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MULTIPLE ANTI-PREDATORY BEHAVIORS IN RED-TAILED MONKEY (*CERCOPITHECUS ASCANIUS*) GROUPS REVEAL DISTINCT LANDSCAPES OF FEAR

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ABSTRACT

Foraging opportunity and predation risk can act as opposing influences on an animal's habitat use. This opposition can be addressed with a "landscape of fear" (LOF), where models predict the spatial distribution of predators or perceived predator presence using prey responses. LOF models are often generated using a single behavioral metric. Here, I expanded on the concept of LOF by measuring three anti-predatory behaviors– aggregation, alarm calling, and vigilance– in two groups of red-tailed monkeys (*Cercopithecus ascanius*). I also looked at the relationship of each type of anti-predatory behavior to habitat characteristics, age/sex class, seasonality, and their relationship to the other types of behaviors. I sought to understand possible factors that affect the expression of different types of anti-predatory behavior at the group level. I constructed LOFs from each of the behaviors to explore differences in the regions of perceived predation risk. I found relationships of anti-predatory behaviors to vegetation coverage, group membership, and seasonality to differ between groups and behavior type. The LOF models generated for each behavior and group mapped non-overlapping regions of perceived predation risk distinct to each anti-predatory behavior. Differences in the number of identified regions, the spatial location of these regions, and the size of these regions produced unique perceived predation risk landscapes for each behavior. This in addition to the different relationships to vegetation, age/sex class, and seasonality inform us of a nuanced perception of risk by prey that may call for multiple behavioral response metrics in future LOF studies.

INTRODUCTION

Predation exerts a strong selective pressure on prey species' morphology, physiology, and behavior (Bidner, 2004, Lima, 1998, Schmitz, 2017). Although lethal effects of predation may drive the evolution of various traits, non-lethal effects can also have substantial impact on prey animals (Brown et al., 1999, Lima, 1998, Peacor et al., 2007, Peckarsky et al., 2008). These include associated costs of a prey's response to predator presence, such as the foraging costs associated with anti-predatory behaviors like vigilance (Lima, 1998). Prey species change their space use as they balance the trade-off between predation risk and foraging opportunities (Brown, 1988, Stephens, 2018). 'Landscape of fear' (LOF) models allow researchers to measure how space use is specifically informed by the prey's perception of predator presence (Brown & Kotler, 2004, Campos & Fedigan, 2014, Laundre et al., 2001, Laundre et al., 2010, Lima & Dill, 1990). This concept relies upon the hypothesis that there are safe and risky areas of an animal's home range that can be mapped by measuring space use and anti-predator response (Laundre et al., 2001, Laundre et al., 2010, Prugh et al., 2019).

Measuring perceived predation risk by examining a prey animal's responses can tell us more about the prey's umwelt than looking at where a predator occurs. Although many studies that focus upon predation risk use predator movement data to directly assess it, sufficient data on predators can be difficult to gather in many systems (Bleicher, 2017, Lima, 1998). One can also use anti-predatory behavior of the prey species to infer their perception of the physical landscape, which can be more informative of the prey itself (Brown & Kotler, 2004, Lima & Dill, 1990). Prey species perceive predators using visual, auditory, and olfactory cues, which are not always identifiable by human observers (Moll, 2017). Indirect cues, for example how open or closed a habitat is, can also influence prey vulnerability (Verdolin, 2006). The information perceived by prey is often partial, imperfect, or context-specific (Blumstein et al., 2004, Bouskila & Blumstein, 1992; Prugh et al., 2019). Therefore, anti-predatory responses are informative metrics for studying prey perception of predation risk.

Prey can respond to predation in multiple ways, therefore providing multiple avenues to measure perceived predation risk (Bleicher, 2017, Prugh et al., 2019). One such measure is known as "giving-up densities" (GUD). In this experimental approach, identical food patches are placed across a prey animal's range and the amount of food the prey animal leaves or "gives up" is used as a measure as its perceived risk: the more it gives up, the higher the risk is assumed to be in that patch (Brown, 1988, Brown & Kotler, 2004). This type of experimentation provides for direct measurement of foraging costs of predation risk. However, it is impractical in systems where the environment is heterogenous, where group foraging diminishes the perceived predation risk that was intended to be measured, and where experimentation is discouraged (Bedoya-Perez et al., 2013, Brown, 1988).

The use of anti-predatory behaviors, such as alarm calling or vigilance, as metrics of perceived predation risk offers a valuable solution to LOF studies on constrained systems (Isbell, 1994, Treves, 2000). Vigilance behavior, which can be measured naturalistically, can be used by prey in concert with giving up food patches to decrease perceived predation risk, therefore vigilance can measure perceived predation risk like GUDs (Brown, 1999). However, anti-predatory behaviors can be context-dependent, influenced by predator types, habitat characteristics, sex and age of the individual, group demography, and conspecific behaviors (Campos & Fedigan, 2014, Hirsch, 2002, Isbell, 1994, Laundre et al., 2010, Moll et al., 2017, Seyfarth et al., 1980, Treves, 2000, Verdolin 2006,).

The characteristics of a prey animal's habitat may affect its perception of predation risk and its response. For example, Jaffe and Isbell (2009) found that arboreal primates are more vulnerable to predation in open forest or at forest edges where they are more exposed and visible. Meta-analysis of GUD experiments demonstrated that habitat characteristics predicted the same effect of predation risk as studies using direct predator observations and odors (Verdolin, 2005). Lastly, hunting by predators can be concentrated in different habitat types (Balme et al., 2007, David & Zuberbühler, 2005).

Many prey animals express multiple anti-predatory behaviors that can influence one another (Lima, 1998, Treves, 2000) which would complicate LOF studies that use only one prey response to construct their models. Larger group sizes are thought to decrease predation risk by increasing group defense while diluting the risk to each individual, but this is not consistently observed in all taxa (Hamilton, 1971, Treves, 2000). Many studies have instead measured distances between aggregated individuals, suggesting it as a characteristic of safety perceivable by the prey (Hirsch, 2002). Many studies have found that closer proximities to conspecifics decrease vigilance behavior, thus replicating the expected trend of group-size (Cowlishaw, 1988, Pöysä, 1994, Robinson, 1981, Treves, 1998). Vigilance is hypothesized to decrease the need of other anti-predatory responses, like giving up densities (Brown, 1999). Vigilance can also increase following alarm calls (Blumstein et al., 2004, Campos & Fedigan, 2014), which are produced when a predator is perceived (Arnold et al., 2007). Findings that suggest that the occurrence of one anti-predatory behavior could diminish another question whether a single anti-predatory behavior would account for each moment of perceived predation risk.

