

Extent of threat detection depends on predator type and behavioral context in wild samango monkey groups

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Abstract

Detecting predators requires information, and many behavioral and environmental features are predicted to enhance or limit an animal's ability to learn about potential danger. Animals living in groups are thought to be at an advantage for learning about predator presence, but individual safety also depends on cues spreading from detectors to non-detectors as unsuspecting individuals may still be vulnerable. In this study we simulated predator presence among two groups of wild samango monkeys (*Cercopithecus albogularis schwarzi*) to mimic natural encounters where only some individuals within a primate social group have access to personal information about potential threats. We did this using visual models of natural predators placed in positions for the monkeys to encounter within the landscape for a limited amount of time. We measured the number of individuals that were observed to detect and respond to these models with antipredator reactions, relative to subgroup size. While initial detectors that were able to spot the model themselves always reacted with overt behaviors such as alarm calling or staring at the model, responses did not typically spread to all group members. The number of initial detectors was also only weakly associated with the number of individuals that responded at the end of a trial. Initial responses to leopards were much stronger and more likely to spread than those given in response to pythons or eagles and the importance of behaviors assumed to have an antipredator function depended on the type of predator the samangos encountered.

Significance Statement

Early detection is critical for prey to survive an encounter with an ambush predator. Social prey have the advantage of being able to rely on cues from conspecifics, though individuals that do not detect a potential threat can still be susceptible to attack. Here we exposed wild samango monkeys to predator models to simulate predator presence to only part of a social group. Habitat visibility was a key predictor affecting collective detection, but the importance of other hypothesized factors— scanning and group spatial cohesion — depended on the predator species. Overall, our results indicate that the social effectiveness of purported risk-sensitive strategies varies based on the type of threat encountered.

Keywords: Predator Detection, Antipredator behavior, *Cercopithecus albogularis*, Social Information

Introduction

In natural settings, the probability that most members of an animal group will respond to the presence of a predator prior to attack depends on multiple factors that can constrain or facilitate social information transfer. The outcome of information transfer from detectors to non-detectors is referred to as collective detection and is an important hypothesized benefit of group-living for social vertebrates (Lima 1996; Bednekoff and Lima 1998). Early collective detection is especially important for avoiding mortality by ambush hunters that rely on remaining hidden until prey animals are within a certain distance (Caro 1995; Cresswell and Quinn 2010). When an ambush predator learns that prey animals are aware of its presence, it may give up on an attack that is likely to be unsuccessful (Woodland et al. 1980; Zuberbühler et al. 1999).

Learning about predator presence is constrained by individuals' abilities to monitor one another and the type of signal or cue given by an initial detector (Hochman and Kotler 2007; Pays et al. 2013). Local habitat characteristics, like visibility, should limit how quickly an initial detector can sense and respond to a threatening cue (Whittingham et al. 2004), but whether this information spreads throughout the rest of a group should also depend on the mechanism by which a species communicates alarm (e.g. visual cues or alarm calls) (Pays et al. 2013). General wariness or risk perceptions of group members might influence how much of a group is monitoring the environment versus engaged in other activities (Hochman and Kotler 2007) or how close individuals are to their conspecifics (Frechette et al. 2014; LaBarge et al. 2020a). Both factors are hypothesized to limit the ability of individuals to personally collect information about potential risks (Fernández-Juricic and Kacelnik 2004). However, several studies indicate that animals typically do not act on social sources of information as readily as they do on their own detection (Lima 1995; Kendal et al. 2004) and that more distant cues given by groupmates may be perceived as less reliable (King and Cowlishaw 2007). As such, the number of individuals who personally detect and conspicuously respond to a threat should subsequently determine whether non-detectors act on signals from conspecifics (King and Cowlishaw 2007; Ward et al. 2008).

In primates, information about predators is often conveyed through alarm calls that can reach a wide range of individuals (Caro 2005; Frechette et al. 2014). Emitting alarms can be risky if they attract the

attention of an approaching predator, but may also function to deter an attack if the signal informs an predator that it has been detected (Zuberbühler et al. 1999; Isbell and Bidner 2016; Adams and Kitchen 2018). These signals may also function to solicit collective action, such as mobbing, which may cause a predator to retreat (Isbell 1994; Arlet and Isbell 2009). Yet, if an initial detection by one member goes unnoticed by the rest of the group, an ambush predator may be able to attack another unsuspecting individual (Lima 1995). In experiments in which individual birds foraging within flocks were exposed to visual cues indicating predator presence, collective responses were more likely when a greater number of individuals initially detected the stimulus and fled, whereas limited responses were common when only one individual was able to detect the cue (Lima 1995). Experiments with fish shoals have similarly revealed that group-wide antipredator reactions require that a threshold “quorum” number of individuals detect and respond to a cue before the rest of the group changes their behavior (Ward et al. 2008). In contrast, field experiments with primates have found evidence that alarms may function to alert non-detectors to a potential threat. Solitary male Thomas langurs (*Presbytis thomasi*) tend to alarm less to experimental tiger models than those within groups (Wich and Sterck 2003). Sooty mangabeys (*Cercocebus atys*) were more likely to emit an alarm to a model snake when fewer conspecifics were nearby at the encounter site and when others had not previously alarmed (Mielke et al. 2019). Similar experiments with chimpanzees (*Pan troglodytes*) and model snakes indicated that subjects were more likely to alarm when with another individual who had not previously encountered the potential threat (Crockford et al. 2012). While these studies focused on individual alarms rather than collective responses, they may indicate that primates are more likely to respond to distant signals if alarms function to inform non-detectors of a potential threat.

Naturally occurring encounters with ambush hunters tend to be brief, and this is especially true if conspicuous indications of detection lead to a predator giving up an attack (Caro 1995; Zuberbühler et al. 1999). In these scenarios it is likely that the accessibility of cues about potential threats will be uneven within large social groups. Several studies have examined the time to predator detection in primates and other animals (e.g. Pays et al. 2013; Janson et al. 2014), but few to our knowledge have actually examined how much of a social group ends up detecting and responding to a predator during a brief encounter. In this study we examined the contexts that lead to variation in detection of predators by wild samango monkey

groups (*Cercopithecus albogularis schwarzi*). We did not aim to completely isolate personal or social information acquisition in our field study, but aimed to mimic a natural scenario where several variables would lead to differences in the number of initial detectors (who could personally spot a predator) and subsequently enhance or limit responses spreading to other group members once a threat was no longer visible. Encounters with terrestrial predators were rare at our study site despite the resident leopard (*Panthera pardus*) population (Williams et al. 2017), probably due in part to the presence of humans (Isbell and Young 1993; Nowak et al. 2014). Therefore, we used experimental methods to overcome this issue following a long tradition of researchers using realistic looking visual models to simulate predator presence to wild primates (van Schaik and Mitrasetia 1990; Pereira and Macedonia 1991) and placed these in the landscape for an oncoming group to detect within a restricted time period. We chose visual models over auditory cues, because most group members would still be unaware of their presence even when one or more close individuals initially detected the potential threat (Arnold et al. 2008). Additionally, given that ambush predators often rely on surprise, the detection of cryptic or partially obscured visual cues would constitute a relatively natural situation.

Primate antipredator responses often vary with predator hunting mode and may also vary with the detectors' perception of danger (Seyfarth et al. 1980; Zuberbühler et al. 1999; Coss et al. 2007). Thus, responses that reach the greatest number of detectors may occur simply when appropriate predator-specific responses are especially conspicuous (e.g. loud alarm calling or mobbing) or may also occur in response to predators that are most feared. The three models we used were replicas of a crowned eagle (*Stephanoaetus coronatus*), leopard, and rock python (*Python sebae*). Among samango predators at our field site, eagles likely pose the greatest threat because previous studies on this population have determined that samangos' perception of eagle risk results in a 'landscape of fear' in which individuals tend to avoid dangerous locations (Coleman and Hill 2014). Leopards also pose a risk, but it is likely they only rarely hunt arboreal samangos (Williams et al. 2018). Finally, snakes pose a risk to many primates, and detection often results in antipredator reactions across a range of species (Shibasaki and Kawai 2009; Isbell and Etting 2017; Mielke et al. 2019), but it is uncertain what risk they pose to samangos relative to other predators. These three

predators rely on concealment to attack unaware prey animals (Shultz 2001; Isbell and Bidner 2016), though eagles can either sit and wait in the forest canopy or attack on the wing (Shultz and Thomsett 2009).

Here we test the hypothesis that characteristics of the social group, local environment, and perception of the predator encountered can constrain or facilitate information transfer within samango groups. Our response variable was the final number of individuals who reacted with risk-sensitive/antipredator behaviors at the end of a trial, relative to subgroup size. Critical to this study is that these experiments occurred on two large groups where most individuals could not personally detect our models within the time limit (see Methods, Predator Exposure). Specifically, we predicted the number of detectors would increase during trials if: 1. Habitat visibility was high; 2. Spatial cohesion, measured as the number of nearest neighbors, was greater; 3. A greater proportion of the group was monitoring the environment prior to a trial; 4. More individuals could personally detect the threat themselves by being near the model before removal; and 5. Predator-specific responses were especially conspicuous (alarm calling or other overt antipredator behaviors). Based on previous observational data, we predicted that the eagle would elicit the strongest reaction, followed by the leopard, and then the python.

