkeys were highly sensitive to social information in determining their own risk perception.

When capuchin monkeys exhibited escape behavior, squirrel monkeys were more likely to also give an escape response; a reaction denoting an elevated level of perceived risk [Coss & Ramakrishnan, 2000]. This is especially evident when capuchins both called and physically escaped (Table IIIa). Moreover, not only did squirrel monkeys react most severely to the most severe capuchin responses, but they were more reactive to capuchin anti-predator behavior than to their own, suggesting social information from capuchins was of higher value, and/or more reliable than that from conspecifics [Seppänen et al., 2007; Table IIa].

The implication here is that one benefit of associating with capuchins is the quality or reliability of information the capuchins provide about predation risk, a mechanism underlying interspecific bird associations [Hetrick & Sieving, 2012; Sridhar et al., 2012].

Animals use social over personal information when the social information is more reliable, or...
provides new information [Rieucau & Giraldeau, 2011; Schmidt et al., 2010]. The higher reactivity to capuchin behavior could mean that capuchins provided more reliable information than squirrel monkeys' own signals concerning risk, a pattern seen in interspecific associations in other taxa [e.g., Schmidt et al., 2008; Sieving et al., 2004]. Squirrel monkeys follow capuchins [not vice versa; Terborgh, 1983] and appear to benefit from association with a species with great vocal complexity that is capable of transmitting potentially higher quality information about threat assessment and predation risk [Contreras & Sieving, 2011; Fragaszy et al., 2004]. Alternatively, it is possible that the reactivity of squirrel monkeys in the presence of capuchins derives from higher uncertainty. That is they may have been overestimating risk because the capuchin reaction yielded incomplete information concerning the predation threat [van der Veen, 2002; and see below]. However, based on our findings we think it more likely that the predictable and strong association of squirrel with capuchin monkeys derived from the likelihood that capuchins were actually better informed and/or more precisely communicative about ambient risks than squirrel monkeys [King & Cowlishaw, 2007; Németh & Moore, 2007].

Group cohesion (spread) played a factor in squirrel monkey reactivity as well. Although its effect varied across habitat and season (Figs. 1 and 2), the general trend was that as the group spread out squirrel monkey reactivity to aerial predation-related stimuli decreased. This pattern is especially evident during the season when squirrel monkeys have dependent babies and are also foraging on more fruit. This may be because while squirrel monkeys have dependent young and ample food they are less likely to be in riskier microhabitats than during the dry season when lack of fruit may drive monkeys to forage more (reduced vigilance) and in riskier microhabitats [Stone, 2007a]. Primates have been shown to increase individual vigilance as group cohesion is reduced [Treves, 2000; Treves et al., 2001]. An increase in vigilance allows for more complete information concerning predation risk, thus squirrel monkeys would be less reactive to predator-related stimuli. The effect of vigilance and group cohesion changes as squirrel monkey's access to complete information on risk is obstructed by habitat (see below).

Role of Incomplete Personal Information

Squirrel monkeys had higher levels of perceived risk when the personal information about the threat of the predator was incomplete. This pattern was consistent across our analyses and appeared to be related to microhabitat, specifically, thicker vegetation occluding sightlines and thus increasing personal risk perception [Embar et al., 2011; Jaffe & Isbell, 2009; Whittingham & Evans, 2004; Whittingham et al., 2004]. In habitat with dense cover predators may be first detected at shorter distances [Boinski et al., 2003]; and close proximity to a dangerous predator can cause prey to react more severely than they would at a distance that ensured a higher probability of avoidance [Sieving et al., 2010]. Similarly, at low heights squirrel monkeys are limited in appropriate anti-predator responses. They are in closer proximity to potential ground predators and (in the case of potential aerial attack) have restricted visual field above [Lima,
1993]. At lower heights squirrel monkeys may also have had a more obstructed view of the canopy and thus aerial predators may be more difficult to detect. This can explain why squirrel monkeys were more reactive at lower heights in most habitats (lack of protection). It remains unclear to us exactly why, when squirrel monkeys were above dense bamboo thickets, they were more reactive except that sturdy branches for climbing and escaping may have been less available above bamboo thickets, accentuating their susceptibility in exposed positions. We must also acknowledge that we may have underestimated the occurrence of escape behavior since the observers own visibility of the monkeys was quite low. This issue may have been especially relevant for very dense habitats, when the monkeys were high in the canopy, and when the groups were very spread out. Thus, we acknowledge that these potential problems should be recognized when considering our conclusions.