In the following study, I wanted to understand how anti-predatory behaviors were impacted by the habitat and the behaviors of conspecifics. I also measured the relationship to two factors of lesser interest: age/sex class and seasonality. Males may alarm call more and vary less in their distance to aggregations (Cheney and Wrangham, 1987, Treves, 1998). The breeding/non-breeding season and rainy/dry season may further influence anti-predatory behaviors, predator occurrence, or movement due to seasonal availability of resources (Lima, 1998, Reyna-Hurtado, 2018). The second major goal of this study was to explore the LOFs constructed from each anti-predatory behavior, visualizing how different anti-predatory behaviors map similar or distinct regions of perceived predation risk. To accomplish this, I focused on red-tailed monkeys (*Cercopithecus ascanius*) in Western Tanzania.

C. ascanius are a socially gregarious forest guenon that expresses three types of anti-predatory behaviors: alarm calling, vigilance, and aggregation (Isbell, 1994, Nilsson, 2010, Treves, 2000). I measured each of these behaviors in group scans (Bleicher, 2017) in two different groups within the Issa valley, western Tanzania. Both anti-predatory vigilance and alarm calling have been used to construct primate LOFs (Campos & Fedigan, 2014, Hirsch, 2002, Willems & Hill, 2009). Aggregation, measured by proximity of conspecifics and not overall group size, has been discussed in relation to other anti-predatory behaviors and perceived predation risk (Cowlishaw, 1988, Hirsch, 2002, Pöysä, 1994, Robinson, 1981, Treves, 2000), but has yet to be integrated into LOF models. Measuring behavior and constructing LOFs in two different groups allowed me to identify group-specific relationships from population-wide trends.

I hypothesized 1) that the behaviors would have unique relationships to environmental and group characteristics as well as the other anti-predatory behaviors because of context-dependent conditions that promote specific behavioral responses and 2) that the anti-predatory behaviors of red-tails would map regions of increased risk within their home-range because red-tails inhabit a home range with safe and risky regions (*landscape of fear hypothesis*: Laundre et al., 2001, Laundre et al., 2010). I tested four predictions under the first hypothesis: 1) that both red-tailed monkey groups would exhibit more anti-predatory behavior in open vegetation; 2) that individuals would show increased vigilance after an alarm call; 3) that there would be less vigilant individuals during closer group aggregations; 4) that more alarm calls will be produced by males as opposed to females. For the second hypothesis, I constructed three LOFs for each anti-predatory behavior to show risky and safe regions and then further explore how the anti-predatory behaviors compare.

METHODS

Study Site

I studied two troops of *C. ascanius* groups in the Issa Valley, Tanzania that have been habituated since 2012 (McLester et al., 2019). The Issa valley lies approximately 100 km east of Lake Tanganyika, inland between Gombe Stream National Park and the Mahale Mountains National Park. Elevation ranges from 1050 to 1800 meters. The Issa valley consists of a variety of vegetation types including miombo woodland, swamp, open and closed riparian forest, thicket, and grassland. The area experiences an average temperature from 11 to 35 °C with a dry season from May-September characterized by less than 100 mm of rainfall per month and a rainy season from October-April (Piel et al., 2014).

Study subjects

The two groups of red-tails, K1 and K2, were comprised of 35 and 15 individuals, respectively. Each group consisted of a single adult male and multiple adult females, sub-adults, juveniles, and infants. Within the study site there is known predation on *C. ascanius* by leopards (*Panthera pardus)* (McLester et al., 2018), chimpanzees (Piel & Stewart, unpublished data; Takahata et al., 1984), crowned-hawk eagles (*Stephanoaetus coronatus*) (Mitani et al., 2001), and possibly snakes (observed at another *C. ascanius* site: Forester, 2008).

Data Collection

I collected data during both the rainy (November-March) and the dry season (April-October) from July 2018 to December 2019. I alternated following K1 and K2 every two weeks. To maintain data collection during this period, field assistants from GMERC also collected data. Although observers changed across the study period, I found that the spread of the observations was similar for the two consistently collected response metrics across the data collection period (Supplementary Figure S1). When under observation, the group was followed from sunrise (~7:00), around the point they left their sleeping site, until when they chose a sleeping site (~19:00).

I collected data on three different anti-predatory behaviors: alarm calling, vigilance, and aggregation. Alarm calls were identifiable by observers and recorded using instantaneous focal sampling. The alarm call types were distinguished by demographic-specific alarm call types (male and female-subadult-juvenile types), however red-tailed monkeys are not known to produce predator-specific alarm calls (Nilson, 2010).

We used 10-minute interval group scan sampling to measure vigilance behavior. During each observation period the total number of individuals being vigilant was noted. Vigilance was defined as an individual looking at an area either above or below its line of sight without another individual (Allan & Hill, 2018, Treves, 2000). This definition allowed us to differentiate between two kinds of vigilance, social monitoring and vigilance of the surroundings presumed to be monitoring for predators (Hirsch, 2002). In addition to the total number of individuals being vigilant, we also recorded the total number of individuals visible to the observer.

To measure aggregation behavior we used a nearest neighbor protocol that was recorded at the same time as the group scan. We selected a random individual for focal observations and classified the distance to its four nearest neighbors in one of four distance bins (0-5 m, 5-10 m, 10-15 m, and greater than 15 m). If four neighbors were not all visible, we recorded a value of greater than 15 m for those out of sight. As individuals in the group were not identifiable and to avoid focalling the same individual over consecutive periods, we changed age/sex classes with each scan. We were able to identify adult males, subadults/juveniles, adult females, and mothers with infants.

For each data point, the latitude, longitude, elevation, and location accuracy were collected using Samsung tablets (Samsung, Galaxy Tab A) and hand-held Global Positioning System (GPS) units (Garmin Rino 2-way GPS radios). GPS points collected on K1 and K2 had mean accuracies of 11.2 m and 10.0 m respectively (median: 6.5 m and 8 m). The observers also identified the vegetation type in which the group was present, classifying the group in closed forest, medium forest, open riparian forest, miombo (woodland), thicket, or edge. When group members were spread across different vegetation types they were coded as either medium forest (individuals in both open and closed forest) or edge (individuals in both open forest and miombo).

To compare each anti-predatory behavior, we matched the alarm calling behaviors to the group scan observations. Scans were recorded every 10 minutes, but sometimes took longer to complete if many monkeys were visible. To account for this I paired alarm calls to the closest group scan following the alarm call within 12 minutes. This was confirmed to only pair alarm calls to the scan after a call occurred and not before. Any alarm call that could not be paired was removed from analysis.

Predicting the frequency of anti-predatory behaviors in the group

Alarm calls were coded as binary; vigilance behavior was recorded as counts of visible individuals exhibiting vigilance behavior. Lastly, aggregating was quantified as the average distance to four nearest neighbors, with smaller values indicating closer aggregation. I conducted all analyses in the statistical program R v.1.0.153 (R Core Team, 2014). I generated generalized linear models (GLM) using the 'lme4' package (Bates et al., 2015). Tukey's HSD post-hoc analysis was completed on the categorical variables, habitat type and demography using the 'multcomp' package (Hothorn et al., 2008). For all models I included season (rainy/dry), breeding season (yes/no), vegetation type, and number of visible individuals as fixed effects. In the aggregation model, we included the age/sex of the focal individual. Since individuals in both red-tail groups were not individually identifiable, age/sex was the best metric to account for the potential of pseudoreplication. Lastly, to compare the demographic of callers in an unidentifiable group, I first averaged the mean number of visible individuals in each group. Then, I subtracted one from each average to account for the single male in the group. I then divided the female/subadult/juvenile calls by this conservative measure of group-size to compare calls per capita.