Methods

Study Site and Species

We conducted our study at the Lajuma Research Centre in the western Soutpansberg Mountains of Limpopo Province, South Africa (23° 02'S, 29° 26'E). The study site encompasses an array of habitat types including tall moist Afromontane forest, deciduous woodland, acacia bush, and rocky grassland/cliffsides. We studied two samango groups, "Barn" group (N~45) and "House" group (N~70-80), that were well-habituated to direct observation. Samango monkeys are medium-sized (adult females ~ 4.4kg, adult males ~ 7.6kg), arboreal guenons that live in single-adult male multi-female groups typically with 10 to 65 individuals (Coleman and Hill 2014). Groups were not always a single unit and would sometimes fission into one or more subgroups during the day. Mean (sub)group size at the beginning of trials was ~55 for House group and ~40 for Barn group. House group contained 16 identifiable individuals and Barn group contained five. Observers could readily distinguish between age-sex classes. Natural predators of samangos

at the site include crowned eagles (*S. coronatus*) and black eagles (*Aquila verreauxii*), the African leopard (Williams et al. 2018), caracal (*Caracal caracal*) (Nowak et al. 2014), and rock pythons.

Predator Models

Leopard and python models were realistic-looking plush toys, while the eagle model was created using mesh wire, papier-mâché, and chicken feathers and painted to mimic the colors of a crowned eagle (Fig S1). The leopard and eagle models were both larger than the python, reflecting their natural variation in size. Observers at this site have witnessed each of these predator types with one of these samango groups. To control for responses to novel but non-threatening stimuli, we used a penguin model which does not resemble any bird native to the Soutpansberg.

Pilot trials

Between May and August 2017, we conducted pilot trials with our leopard model to assess whether samangos would respond to a visual model similarly to a live predator encounter. We used these preliminary trials to determine an adequate time between initial detection and covering the model that would minimize the possibility that the entire group could see it personally. This was necessary to avoid conflating social transmission of information with ongoing personal information acquisition. We placed the models approximately 100 m ahead of an oncoming group based on the direction individuals seemed to be moving and found it typically took 4 – 6 minutes following an initial detection for all of the remaining members of the (sub)group to respond. Detection was indicated by alarm calling, approaching, staring and/or bobbing their heads at the model. Thus, we determined that an exposure of 90 seconds after the initial reaction would be enough time to ensure that much of the group could not see the model, but that the response of the initial detector(s) would still be strong enough for others to respond.

Predator Exposure

Following the pilot study, we conducted one or two predator model presentations per month on each group between June 2018 and June 2019. Experiments took place between 9:00 and 13:00. A research assistant followed the group from their sleeping site before dawn and collected behavioral data following the normal long-term research protocol (see Behavioral Data). Communication between the assistant and experimental researchers via two-way radio allowed us to ensure that we did not place predator models

during or following any natural predator encounters. Samango groups were generally cohesive (single group), but sometimes split into two or more subgroups. Our measure of ‘collective’ detection (our dependent variable) was linked to the size of the observable (sub)group, rather than absolute group size. Therefore, prior to initiating the trials, observers recorded the number of visible individuals within the subgroup. This was completed by LRL and/or one or more field assistants.

We placed models beyond the visual range of the samango monkeys and approximately 75 – 150 m ahead of an oncoming group and according to the predator’s respective hunting styles. The eagle model was placed on a branch or large boulder >2 m above the ground, the leopard was placed on the forest floor, and the python was placed either on the ground or on rocks/logs <1 m from ground level. Subsequently, observers that initiated the trial hid behind large rocks or trees to avoid subjects associating model predators with humans. Observers collecting general behavioral data made no attempt to conceal themselves. A video recording was made to confirm an identity and/or age-sex class for the initial detector (Sony handycam). At the time of this initial detection, observers recorded the number of individuals within 25 m of the model (at first detection and again at 90 sec) and the ID and age-sex class of the detector(s). The mean distance of the initial detector from the predator model was 10.3 m (standard deviation(SD): 7.49 m) for the eagle, 19.3 m (SD: 7.7 m) for the leopard, and 5.2 m (SD: 4.6 m) for the python. All of these initial detectors were within the understory or subcanopy when we observed their response. Thus, it was unlikely that individuals beyond 25 m could typically personally detect a threat in this densely vegetated habitat. Immediately following the first detection of the model, the observers waited 90 sec and then covered the model using a green canvas tarp. For leopard trials, the tarp was attached to ropes that allowed us to cover the model remotely. This was necessary because pilot trials indicated that detectors would approach this model, and we aimed to avoid being close to any of these individuals. For eagle and python trials, one of the observers would cover the model rapidly at 90 sec. Once models were covered, observers continued to monitor groups for delayed responses and, when necessary, agreed on a final count of responders. Following trials, we used data from the nearest preceding group scan sample (collected between 5-15 minutes prior) to obtain information on relative levels of cohesion and scanning behavior (see Behavioral data).

In total, we completed 30 trials with 10 on each predator type (5 on each samango group). To control for potential reactions to novel stimuli, we also completed 10 trials with a non-threatening bird model (penguin). We did not repeat trials on the same group in the same location (<50 m) and recorded all the same behavioral and habitat data (see below) for both predator and control trials. Additionally, we left approximately two - three weeks, on average, between trials of the same predator type to minimize the potential for habituation. Our response measuring the variability in collective detection was the number of individuals within an immediate (sub)group reacting with obvious risk-sensitive behaviors before the end of a trial. We recorded the number of initial detectors and subsequently recorded the number of individuals who responded by the end of each trial. We note that these counts may slightly underestimate the true number as there may have been more responding individuals high in the trees or far out of sight.

Following each trial, we measured understory visibility by photographing a black and yellow 1 m² 225-square checkerboard 10 m from where the model was placed at two meters high in each cardinal direction with the percentage of the squares visible recorded (each square = 6.6cm²) (LaBarge et al. 2020a). As groups tended to come down from the canopy during mid-morning to lower forest strata, this was a good proxy for the degree of visibility most samangos would have in that habitat.

Every predator trial resulted in detection by at least one individual as indicated by alarm calling, visual inspection, head bobbing, and/or approaching the model. All but three of the initial detectors were unmarked individuals; however, in most of these unmarked individuals, observers could confirm that their age/sex class was different than previous detectors of the same predator type. The exceptions to this were two of the eagle trials which resulted in an initial detection by unidentified subadults from the “House” group and two of the leopard trials resulted in detection by unidentified adult females in the “Barn” group. Because both groups were large, and because we left three to four weeks between predator trials of the same type, it is likely that these were not the same individuals. One python trial in January 2019 was terminated early because the model fell out of a tree, resulting in immediate alarm calls from all visible “House” group members. We did not use data from this trial. The control model trials did not result in apparent behavior changes in adult or subadult individuals, but in three instances (two in “House” group , one in “Barn” group) juveniles approached the model on the ground and investigated it before moving on. Thus, we assumed that

the novelty of predator models did not evoke antipredator reactions and that the responses recorded for other trials were appropriate for samangos encountering danger.

Behavioral Data

Behavioral and location data were collected before, during, and following all predator trials via scan sampling (Altmann 1974) in a five-minute window every 20 minutes throughout the day. Day length ranged 10.5 hours (06:40 – 17:20) to 14.5 hours (04:40 – 19:00). Each sample location was recorded with a handheld GPS (Garmin GPSmap 60Cx or 62s, Garmin, Olathe, Kansas, US). Within a scan sample, we attempted to record the behavior of as many individuals as possible within the group and minimized repeating individuals by moving throughout the group and collecting data only when certain an individual had not been previously observed (mean: 10.8 individuals; range: 6-14). Moving between spatial subsections, and between the periphery and center of the group minimized oversampling intra-group cliques. Thus, these group scans were comprised of information on individuals found in various positions throughout the group. Within these samples we recorded the date, time, group ID (“House” or “Barn”), individual age/sex class, and individual ID when known. For each subsampled individual, we recorded the number of non-infant neighbors each individual had within five meters (LaBarge et al. 2020a). Finally, we recorded whether an individual was scanning beyond an arm’s reach (Treves 1998). Data from each of these individuals within a group scan was converted into a proportion (of sampled individuals) as a proxy for how much of the group was monitoring the environment or conspecifics prior to an initial detection. Blinded methods were not possible for this study as we collected data on wild, habituated animals in their native habitat.

Data Availability

All data used in this manuscript and corresponding R code can be found within supplementary materials.