Our conclusion that habitat cover increases squirrel monkey reactivity to predator-related stimuli, may appear contradictory to previous work showing that squirrel monkeys preferred thicker habitat for the safety it offers from predators [Boinski et al., 2003; Stone, 2007a]. However, our conclusions are not mutually exclusive because we looked specifically at predator-related events across habitats rather than patterns of preference. We found when squirrel monkeys lack complete information concerning the actual threat level due to habitat obstruction they will react more intensely. Similarly, baboons have been shown to prefer open habitat because it allows for the detection of ambush predators at greater distances [Cowlishaw, 1997].

Squirrel monkeys’ strong reactions to stimuli whose identity observers could not determine in the field highlight prey overestimation of risk when only incomplete information is available. If we assume that most monkeys in the troop under observation, with the exception of the first responder exhibiting an aerial or terrestrial anti-predator response, were also unable to identify the same threats, then our findings are consistent with the hypothesis that it is far less costly to overestimate predation risk than to underestimate it [Abrams, 1994; Stanford, 2002]. Prey species must be able to make an appropriate response to predators to reduce the probability of death [Lima, 1993; Lingle & Pellis, 2002; Mirza & Chivers, 2000]. The inability to assess the identity of a detected (potential) predator heightens the perceived level of threat to an individual and, in our study species, enhanced the probability of a more intense alarm response.

Critical to the anti-predator decision-making process, and the correct assessment of risk, is the completeness of information about the threat [Liley & Creel, 2008]. Social information can vary in completeness or quality if, for instance a signaler is inexperienced [McCowan et al., 2001] or conveying second-hand or outdated information [Fletcher & Sieving, 2010]. Similarly, personal information can be more or less complete depending on environmental conditions (see above). It is also increasingly clear that individual animals simultaneously weigh the relative importance (completeness/quality) of personal and social information that is available when deciding how to react to a situation [Barrera et al., 2011; Hetrick & Sieving, 2012; King & Cowlishaw, 2007]. In cases where the consequences of making the wrong decision are dire (as when lethal attack is potentially imminent), and when neither social nor personal information regarding the threat parameters is complete, it appears that prey may strategically default to perceive a high risk, and react accordingly [Barrera et al., 2011]. Given that severe anti-predators (escape, cessation of feeding) are energetically expensive and potentially predator-attracting (i.e., of high fitness importance), a complete understanding of the social and environmental conditions that lead to the most costly anti-predator behaviors is of interest in primate behavioral ecology and conservation.

**CONCLUSIONS**

An inferential strength of our longitudinal design is in establishing that anti-predator behaviors are a common and consistent characteristic of the subjects’ behavioral repertoire. Moreover, seasonal and environmental changes and social factors that characterize the lives of the animals we studied clearly influenced these behaviors in repeatable and consistent ways. However, while we feel our study is robust in terms of temporal and environmental coverage, it is based on only two habituated groups. Though these two troops occupied undisturbed and unaltered habitats supporting a complete predator community, and are therefore likely to be “typical,” we must caution against generalizations. Secondly, although major efforts were made to avoid biases, there is a chance that the patterns observed were a result of pseudoreplication. Since, we were not able to identify each individual there is a possibility that our observations were only representative of a few highly visible individuals rather than the entire troop. In this context, the true value of our conclusions lays in providing a strong and potentially productive set of predictive hypotheses concerning risk perception and information use for future testing.

Information use in many ways defines animal life and its likelihood of success in changing environs [Danchin et al., 2008]. Our work confirms that information use by higher vertebrates is complex and difficult to measure. But also, we show that with forethought concerning the environmental and social complexity of vertebrate information production and detection, its use in decision-making can be measured
in the natural environment of free-living primates. To that end, we would encourage further determination of (1) the nature and importance of interspecific information exchange for coping with changeable predation risk (see Seppänén et al., 2007 discussion of its importance in animal community ecology), and (2) how uncertainty in predator identification via social and personal information pathways influences risk perception.

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