Perceived predation risk landscapes of fear

To create LOF models using three different behavioral metrics of perceived predation risk, I calculated the relative risk of each anti-predatory behavior in each region. Relative risk models have been applied to previous landscape of fear studies and maps the ratio of presence to absence of the behavior (Campos & Fedigan, 2014, Davies et al., 2017). I dichotomized each behavior into presence and absence to calculate the probability of its occurrence.

For the alarm calling LOF model I was not interested in the relationship to other anti-predatory behaviors collected during scans and therefore used all data available(not only those that could be paired with group scans). All group scans without an alarm call were scored as absence while all observations of alarm calls were coded as presence. For vigilance, each scan was contained in a row that had the GPS point of the observer. To account for the number of vigilant and non-vigilant monkeys, each row, and thus GPS point, was replicated by the number of visible monkeys during the scan. For X number vigilant monkeys during the scan, there were X number of coded rows for vigilance or presence. The remaining rows left un-coded were equal to the number of non-vigilant individuals or absence. To code aggregation, I defined neighbors within 10 meters as evidence of anti-predatory aggregation (presence) and neighbors outside of that range as controls of absence of aggregation behavior (see Supplementary Materials for justification of 10 m cutoff). Using the 'sparr' package in R, we constructed asymptomatic tolerance contours using bootstrapping to define the limits of the polygons (Davies et al., 2017). Boundaries for these models were defined as 95% kernel density estimations of home range, using the ‘adehabitatHR’ package in R (Calenge, 2006). One caveat of the relative risk models is that area of regions are unable to be calculated or put into a spatial regression model, but contours were overlapped in attempt to aid in comparison.

RESULTS

Predicting the frequency of anti-predatory behaviors in the group

Monkeys of both groups were the most vigilant in edge vegetation and the least vigilant in closed forest vegetation (Figure 1 & Table 1). In K1, only closed forest significantly differed from edge vegetation and edge from open forest. In K2, closed forest monkeys were less vigilant than in other vegetation types and more vigilant at the forest edge compared to the open forest (Figure 1 & Table 2). Vegetation types differentially predicted aggregation behavior as well (Table 3 & 4). Monkeys were most closely aggregated in medium and open forest (Figure 2). Vegetation type did not predict alarm calling behavior (Table 5 & 6).

There were more alarm calls by males compared to calls by females, subadults, or juveniles (*K1*: males = 34 calls/ind., female/sub-adult/juv. = 9.63 calls/ind.; *K2*: males = 26 calls/ind., female/sub-adult/juv. = 4.05 calls/ind.). An animal’s age/sex also predicted aggregation behavior (Table 3 & 4; Figure 3). Mothers with infants and subadults had the closest aggregations in both K1 and K2. In K2, juveniles also had the closest aggregations and did not significantly differ from subadults and mothers with infants. In K1 and K2 adult males had the farthest average distance to neighbors. This was not significantly different from females in K2 or juveniles in K1.

There was significantly more vigilance observed during the non-breeding season and the dry season for K2 (Table 2). There were significantly more observations of closer aggregations during the breeding season and the rainy season in K2 (Table 4). Season did not affect alarm calling behavior (Table 5 & 6) and no relationship in K1.

More individuals visible predicted more individuals observed doing vigilance behavior (Table 1 & 2). Closer aggregations were observed when more individuals were visible (Table 3 & 4). There was no relationship between the number of individuals visible and alarm calling behavior (Table 5 & 6).

Only in K1 were there significant relationships between anti-predatory behaviors. Vigilance and average distance to nearest neighbor were negatively correlated, as closer aggregations correlated with more vigilance behavior (Table 1 & 3; Figure 4). Closer aggregations also correlated with a higher probability alarm call production in K1 (Table 3 & 5; Figure 5). In K2, the relationship between vigilance behavior and alarm calling was not significant, but had a p-value less than 0.1 (Table 2 & 4). No other relationships were significant.

Perceived predation risk landscapes of fear

A 95% kernel density estimation (kde) of the home range of both groups was constructed (Figure 6). There was overlap between the two groups' home ranges. The area of the home range of the larger group, K1, is approximately 9.8 times that of the smaller group, K2 (9.85, calculated form 95% isopleth polygons). Using the kde models as boundaries, relative risk models were created for each behavior (Figure 7). I observed multiple regions of perceived predation risk throughout the monkeys' home ranges. The amount of contours, or regions of significantly increased risk, reflect the amount of distinct regions of increased perceived predation risk. Looking at the more conservative alpha level of 0.01, I compared the number of distinct regions identified by each behavior. There were the fewest contours in the alarm calling behavior models, with two contours in the K1 model and four in K2. Vigilance models had five contours for each group. Finally, aggregation produced the most distinct contours with seven in K1 and six in K2. In K1, there are two locations that overlap at the 0.01 level in all three models (Figure 8a).There was only one region of overlap between only vigilance and alarm calling, one region between vigilance and aggregation, and five regions between alarm calling and aggregation. In K2, there is only one region of overlap for all three behaviors (Figure 8b). There are three regions of overlap between vigilance and alarm calling models, two regions between alarm calling and aggregation, and one region between aggregation and vigilance. All models have contours or parts of contours that do not overlap. These models suggest that each behavior maps distinct regions of perceived predation risk, differing in the spatial location, the size, and the number of regions of relative risk.

DISCUSSION

The expression of anti-predatory behaviors in both red-tailed groups was found to be dependent on environmental characteristics, the group, and home range. I found that veg type was associated with anti-predatory behaviors in both K1 and K2, with monkeys being more vigilant and closely aggregated in open veg types. Additionally, in K1, anti-predatory behaviors were found to be associated with one another, e.g. aggregation and vigilance. When alarm calls occurred, the group was also more closely aggregated. The LOF models had distinct contours depending on the anti-predatory behavior metric used. No single behavioral response overlapped in all, or even most, of the contours of the LOF models, thus there is no evidence that one behavior reflects all of the prey's perceived predation risk. Considering past metrics used to construct primate LOFs, studies tend to use alarm calling the most, vigilance second, and aggregation the least as there had yet to be an LOF model constructed with aggregation data. Benefits, concerns, and background for each of these behaviors will address how they are all ultimately valuable to understand perceived predation risk in full.