Analysis

To analyze these data, we used regression with a binomial distribution and logit link in the stan computational environment accessed through the R package brms (Bürkner 2017). We considered the count of the number of individuals that responded as the number of k successes in a binomial trial (relative to n

subgroup size). While frequentist methods might use an ‘exact’ logit for small-sample data, Bayesian analysis can also improve accuracy and minimize the risk of Type 1 and Type M errors at small sample sizes by incorporating information about prior probabilities, along with the likelihood, to form a posterior probability distribution. For additional details on our model fitting methods, see Supplementary Materials, *Detailed Analysis Methods*.

We did not fit any random factors into our model because we did not knowingly repeat trials on the same initial detector. Additionally, our data were clustered into two groups which is too few levels to include as a random factor. At best, random effects with too few levels produce similar estimates as models including the same term as a fixed effect (Moen et al. 2016). We assessed how much variation was due to “group” by calculating an intra-class correlation coefficient (ICC) with the package sjstats (0.24, Lüdtke 2018) and retained this in our model as a fixed effect as this would help account for this between-group variation in this repeated-measures field experiment (Moen et al. 2016). Thus, we focus on population-level inferences and cannot make inferences about the differences between these two samango groups with this analysis.

Additional fixed effects were the categorical predator type (eagle, leopard, python, control), percentage understory visibility, mean number of nearest neighbors, the proportion of sampled individuals scanning/monitoring their surroundings, and the number of individuals within 25 m from the model at initial detection. The proportion scanning included individuals monitoring their surroundings or those that may have plausibly been looking in the direction of another monkey. We included ‘control’ trials so that this categorical level could serve as reference for the predator trials. Trial number was also included as a fixed effect to account for potential habituation to the same predator type. 80% of initial predator reactions came from adult female or subadult individuals, thus we did not include age-sex class within our model. Results of previous studies led us to include interactions between predator type and number of neighbors and the proportion of the group scanning (Whittingham et al. 2004; Frechette et al. 2014).

We used Markov Chain Monte Carlo sampling (MCMC) to obtain posterior estimates. We ran 450,000 iterations across five unthinned chains with a warmup of 425,000 for a total of 25,000 samples because larger effective MCMC sample sizes can produce more stable and reliable estimates for small

sample problems (Forster et al. 2003; Kruschke 2014) (Fig. S1). We checked model residuals using the package DHARMA (Hartig 2016) and applied posterior predictive checks with brms by visual inspection (Bürkner 2017). Variance Inflation Factor (VIF) was <2.7 for all parameters and Monte Carlo standard errors were all under 1%. Finally, we used 95% credible intervals (CIs) along with probability of direction (PD) values to evaluate the relative level of evidence for each parameter. PD values range from 50-100% and describe how much of a posterior distribution is entirely positive or negative. Here we considered a parameter to have supporting evidence if a CI did not include zero and its PD was above 99.5%.

Results

The probability of an initial reaction spreading to more of the group depended on the predator type (Fig. 1, Table 1). In eagle trials, a mean of 25.9% (1.7-100%) of “House” group and 39.7% (2.9 -100%) of “Barn” group responded during trials. In python trials a mean of 14.7% (1.7-35%) of “House” group and 32.6% (6.7-71.4%) of “Barn” group responded and only one out of the total 10 trials resulted in more than 50% of the (sub)group clearly reacting. Responses to leopard models were more intense, and a mean of 80.80% (60-100%) of “House” group responded and 63.56% (8.88-86.66%) of “Barn” group responded to these trials. Only three out of the 30 predator trials resulted in 100% of visible subgroup members clearly responding – two of these responses were to eagle trials and one of these was a leopard trial. Nevertheless, leopard responses were more consistently strong (resulting in more individuals responding overall) and contained an entirely positive CI and PD of 99.98% which was not the case for either the eagle or python.

Reactions to all three predator types resulted in alarm calls, but leopard trials resulted in individuals approaching the model from trees, potentially providing an additional auditory or visual cue to non-detectors that were able to view conspecifics, but not the predator model. Four of 10 leopard trials resulted in male “pyow” and “ant” alarm calls. We did not record any male alarms during eagle or python trials, but males are known to alarm at these predators during natural encounters. Males were typically found towards the center or rear of an oncoming group and, to our knowledge, were not the initial detectors in any of these trials (Table 1).

Greater visibility in understory habitat tended to positively predict wider responses overall (Fig. 2, Table 1); however, this trend was strong for just eagle and leopard trials. In contrast, the number of individuals within 25 m of the model during initial detection may have had a small positive effect on the percentage of the group engaged in antipredator responses at the end of the trial, although the CI for this value included zero and the PD for this parameter was lower than our threshold (Fig. S2, Table 1). We note that the mean number of individuals within 25 m at initial detection was 11.13% of the total subgroup and ranged from 2-28.8%. All of these individuals would have likely been able to personally detect the model before it was concealed after 90 sec.

Interactions between scanning behavior or number of neighbors and model used revealed predator-specific differences. When a greater proportion of the group was engaged in scanning behavior prior to a leopard trial, more individuals tended to detect the model by the end, but this was not the case for the other predator types. Although this value had a PD below 99.5%, its CI did not cross zero (Fig. 3 and Table 1). Similarly, number of neighbors (spatial cohesion) was apparently a positive predictor of widespread detection for eagle models and, potentially, python responses as well. However, while values tended to be positive for leopard trials (Fig. 4), there was less evidence overall (Table 1).

Although we could not test explicitly for differences between the two study groups, we had no evidence indicating substantial differences between them. Trial number was weakly negatively associated with the percentage of a group that would respond at the end of a trial but did not reach our importance threshold (Table 1, Fig. S3).

Discussion

While group living is hypothesized to be an effective strategy for mitigating predation risk, individuals within a group may still succumb to an attack if unaware of a predator. The goal of this study was to better understand whether factors hypothesized to facilitate or constrain information acquisition and transfer would predict the extent to which antipredator responses would spread in samango groups. Samango monkey groups that detected visual predator models reacted to all three with alarm calling, staring, and, in some cases, approaching the model, providing potential cues to non-detectors. Habitat visibility was a strong

predictor of the outcome of our trials, potentially because more individuals were able to personally detect the model prior to the 90 sec time limit. Yet, the number of individuals that were likely able to detect the model personally – those within 25 m of it upon first detection – was not a good predictor of trial outcome. Given the size of our study groups, the density of these forest/acacia bush habitats, and time-limited predator exposures, most individuals would likely have had to rely on cues from conspecifics to learn about the potential threat. Thus, once initial detection had occurred, information about the threat would have to travel throughout the group. Additionally, we found that the effectiveness of purported risk-sensitive behavioral strategies which should enhance collective detection, depended on the type of threat these samangos encountered. Specifically, scanning behavior prior to the trial was only a positive predictor for the extent of responses to leopard trials, but not the other predators. Spatial cohesion, as measured by the number of neighbors an individual had nearby (within 5m), was also a potential predictor for group responses to the eagle or python models, but not the leopard. Finally, differences between the predator types (holding other variables constant) indicated that there were differences either in samango monkeys' ability to detect these predators or in the conspicuousness of predator-specific responses.

We assumed that high within-habitat visibility would lead to greater personal detection (Prediction 1), but also that the number of individuals within close proximity to the model (<25 m) at initial detection would positively predict the extent of responses due to the higher likelihood that these individuals could personally detect the model (Prediction 4). Yet, we found positive support only for the former. This result is consistent with experiments conducted with birds and fish that suggest the importance of personal information to group-wide predator detection (Lima 1995; Ward et al. 2008; Conradt 2011), but contrasts with experiments with other primate species in which individuals were more likely to alarm call when conspecifics were presumably unaware of a predator (Crockford et al. 2012; Mielke et al. 2019). Our result likely stemmed from visibility enhancing detection for a few initial detectors at the start of a trial, but also allowing conspecifics to better monitor their neighbors. In this study we were not able to repeatedly measure responses from the same known individuals over time due to habituation concerns and a relatively low number of consistently identified individuals within these study groups. Yet, it is possible that potentially heritable inter-individual differences in anxiousness or similar traits would result in certain individuals being

particularly reactive (Brent et al. 2014; Watson et al. 2015). If this information was known to conspecifics, it could have influenced overall responses (Couchoux et al. 2018).

Many studies have suggested that social information is often perceived as less accurate than personal information (Kendal et al. 2004; King and Cowlshaw 2007). The exception to this may be that individual prey animals are more likely to act on social information when it comes from neighbors at close distance (Fernández-Juricic and Kacelnik 2004). Frechette et al. (2014) found that groups of squirrel monkeys (*Saimiri sciureus*) were more likely to react with escape responses to predator encounters when group spatial cohesion (measured as group spread) was high. Cohesion itself is likely also important for baseline levels of risk perception (Treves 1998; Fernández-Juricic et al. 2007), because individuals with more neighbors are hypothesized to be able to learn about potential threats earlier than individuals further from groupmates (Prediction 2). We only found support for cohesion-enhancing responses to eagle and snake models. Personal detection of these two predators may have been more challenging if they were better hidden within these densely vegetated habitats (Fig. S1) as detection distance and the extent of collective response tended to be greater for leopard trials. Thus, social information may have been more important to the outcome of eagle or snake trials compared with leopard trials. This may also explain why scanning behavior was a good predictor for the outcome of leopard trials, but not eagle or snake trials (Prediction 3).