Anti-predatory behavior may be influenced by other anti-predatory behaviors expressed in the group at any one time, e.g. a scripted or sequence of behavior. I found closer aggregations to predict greater vigilance and alarm calling, which would suggest that closer aggregations occur in concordance with the other two behaviors. This is further supported by the overlap of three of the six regions of risk in the aggregation model to other behaviors. However, closer aggregations are also used in regions where other prey responses such as calling and vigilance are not used. One possibility is that aggregation did decrease the need of other anti-predatory behaviors, as predicted in past research (Cowlishaw, 1988, Hamilton, 1971, Pöysä, 1994, Robinson, 1981, Treves, 2000), up until moments where there were stronger or more direct cues of predation. Finally, it is possible that alarm calls will drive the group to move from the region, preventing further anti-predatory behavior from being produced in that location (Seyfarth et al., 1980, Zuberbühler et al*.,* 1997). If the use of anti-predatory behaviors by the group influences the expression of other behaviors, then any LOF model that uses only one behavioral response is likely to overlook areas of perceived predation risk in animals' home ranges.

Anti-predatory behaviors may be more effective or less costly against different predator types (Isbell, 1994). When introduced to different predator-specific alarm calls, vervet monkeys increased vigilance after raptor or snake alarm calls and fled into the trees following leopard alarm calls (Seyfarth et al.,1980). If prey exbibit predator-specific responses, this could explain why each behavior failed to map many of the same regions, as they reflect the perception of different predators. Additionally, if predators are influenced by the habitat structure, then LOF models could have an interaction between predator-types and habitat types. The two major predators of *C. ascanius*, leopards and crowned-hawk eagles, could hunt in different habitat characteristics given the arboreal and terrestrial differences (Eason, 1989, Isbell, 1994). Observation of a leopard predation event on *C. ascanius* in the Issa Valley cited that the leopard originated from the miombo woodland habitat (McLester et al., 2018). Eason (1989) suggests that Harpy eagles, a closely related raptor to crowned-hawk eagles, also hunt in open habitat types. Both offer support for a preference by predators for the same open habitats. In order to show this in the Issa Valley, more observations of predator-prey interactions are needed, albeit difficult to acquire.

I found that vegetation type had different relationships to each anti-predatory behavior, which could consequently be driving the LOF differences between each behavior. *C. ascanius* groups were more vigilant in open habitat types consistent with past findings on *C. ascanius* in Kakamenga (Cords, 1990). In contrast to vigilance, monkeys did not produce more alarm calls specific to any habitat type. Open habitat types increase visibility and thus prey's vulnerability, however it may also influence the effectiveness of vigilance behavior (Isbell, 1994) as monkeys have further sight-lines in locations with less foliage (Jaffe & Isbell, 2009). The spacing of trees could also shape the proximity that individuals can have to one another. The greater distance between trees in the miombo could drive monkeys to aggregate farther apart in the miombo woodland compared to medium forest, despite it being the most open habitat type. If the structure of the habitat influences the ability to aggregate closer, this may also impact alarm calling and vigilance behaviors that are influenced by closer aggregations. Lastly, the miombo woodland has canopy heights of about 15m or lower (Frost, 1996) which could further impact the safety of prey under attack from terrestrial predators. More data would be then useful to construct non-overlapping habitat-type contours within the home-range, allowing for such visualizations.

Next, the structure of the social group may drive which behaviors are expressed. Alarm calls can serve two functions– either to inform the group of danger or expose the predator (Zuberbühler et al., 1997, Zuberbühler et al., 2009). The relationship between proximity to conspecifics and alarm calling that I observed in K1 suggests that alarm calling in *C. ascanius* is influenced by the presence of conspecifics. The relationship to aggregation proximity could be driven by a proximity to kin and future mates of the caller, who are the suggested beneficiaries of alarm calling (Charnov & Krebs, 1975, Sherman, 1985). However, this relationship was not present in the smaller (K2) group. A smaller group size could decrease the benefit of calling, as the group contains fewer individuals from which an alarm call would benefit. It is possible as well that the smaller group would have fewer individual that could be related or fewer possible mates. The two groups recently split and whether K2 has many closely related individuals compared to the larger group is unknown. I would hypothesize that K2 consists of more distantly related individuals. Genetic analyses could easily confirm this.

A final explanation for the distinctions seen in each LOF model is that they are measuring responses to different stages of risk perception. Aggregation and vigilance serve to detect risk when prey perceive cues of vulnerability, such as open vegetation (Isbell 1994, Makin et al., 2012). While individuals may produce alarm calls once they detect a predator (Arnold et al., 2007), vigilance and aggregation may act as preventative measures (Treves, 2000). This idea is supported by the finding that open vegetation correlates with increased vigilance and closer aggregations, but had no relationship with alarm calling. Alarm calling may measure the most urgent situations of predation perception given the high risk it incurs on callers (Charnov &

Krebs, 1975). In comparison to the other behaviors, alarm calling may be highly dependent on the presence of more direct cues of predators. However, it is important to note that alarm calls in primate taxa can be unreliable, produced in situations of no predator occurrences (Blumstein et al., 2004, Cheney & Seyfarth, 1988). Alarm calls may also be dishonest or ignored by the rest of the group (Cheney & Seyfarth, 1988), which would prevent anti-predatory response by conspecifics, limit the density of alarm calls, and shrink the overlap between response metrics.

Although this was not a major focus of this study, age/sex class biases that affect the expression of anti-predatory behavior would further threaten the use of single response metrics for predator perception. Similar to my findings, Cheney and Wrangham (1987) concluded that more males alarm call than females, even in single-male groups. One explanation could be a sex difference in mortality by predators between males and females, as observed in some of the monkey species of Kibale (Struthsaker & Leakey, 1990). Males also stand to benefit the most from alarm calls as they have more potential kin or mates in single-male multi-female groups. LOF studies solely measuring the alarm calls as a metric for perceived predation risk may further skew their LOFs in favor of the male's perception instead of the entire group.

Vigilance has been previously used in primates to create LOF models (Campos & Fedigan, 2014) and studied in relation to GUDs and alarm calling (Brown, 1999, Seyfarth et al., 1980, Willems & Hill, 2009). Vigilance can take two forms, anti-predatory vigilance and social monitoring (Hirsch, 2002, Treves, 2000). Although we restricted vigilance in our definition to exclude glancing at another individual, there is still the possibility that some vigilance behaviors observed were attempting to serve a social purpose (Hirsch, 2002). However, this social monitoring can still aid to detect predators when individuals monitor others that are being vigilant (Treves, 2000). One benefit of group-living is the improved detection of predators, which assumes that added individuals in a group will increase the number of individuals being vigilant (Pays et al., 2007, Pulliam, 1973). Although group-size and proximity to individuals correlates to vigilance, our vigilance LOF models show regions of increased perceived predation risk are not only relative to the group size; if they were there would be no areas of increased risk. Inconsistencies in the literature on vigilance challenge how it relates to group size, neighbor proximity, and group demography (Allan & Hill, 2018). Concerns with vigilance measuring social monitoring or whether it produces enough variance to create contours reflective of all perceived predation risk would add value to the use of multiple behaviors.

The measurement of aggregation behavior may be influenced by the structure of the environment and the group. I observed that groups were less aggregated in more open habitat types, which could be a result of the farther more widely distributed food sources in open habitat types. The inability to identify individuals when measuring aggregation threatens pseudoreplication of focals (see methods for precautions taken). Looking at the relationship between aggregation and age/sex class, I also noted that closer aggregations occurred in mothers with infants, which was biased by the infant included as the first neighbor. Any future work using aggregation would exclude the infant as a neighbor given its dependence on the mother. It is important to note that aggregation metrics would also measure individuals that are proximate for non-predatory reasons, such as grooming or mating, which is an inevitable downside of measuring proximity. However, given its relationship to other anti-predatory behaviors and its potential role in diluting risk (Cowlishaw, 1988, Hamilton, 1971, Hirsch, 2002, Pöysä, 1994, Robinson, 1981, Treves, 2000), I argue that even during grooming or mating proximity can combat predation risk. Although, this LOF should not stand alone to demonstrate perceived predation risk landscapes, along with other behavioral response metrics it provides insight into the relationship that individual proximity within the group can have on the group's relative perceived risk.

Lastly, all models, both linear and spatial, differed between groups K1 and K2. A number of relationships were only seen in one group. K1 showed significant relationships between the anti-predatory behaviors when K2 did not. Seasonality was only significant in K2. These differences could be due to group kinship, size, or home range. If the differences are driven by relatedness, I may expect alarm calling to be significantly related to aggregation in K2 when relatedness of the caller to others in the group is accounted for as a random effect. Group size in *C. ascanius* has been shown to not affect vigilance behavior (Treves 1999a, Treves 1999b). Yet in all three LOF models, including vigilance models, regions where K1 and K2 overlap in their home range do not overlap in their contours. A possible effect, like group size, would be measurable using a multi-group study possibly across populations. Overall, although the two groups provide further insight into the context-specific nature of LOF models and anti-predatory response, no strong comparisons can be made with such a vast number of possible factors driving any of the differences.

In summary, red-tailed monkey anti-predatory behavior varies with vegetation, age/sex class, and home range, and drives variability in LOFs. I offer multiple alternative explanations for the differences in perceived predation risk contours produced in each LOF model. These differences suggest that each behavioral response informs a different aspect of perceived predation risk. Because primates are social, anti-predatory behavior may respond to not just the physical environment – as I showed here – but also the social environment, with individuals responding to each other's behavior. Future LOF studies would benefit from using multiple anti-predatory response metrics and especially across multiple groups to help identify causative influences on these key behaviors.

TABLES

Table 1: Results from GLM predicting vigilance bouts for group K1. Asterisks indicate significance at the following alpha levels: ‘***’ 0.001; ‘**’ 0.01; ‘*’ 0.05.

Fixed Effects	**Estimate**	**LR Chisq**	**Df**	**P-value**
Average distance to nearest neighbor (m)	**-0.056906**	**20.830**	**1**	**5.019e-06 *****
Alarm calling (absence vs. presence)	0.053172	0.166	1	0.6836
Habitat Type	**-**	**26.365**	**5**	**7.581e-05 *****
Breeding Season (non-breeding vs. breeding)	0.083122	0.419	1	0.5172
Season (dry vs. rainy)	0.084552	0.484	1	0.4867
Total number of visible individuals	**0.059366**	**103.498**	**1**	**< 2.2e-16 *****

Table 2: Results from GLM predicting vigilance bouts for group K2. Asterisks indicate significance at the following alpha levels: ‘***’ 0.001; ‘**’ 0.01; ‘*’ 0.05.

Fixed Effects	**Estimate**	**LR Chisq**	**Df**	**P-value**
Average distance to nearest neighbor (m)	-0.01727	2.355	1	0.12489
Alarm calling (absence vs. presence)	0.26068	3.290	1	0.06972 .
Habitat Type	**-**	**79.778**	**4**	**< 2e-16 *****
Breeding Season (non-breeding vs. breeding)	**3.00000**	**86.967**	**1**	**< 2e-16 *****

Season (dry vs. rainy)	**-3.06339**	**91.758**	**1**	**< 2e-16 *****
Total number of visible individuals	**0.08466**	**139.246**	**1**	**< 2.2e-16 *****

Table 3: Results from GLM predicting average distance to nearest neighbor (m) for group K1. Asterisks indicate significance at the following alpha levels: '***' 0.001; '**' 0.01; '*' 0.05.

Fixed Effects	**Estimate**	**LR Chisq**	**Df**	**P-value**
Number of observed vigilance bouts	**-0.18705**	**8.466**	**1**	**0.003619 ****
Alarm calling (absence vs. presence)	**-0.91686**	**9.770**	**1**	**0.001774 ****
Habitat Type	**-**	**72.438**	**5**	**3.184e-14 *****
Breeding Season (non-breeding vs. breeding)	-0.06283	0.051	1	0.821271
Season (dry vs. rainy)	0.16127	0.385	1	0.535019
Total number of visible individuals	**-0.21180**	**240.994**	**1**	**< 2.2e-16 *****
Demographic of focal individual	**-**	**101.860**	**5**	**< 2.2e-16 *****

Table 4: Results from GLM predicting average distance to nearest neighbor (m) for group K2. Asterisks indicate significance at the following alpha levels: '***' 0.001; '**' 0.01; '*' 0.05.

Fixed Effects	**Estimate**	**LR Chisq**	**Df**	**P-value**
Number of observed vigilance bouts	0.09402	1.344	1	0.246245

Alarm calling (absence vs. presence)	0.08943	74.237	1	0.781324
Habitat Type	**-**	**72.438**	**4**	**2.889e-15 *****
Breeding Season (non-breeding vs. breeding)	**-0.84713**	**9.052**	**1**	**0.002623 ****
Season (dry vs. rainy)	**1.23006**	**17.704**	**1**	**2.581e-05 *****
Total number of visible individuals	**-0.31726**	**175.067**	**1**	**< 2.2e-16 *****
Demographic of focal individual	**-**	**98.732**	**5**	**< 2.2e-16 *****

Table 5: Results from binomial GLM predicting presence of an alarm call for group K1. Asterisks indicate significance at the following alpha levels: ‘***’ 0.001; ‘**’ 0.01; ‘*’ 0.05.

Fixed Effects	**Estimate**	**LR Chisq**	**Df**	**P-value**
Number of observed vigilance bouts	0.03768	0.1685	1	0.681429
Average distance to nearest neighbors (m)	**-0.12963**	**10.6272**	**1**	**0.001114 ****
Habitat Type	-	9.4035	5	0.094012 .
Breeding Season (non-breeding vs. breeding)	-0.21987	0.2860	1	0.592805
Season (dry vs. rainy)	0.31513	0.6924	1	0.405339
Total number of visible individuals	-0.02438	1.2745	1	0.258933

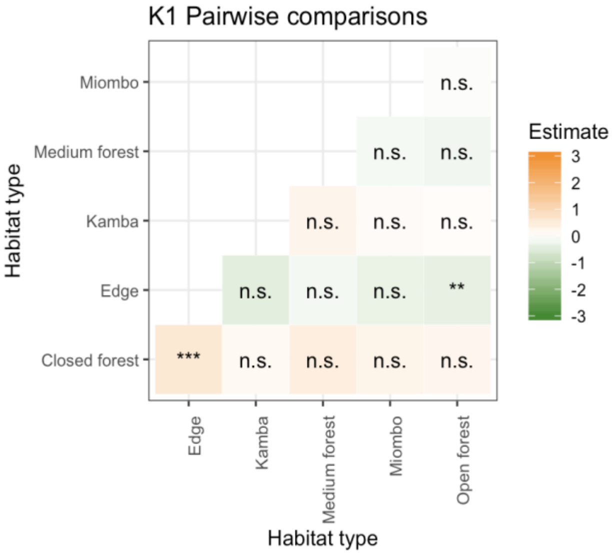
Table 6: Results from binomial GLM predicting presence of an alarm call for group K2.