Trials with leopard models were the only ones that elicited consistently extensive responses and male alarm calls, although male responses were likely due to greater detection distances and the tendency for samango males to occupy positions near the center or rear of the group during the trials (LRL, personal obs.). This particular result does not fit with our initial prediction that perceived risk would be highest for eagles based on previous studies indicating their importance for samango landscape use (Prediction 5; Coleman and Hill 2014). This is compared with responses of vervets (*Chlorocebus pygerythrus*) at this site who appear to preferentially avoid high leopard and baboon risk, but do not respond similarly to eagle risk (Willems and Hill 2009). One potential explanation is that the post-detection strategies for avoiding these predators differ in their conspicuousness, because alarm calls and other overt antipredator reactions can serve as a particularly effective predator deterrent for leopards (Woodland et al. 1980; Isbell and Bidner 2016; Adams and Kitchen 2018). As such, widespread and repeated alarm calling may not deter eagles or

snakes to the same extent. In each leopard trial, detecting individuals also tended to approach the model; however, this was the case in only one of the eagle trials that led to a collective response. In contrast, remaining in place may be a relatively effective strategy to avoid being taken by an eagle (Arlet and Isbell 2009). Yet, we cannot rule out that these differences may be due to samangos perceiving a perched eagle as less dangerous than one flying overhead. While crowned eagles do drop down from dense canopy onto monkeys, samangos may not see these predators as often prior to an attack, which could explain this discrepancy.

Approaching a leopard, as we witnessed here, may help individuals avoid mortality as ambush predators are often less likely to continue a hunt if prey signal that they are aware of present danger (Woodland et al. 1980; Adams and Kitchen 2018). This response may also deter a leopard from concealing itself nearby but may also be a more noticeable reaction to other group members unaware of potential danger, leading to more widespread responses. In some instances, alarm calling may solicit help for mobbing (Isbell 1994). While we did not observe mobbing or harassment behavior following approaches, this was potentially due to our time-limited trials. Given that leopard models were approached more often, increased alarming could have also functioned to recruit more group members to participate in this potentially costly behavior. We also observed that initial detectors often continued alarming long after both eagle and leopard models were removed, but this was generally not the case with the python model. This may indicate that once detected, snakes pose less risk than the other ambush predators. For example, Mielke et al. (2019) found that sooty mangabeys (*C. atys*) react mildly to stationary snakes or snake models, potentially indicating that, once detected, a non-moving snake poses little risk.

Previous experiments with this population showed that samangos spend more time foraging on the ground while being observed by humans (Nowak et al. 2014). This is likely due to a “human-shield” effect where predators avoid contact with humans, and samangos take advantage of this increase in safety. Leopards may infrequently hunt samangos in this habitat compared with other available mammals (Williams et al. 2018), but it is uncertain where they are most frequently encountered on the landscape compared with eagles that are encountered more frequently (LaBarge et al. 2020a). From a prey animal’s perspective, encounters with a potential predator should elicit a response (including freezing or other cryptic reactions)

even if the predator itself is not engaged in an attack. Additionally, sit-and-wait terrestrial predators with relatively small hunting domains are expected to produce outsized risk effects in their prey (Schmitz 2007; Miller et al. 2014). It is possible here that our presence through general observation throughout the day would have led to relaxed risk perceptions prior to initiating trials. This could have led to delays in responses if most individuals are less reactive when humans are present. Conversely, if human presence produces relaxed perceptions of leopard risk across the landscape, this could lead to stronger responses if an unwary individual happens to encounter a predator while in a more vulnerable position. At minimum we have demonstrated here that observed encounter frequency does not necessarily track with the magnitude of antipredator response in this population of samangos.

Predator-primate interactions are difficult to observe because they are unpredictable, rapid, and relatively rare (Isbell 1994; Janson et al. 2014). Compounding this issue is that many unhabituated predators tend to avoid proximity to potentially dangerous humans (Ngoprasert et al. 2007; LaBarge et al. 2020b), minimizing the chances that an observer witnesses an encounter during data collection. Observational studies that look for correlations between antipredator behaviors and habitat or location-specific risk often overlook the possibility that prey perceive themselves to be relatively safe while accompanied by an observer (Nowak et al. 2014). Field experiments can ameliorate this problem by allowing researchers to control when and where predator cues are used (Adams and Kitchen 2018; LaBarge et al. 2020b).

Limitations to our study included the presence of an observer collecting behavioral data on our habituated subjects while we conducted these experiments. This is because these samangos may have already perceived themselves to be relatively safe from certain predators while in proximity to humans (Nowak et al. 2014). This potential effect on perceived risk could have altered initial detection times. Nevertheless, these realistic reactions to visual models indicate that experiments are an effective means of simulating these encounters. Future studies with expanded numbers of groups should investigate whether presence/absence of an observer influences detection time and overall probability of collective response. Finally, we could not test how group size might have limited or enhanced the probability of a collective response, but future studies using random slopes models with many groups (>10) of varying sizes could provide information on the importance of this trait for samango predator detection (Grueber et al. 2011). Studies that can further

minimize the presence of observers or eliminate direct observation would be better positioned to investigate whether underlying spatial patterns of risk from various predators result in variation in detection time or overall response.

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Compliance with Ethical Standards

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Conflict of Interest: The authors declare they have no conflict of interest.

Ethical approval: We followed all animal research (IACUC) guidelines from The State University of New York as well as all applicable South African and international guidelines. We received research permission from the Limpopo Province Dept of Economic Development and Tourism (Permit # ZA/LP/81996), University at Buffalo IACUC (#ANT07037N) and Durham University Animal Welfare Ethical Review Board.

Informed consent: No human subjects were involved in this research.

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Table 1 Coefficients from the joint posterior distribution, estimated errors, and 95% credible intervals.

Num. w/in 25 m is the number of individuals near the predator model during the initial detection (max. end of apparent visual range). Scanning refers to the proportion of the sampled group scanning prior to the trial.

Pred.Type * Neighbors refers to the interaction between the type of model predator and the number of nearest neighbors per individual. Pred.Type*Scanning refers to the interaction between predator type and scanning. Rhat is the potential scale reduction factor on split chains which indicates convergence at 1.00

(Gelman-Rubin Diagnostic). PD is the probability of direction where values above 99.5% are bolded

		Estimate	Est.Error	L. 95%	U. 95%	Rhat	PD
Intercept		-5.46	1.37	-8.39	-2.99	1	100.00%
Group		0.11	0.19	-0.26	0.47	1	72.24%
Predator Type	<i>Eagle</i>	1.93	1.38	-0.57	4.88	1	93.02%
	<i>Leopard</i>	4.21	1.37	1.74	7.15	1	99.98%
	<i>Snake</i>	2.00	1.39	-0.52	4.95	1	93.61%
Habitat Visibility		2.73	0.8	1.18	4.30	1	99.96%
Num. of Neighbors		-1.28	0.98	-3.42	0.46	1	91.92%
Num. w/in 25m		0.05	0.02	-0.00	0.10	1	97.06%
Scanning		-0.69	1.22	-3.19	1.63	1	71.17%
Trial Number		-0.11	0.06	-0.22	-0.00	1	97.61%
Pred. Type * Neighbors							
	<i>Eagle</i>	2.76	1.00	1.00	4.91	1	99.91%
	<i>Leopard</i>	1.51	0.98	-0.22	3.66	1	95.39%
	<i>Snake</i>	1.99	0.99	0.25	4.14	1	98.86%
Pred. Type * Scanning							
	<i>Eagle</i>	1.28	1.28	-1.14	3.90	1	84.55%
	<i>Leopard</i>	3.58	1.33	0.01	5.27	1	97.53%
	<i>Snake</i>	0.32	1.31	-2.19	2.96	1	59.13%