Asterisks indicate significance at the following alpha levels: ‘***’ 0.001; ‘**’ 0.01; ‘*’ 0.05.

Fixed Effects	**Estimate**	**LR Chisq**	**Df**	**P-value**
Number of observed vigilance bouts	0.14887	0.31226	1	0.2058
Average distance to nearest neighbors (m)	0.02160	1.60092	1	0.5763
Habitat Type	-	2.30743	4	0.6026
Breeding Season (non-breeding vs. breeding)	-0.43884	0.98743	1	0.3204
Rainy/Dry Season (dry vs. rainy)	-0.04262	0.00998	1	0.9204
Total number of visible individuals	0.05580	2.30743	1	0.1288

FIGURES

a)



b)

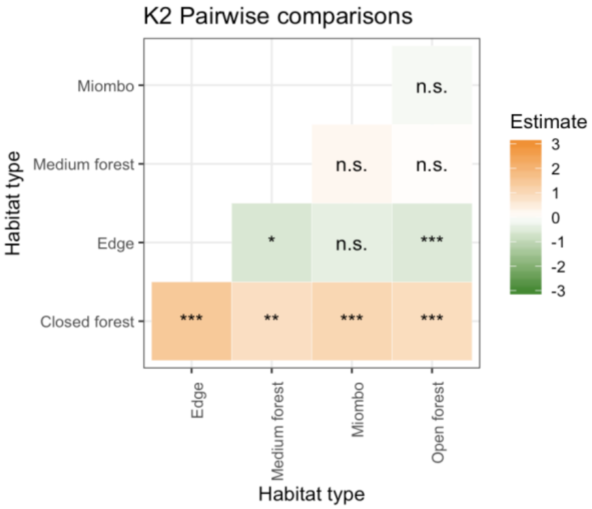
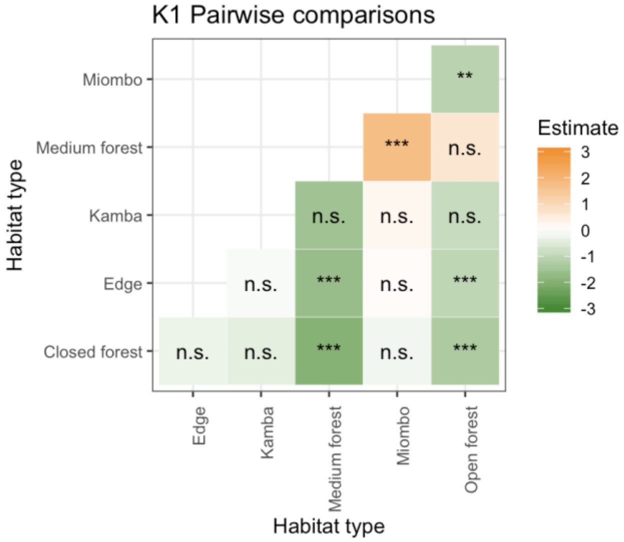


Figure 1: Heatmap demonstrating the pairwise comparisons, pulled from a Tukey's HSD, between habitat types as predictors of vigilance behavior by group a) K1 and b) K2. Estimates are shown by gradient, comparing the x-axis to the y-axis values. Text indicates p-values for the comparisons: '***' 0.001; '**' 0.01; '*' 0.05; 'n.s' > 0.05.

a)



b)

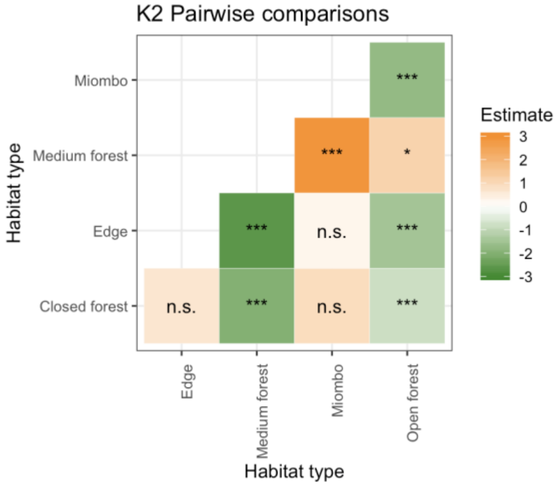


Figure 2: Heatmap demonstrating the pairwise comparisons, pulled from a Tukey's HSD, between habitat types as predictors for average distance to nearest neighbors (aggregation) by group a) K1and b) K2. Estimates are shown by gradient, comparing the x-axis to the y-axis values. Text indicates p-values for the comparisons: '***' 0.001; '**' 0.01; '*' 0.05; 'n.s' > 0.05.

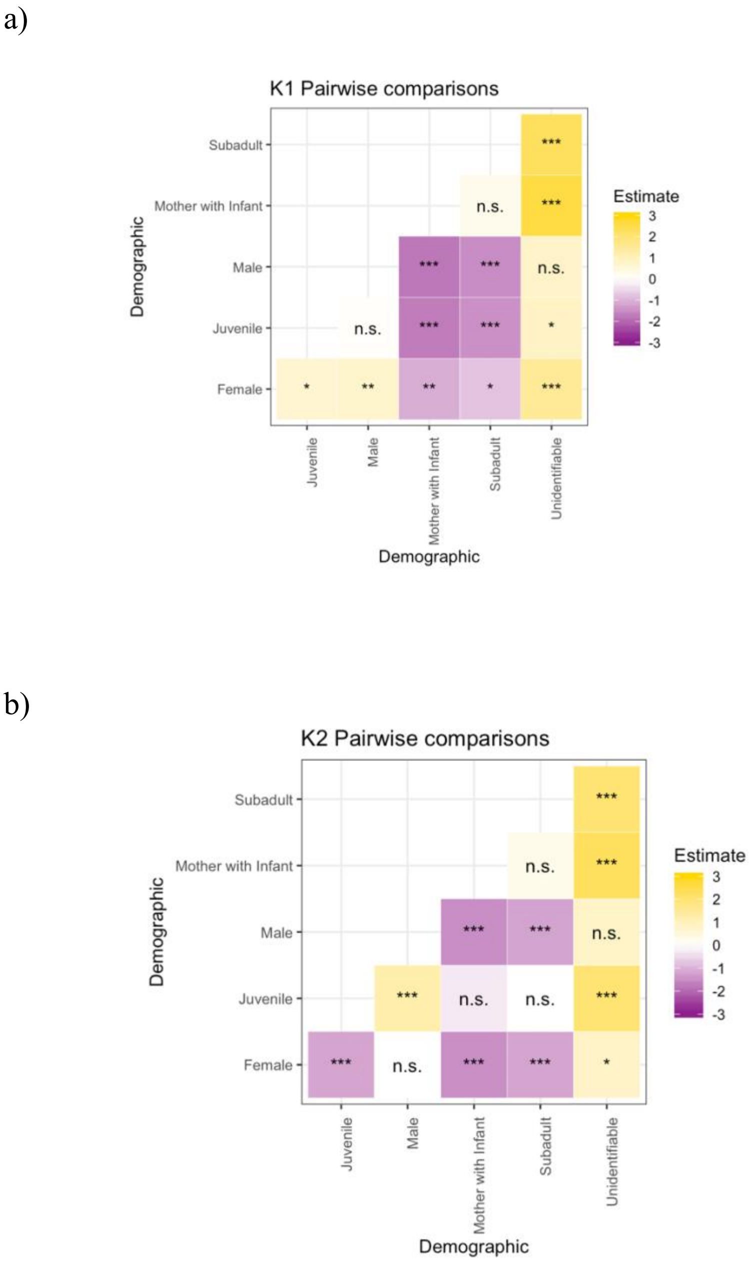


Figure 3: Heatmap demonstrating the pairwise comparisons, pulled from Tukey's HSD, between demographic categories as predictors for average distance to nearest neighbors (aggregation) behavior by group a) K1and b) K2. Comparisons shown between males as each group had a single individual. Estimates are shown by gradient, comparing the x-axis to the y-axis values. Text indicates p-values for the comparisons: '***' 0.001; '**' 0.01; '*' 0.05; 'n.s' > 0.05.

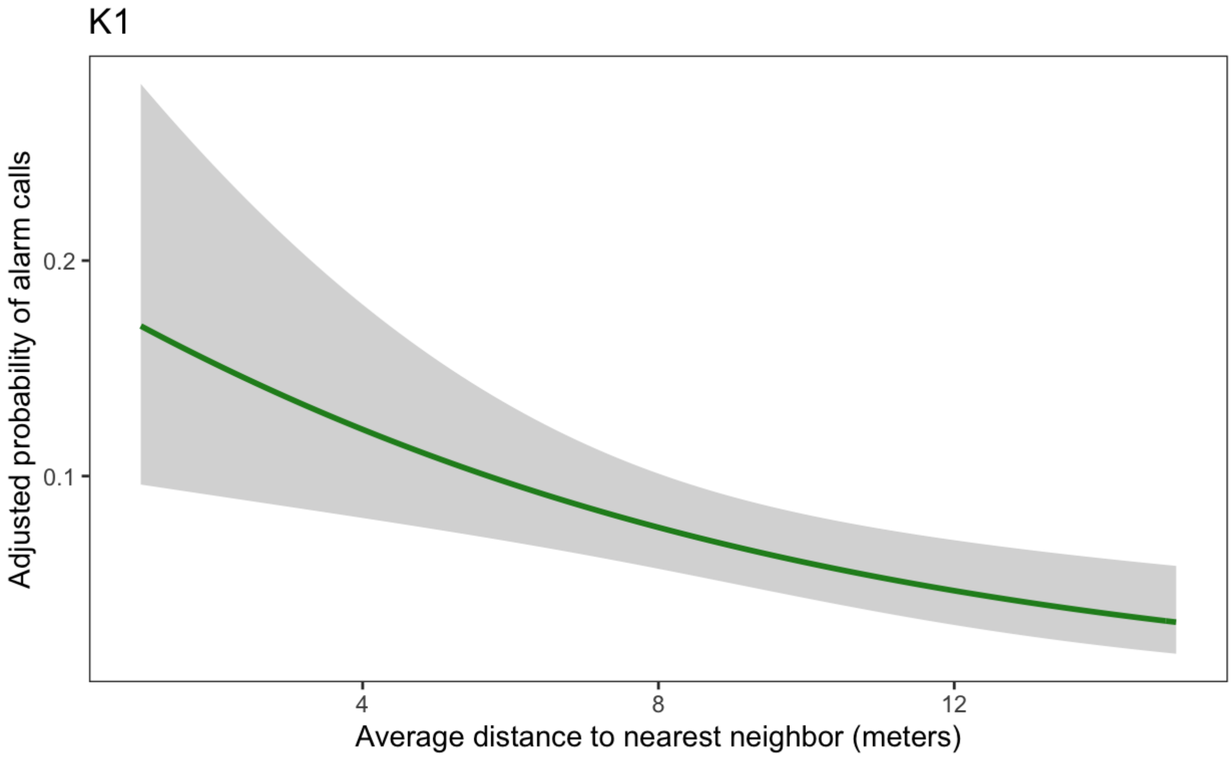


Figure 4: Closer aggregations of conspecifics (meters) predict greater probability of an alarm call in K1 only. Visualization contains +/- standard error as gray bands around the estimate line, rendered from GLM.