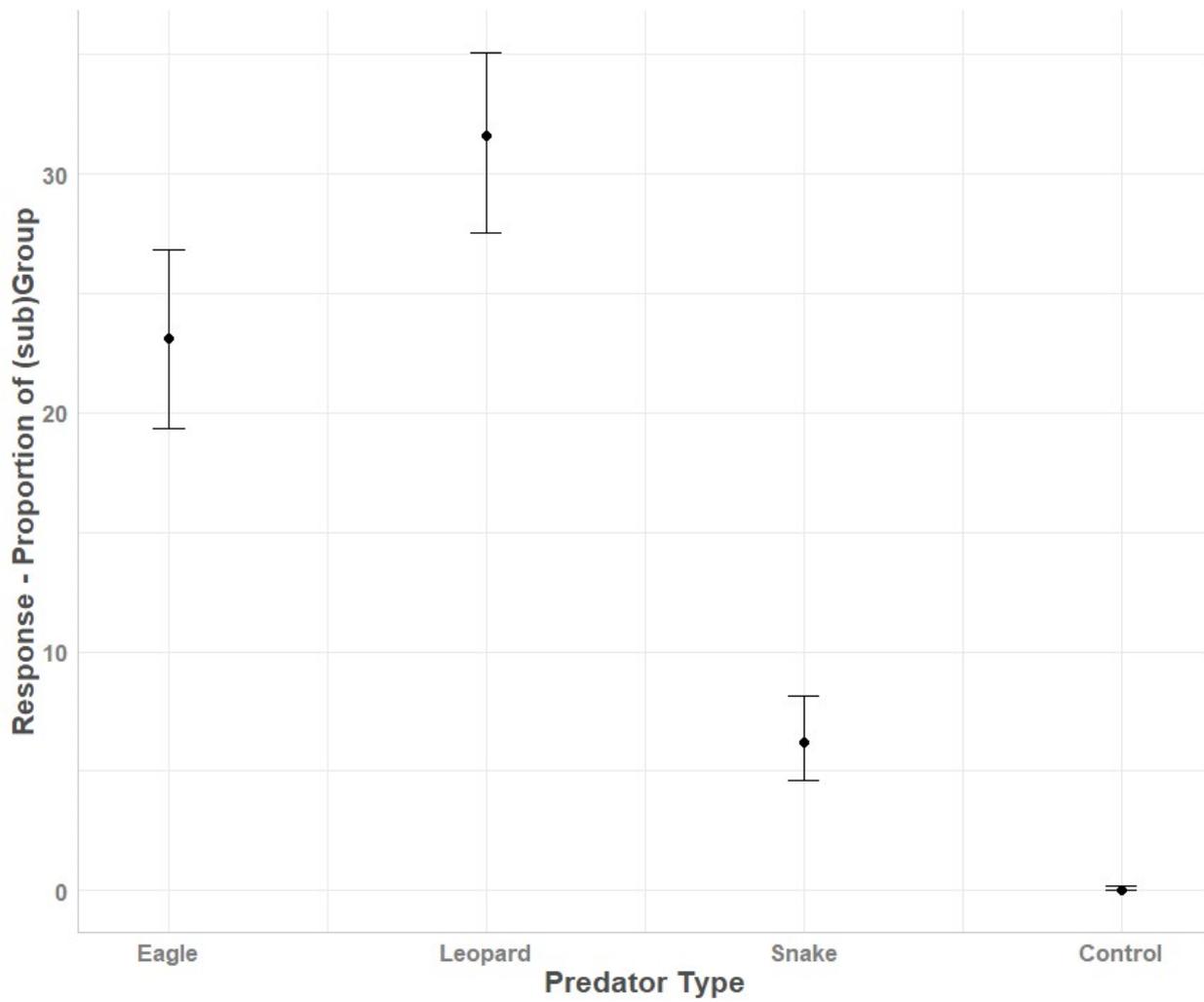


Fig. 1 Marginal effects plot of differences in response (proportion of (sub)group responding) between the predator types. All other predictors held at their mean or reference values. Bars represent 95% CI

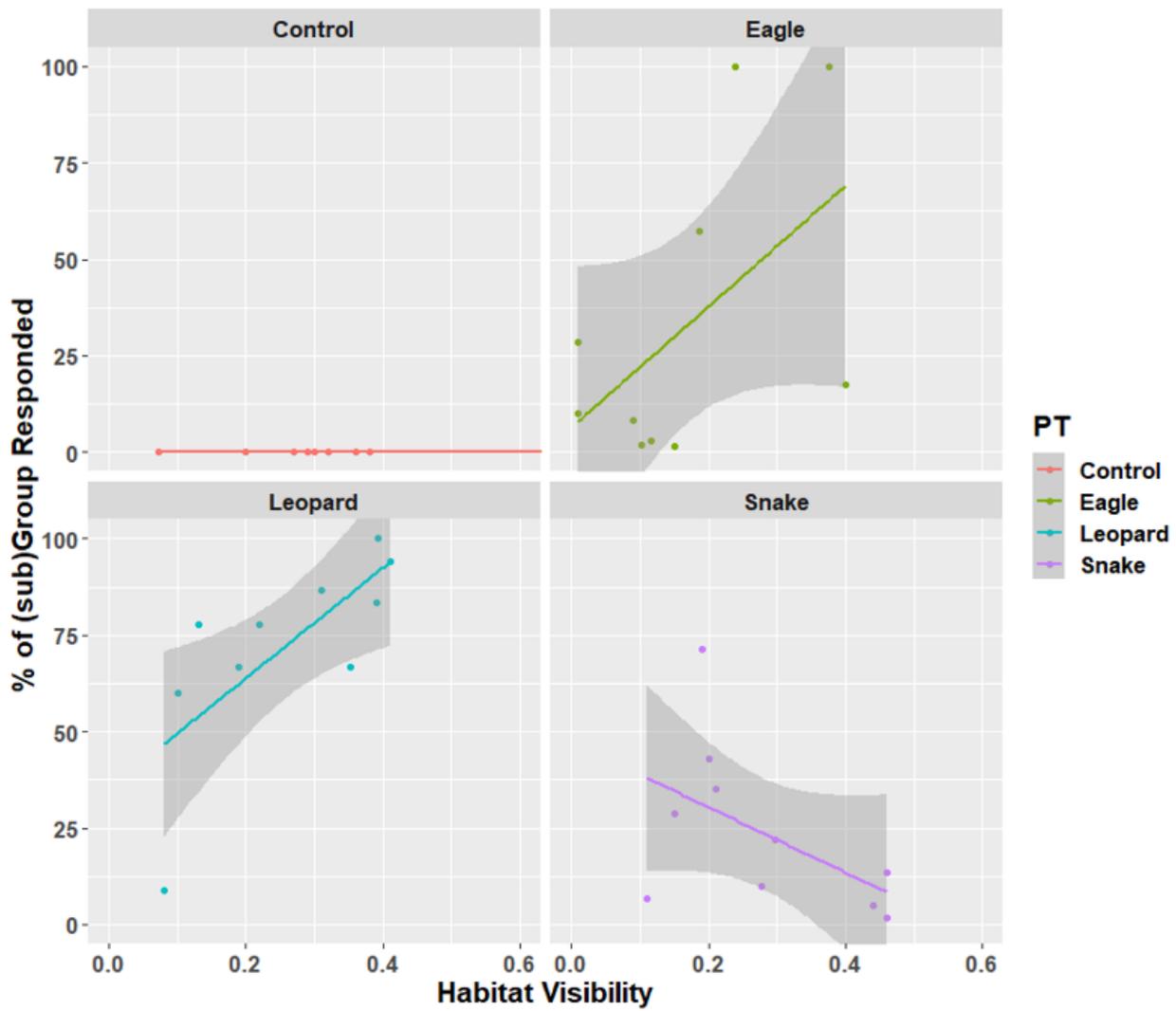


Fig. 2 Habitat visibility and the proportion of the group that responded at the end of a trial. PT is the predator type. Shaded area is 95% CI (credible interval)

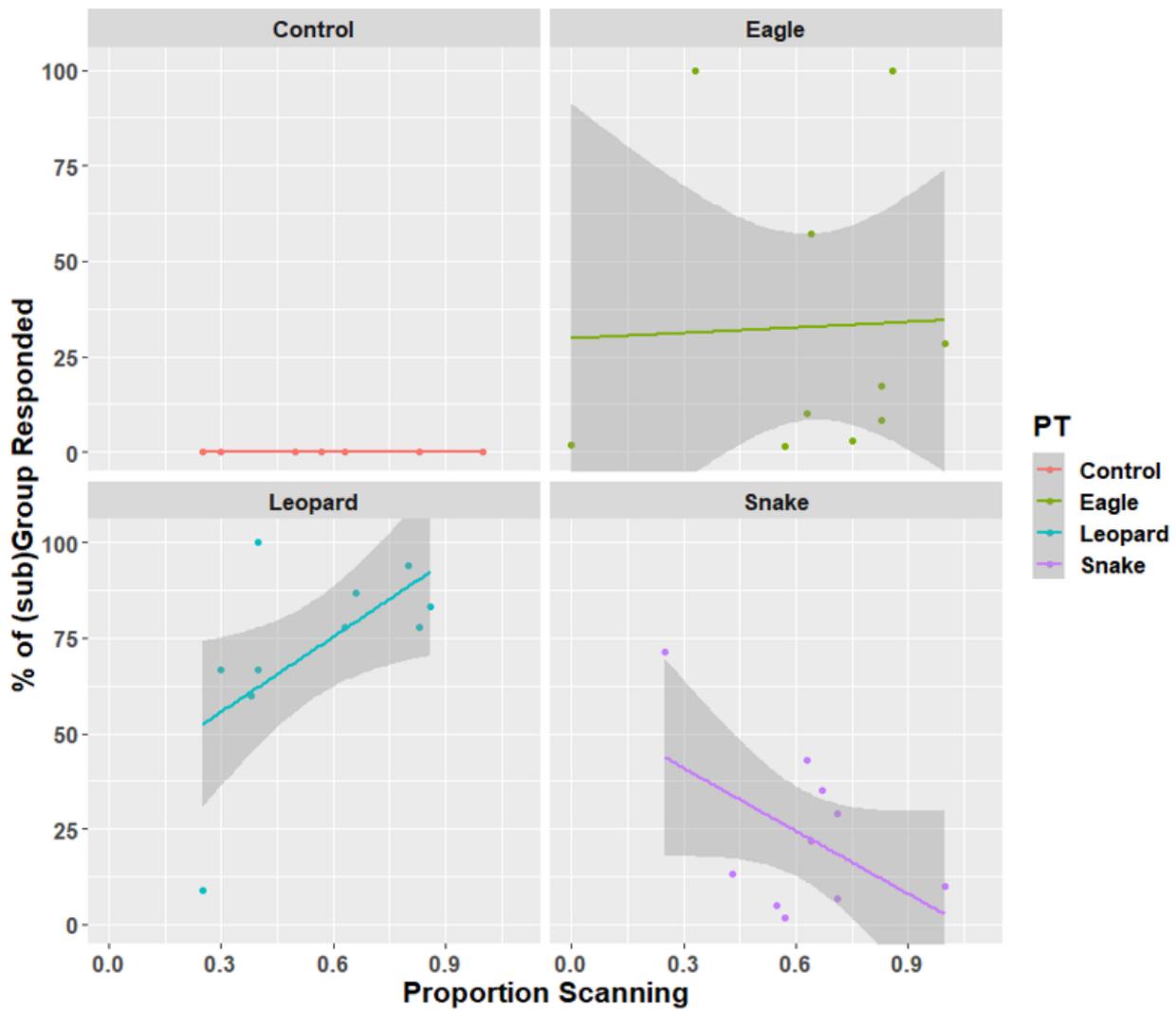


Fig. 3 Proportion of sampled individuals scanning their environment / monitoring others prior to trial and the percent of the group that responded. PT is predator type. Shaded area is 95% CI

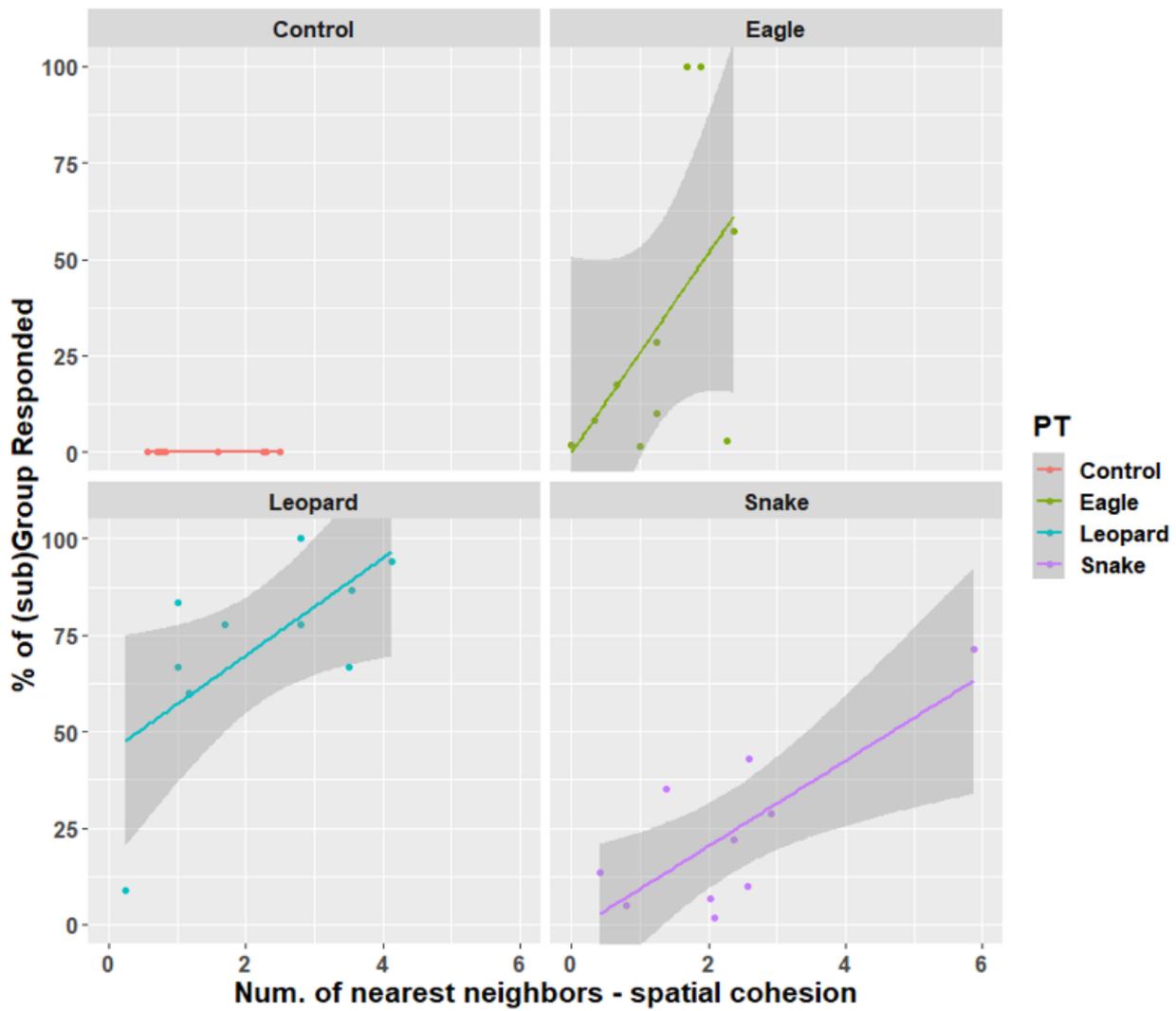


Fig. 4 Mean number of nearest neighbors/individual prior to detection and percent of the group that eventually detected/responded. PT is predator type. Shaded area is 95% CI

Electronic Supplementary Material

Behavioral Ecology and Sociobiology

Extent of threat detection depends on predator type and behavioral context in wild samango monkey groups

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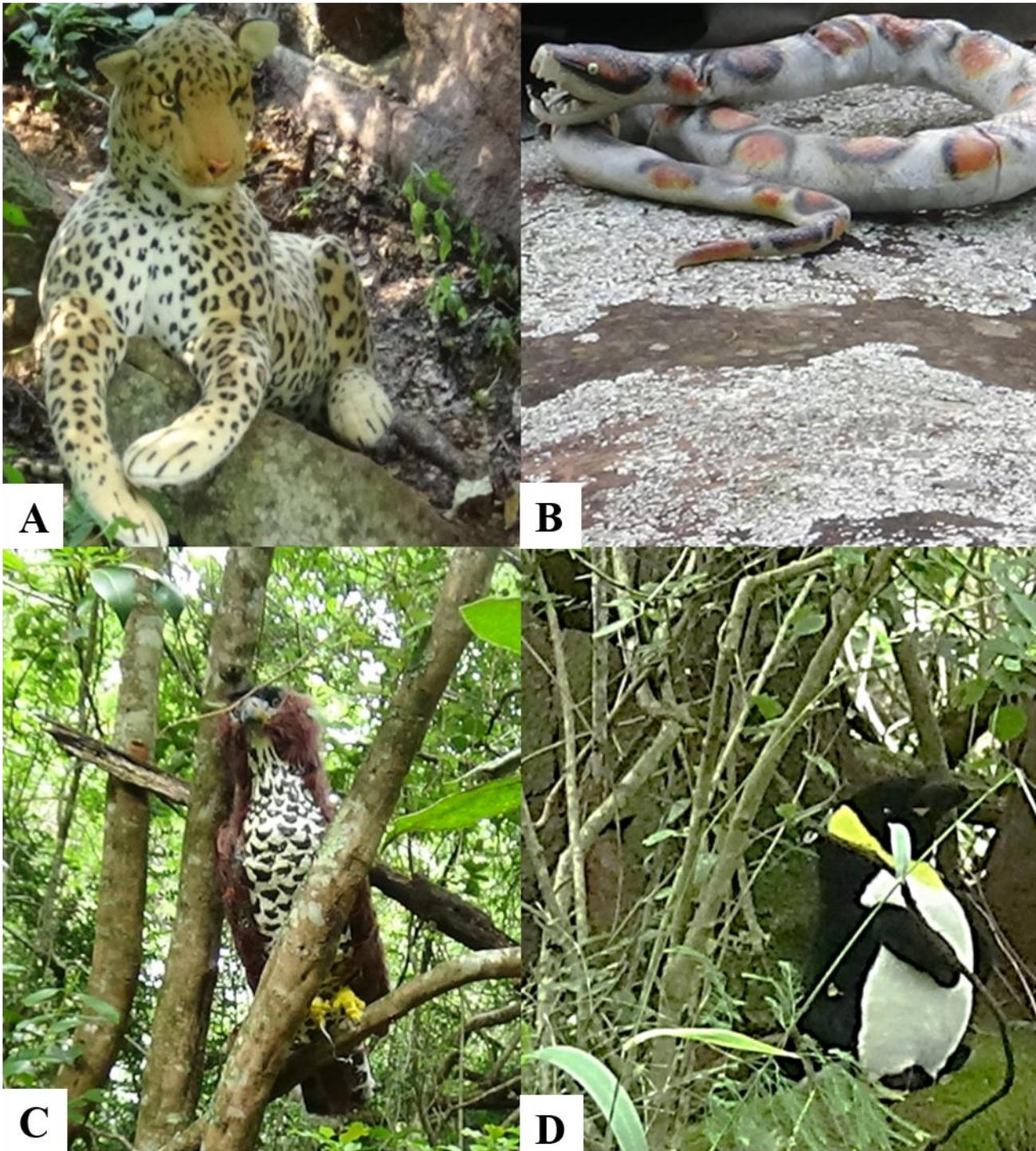


Fig S 1 Predator models A) leopard; B) python; C) Crowned eagle; D) control (penguin)

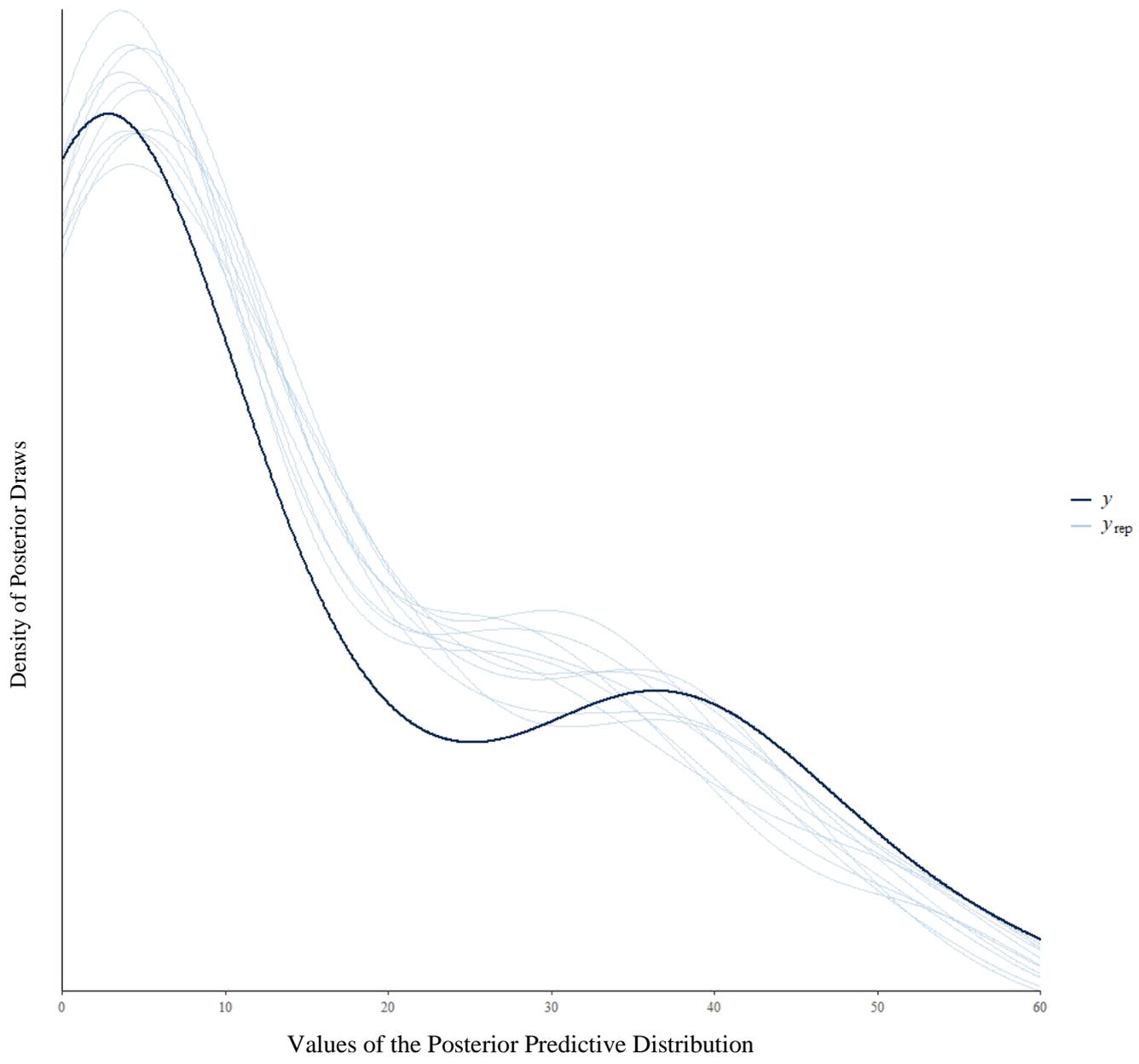


Fig S2 Observed data y versus the suggested distribution of the data y_{rep} from the model

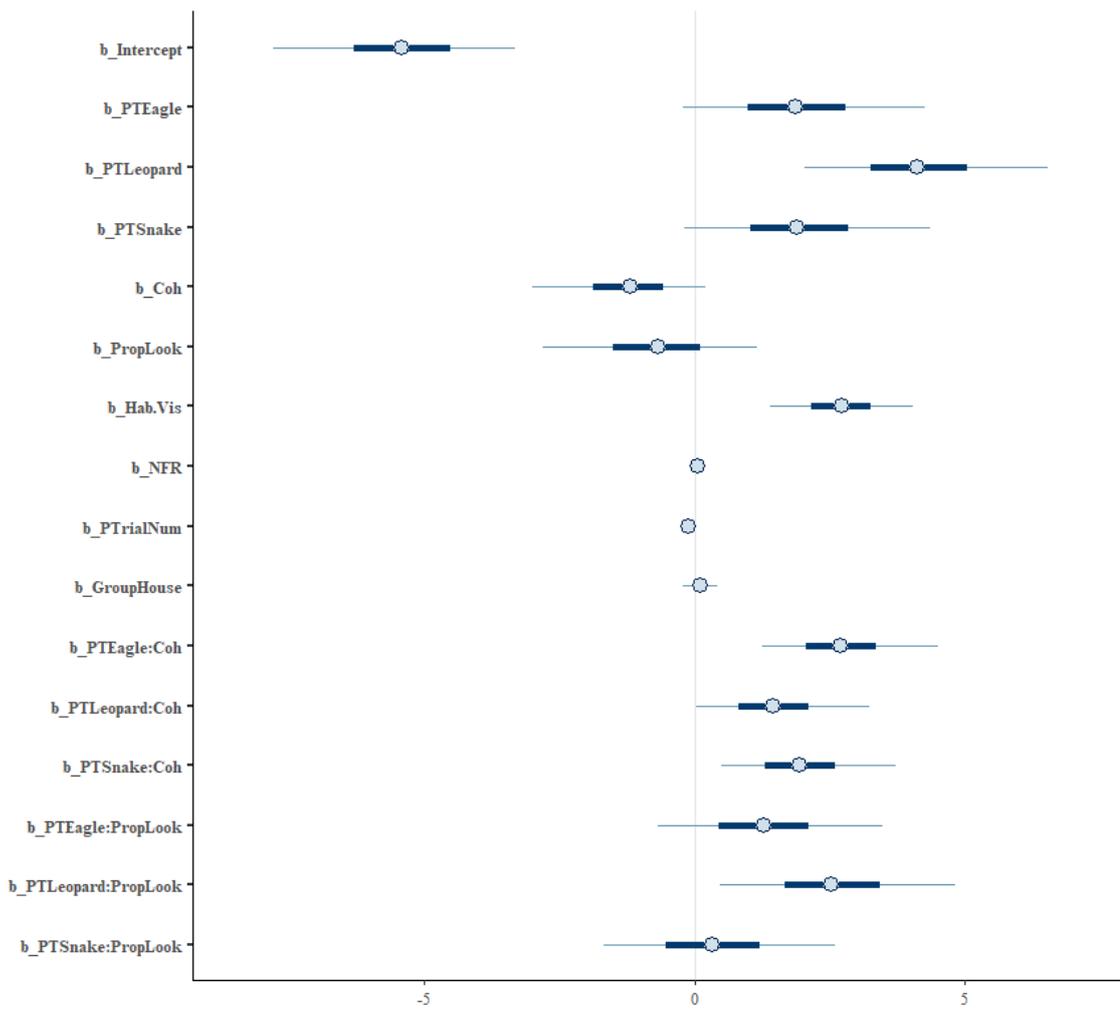


Fig S3 Coefficient plot with highest density intervals (dark blue) and 95% credible intervals (light blue). PT is predator type; Coh is number of neighbors (proxy for cohesion); PropLook is the proportion scanning prior to the trial as a proxy for how much of the group was looking around Hab.Vis is habitat visibility; PTrialNum is trial number

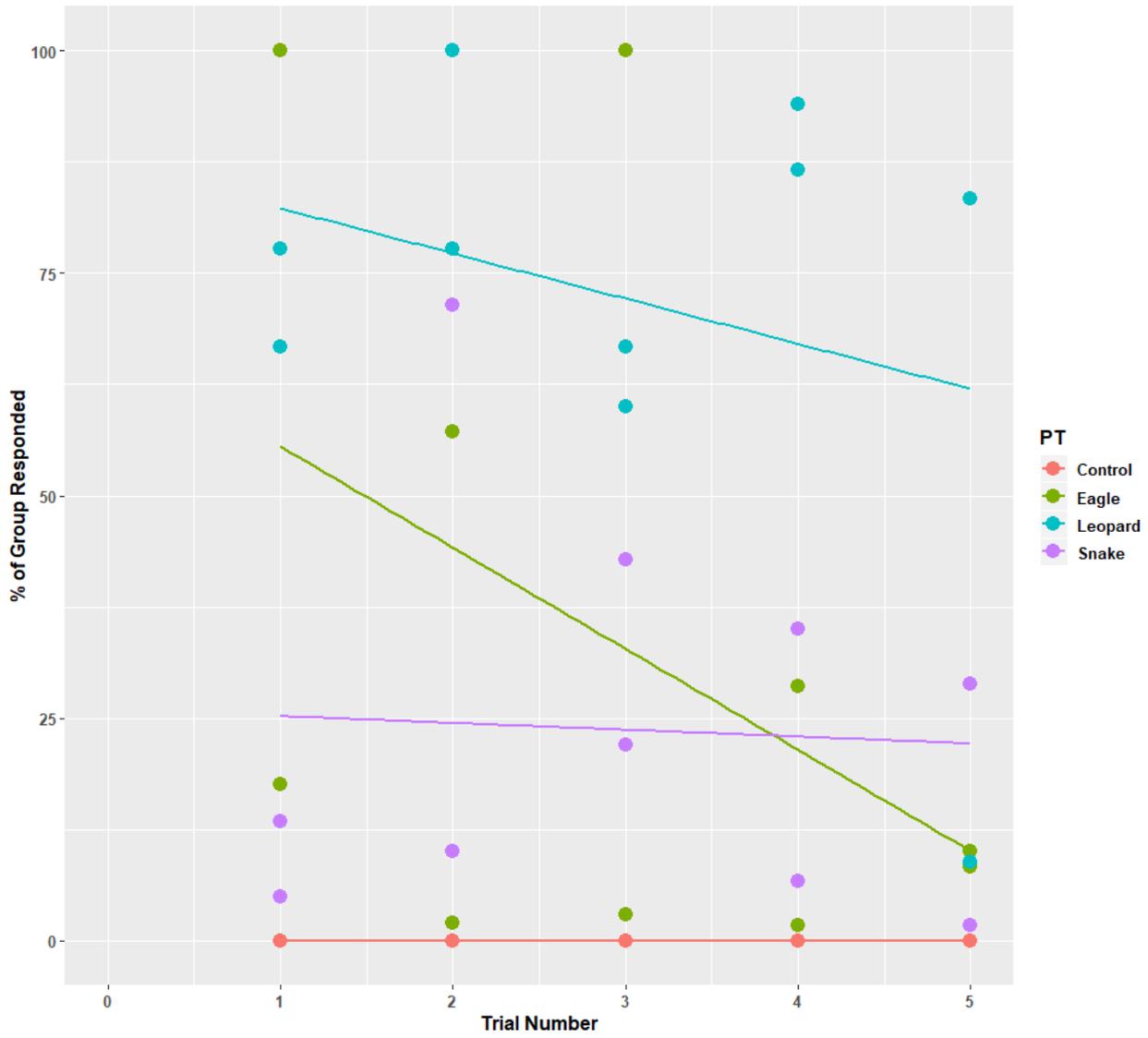


Fig S4 Raw data points for the percent of the group that responded during trials and trial number on each predator type within each group

Analysis Methods Continued:

While we knew before running these trials that samangos would react with antipredator responses to the predator models given an unlimited amount of time, we did not have prior knowledge about the predictors' effect on the probability of collective response in 90s trials. Thus, we determined that setting the prior distribution for β_0 and β_i as Cauchy or half student-t(5, 0, 2.5) would be justifiable as 'weakly informative' following Gelman et al. (2008) and is appropriate when researchers do not have extensive data from previous studies. Weakly informative priors are helpful for regularizing parameter estimates, and shrinkage is greater when power is low, which serves as a check on potentially noisy, small-sample data (Gelman et al, 2008; Lemoine et al. 2016; Lemoine, 2019). This prior assumes most effects are unlikely to be far from zero which we believed was more biologically plausible than uninformative, flat priors with wide variances, which have been shown to bias estimates away from zero when sample size is small (Van Dongen, 2006).

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R Code:

```
library(brms)
library(readxl)
PredModData <- read_excel("C:/Users/l/Documents/PredModData.xlsx")
m1priors <- c(prior(student_t(5,0,2.5), class = "Intercept"), prior(student_t(5, 0,2.5), class = "b"))
mod = brms::brm(Num.Res | trials(Subgroup.size) ~ PT*(Coh + PropLook) + Hab.Vis + NFR +PTrialNum
+ Group, data = PredModData, family = 'binomial',
  prior=m1priors, iter =450000, warmup = 425000, chains = 5,
  thin = 1, cores = 5, control = list(adapt_delta = 0.99, max_treedepth=15))
```

> summary(mod)

Family: binomial

Links: mu = logit

Formula: Num.Res | trials(Subgroup.size) ~ PT * (Coh + PropLook) + Hab.Vis + NFR + PTrialNum + Group

Data: PredModData (Number of observations: 40)

Samples: 5 chains, each with iter = 450000; warmup = 425000; thin = 1;

total post-warmup samples = 125000

Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ES
Intercept	-5.46	1.37	-8.39	-2.99	1.00	45425	5181
PTEagle	1.93	1.38	-0.57	4.88	1.00	46214	5490
PTLeopard	4.21	1.37	1.74	7.15	1.00	45700	5218
PTSnake	2.00	1.39	-0.52	4.95	1.00	47510	5446
Coh	-1.28	0.98	-3.42	0.46	1.00	38153	4260
PropLook	-0.69	1.22	-3.19	1.63	1.00	48825	5823
Hab.Vis	2.73	0.80	1.18	4.30	1.00	97204	9062
NFR	0.05	0.02	-0.00	0.10	1.00	119701	8560
PTrialNum	-0.11	0.06	-0.22	-0.00	1.00	122474	8989
GroupHouse	0.11	0.19	-0.26	0.47	1.00	102406	9343
PTEagle:Coh	2.76	1.00	1.00	4.91	1.00	38480	4357
PTLeopard:Coh	1.51	0.98	-0.22	3.66	1.00	38454	4311
PTSnake:Coh	1.99	0.99	0.25	4.14	1.00	38200	4265

PTEagle:PropLook	1.28	1.28	-1.14	3.90	1.00	52021	6152
PTLeopard:PropLook	2.54	1.33	0.01	5.27	1.00	52870	6332
PTSnake:PropLook	0.32	1.31	-2.19	2.96	1.00	53271	6439

Samples were drawn using sampling(NUTS). For each parameter, Bulk_ESS and Tail_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

```
library(BayestestR)
```

```
pd <- p_direction(mod, method="direct")
```

```
pd
```

```
parameter      | pd
-----
Intercept      | 100.00%
PTEagle        | 92.92%
PTLeopard      | 99.98%
PTSnake        | 93.49%
Coh            | 91.86%
PropLook       | 71.01%
Hab.Vis        | 99.97%
NFR            | 97.26%
PTrialNum      | 97.55%
GroupHouse     | 72.24%
PTEagle.Coh    | 99.92%
PTLeopard.Coh  | 95.46%
PTSnake.Coh    | 98.97%
PTEagle.PropLook | 84.56%
PTLeopard.PropLook | 97.53%
PTSnake.PropLook | 59.
```