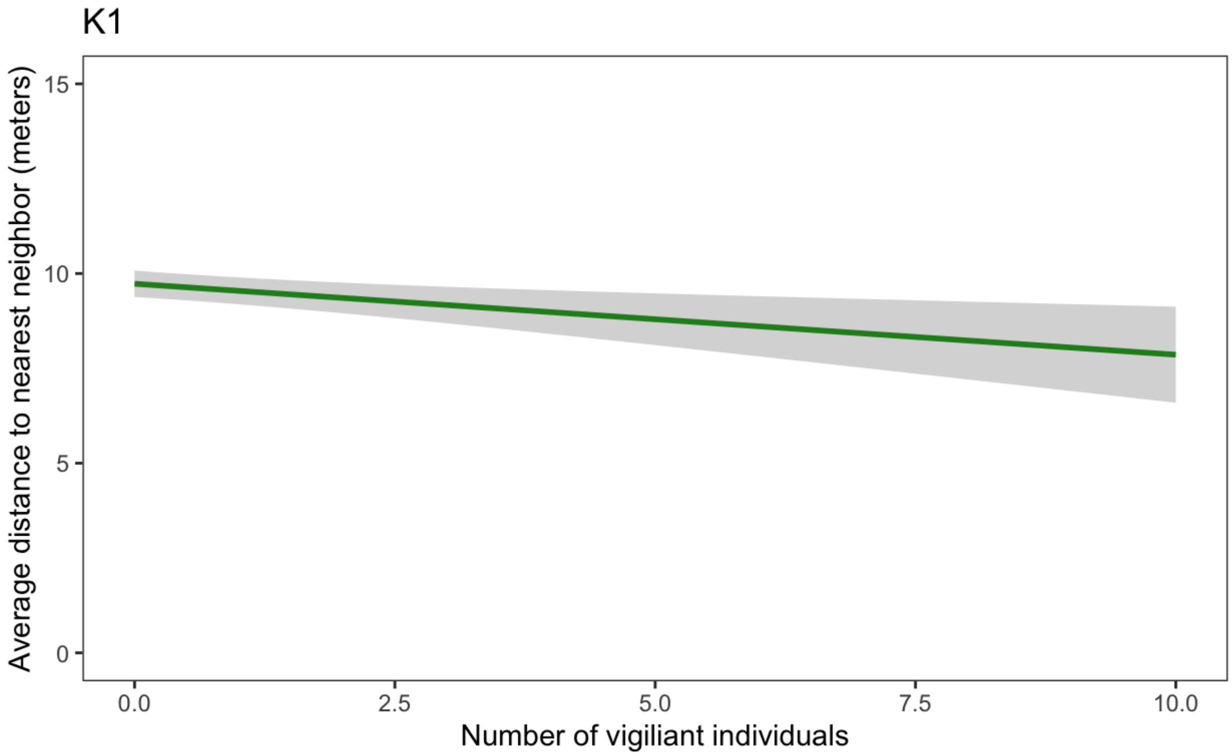


Figure 5: Closer aggregations of conspecifics (meters) is predicted by observations of more vigilant individuals in K1 only. Visualization contains +/- standard error as gray bands around the estimate line, rendered from GLM. This model differs qualitatively from the model with vigilance as a response variable given the additional control of demographic, however both models show the same direction of the relationship between vigilance and aggregation behavior.

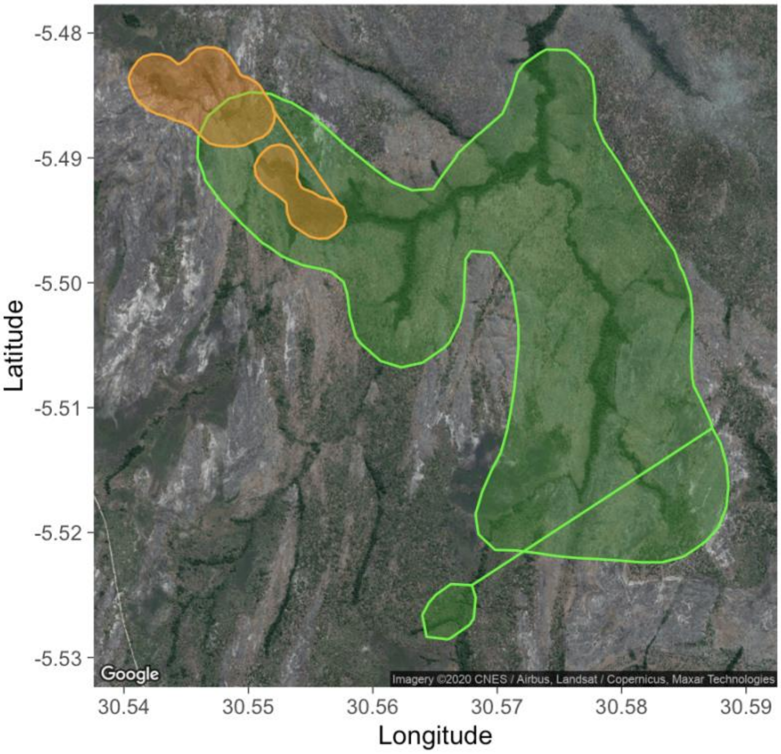


Figure 6: The 95 % kernel density estimation of habitat utilization from July 2018-December 2019 of group K1 (orange) and group K2 (green). The line between polygons connects regions in which no significant observations were made to connect the regions.

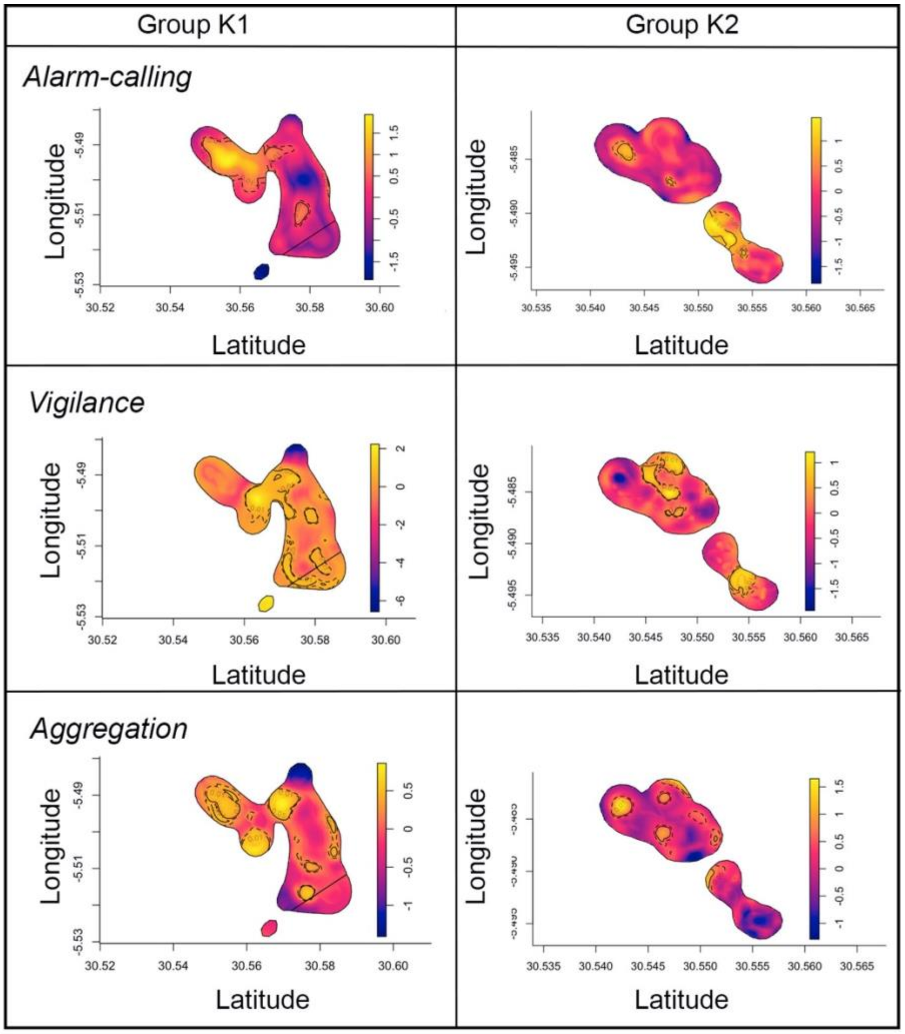


Figure 7: Relative risk models of the occurrences of anti-predatory behavior relative the monkey's home range. Contours reflect significantly increased predation risk at the p= 0.05 alpha-level (dashed line) and the p = 0.01 alpha-level (solid line). The models were mapped using a log-scale and confined to a polygon representing a 95% kernel density estimation of the group's home range.

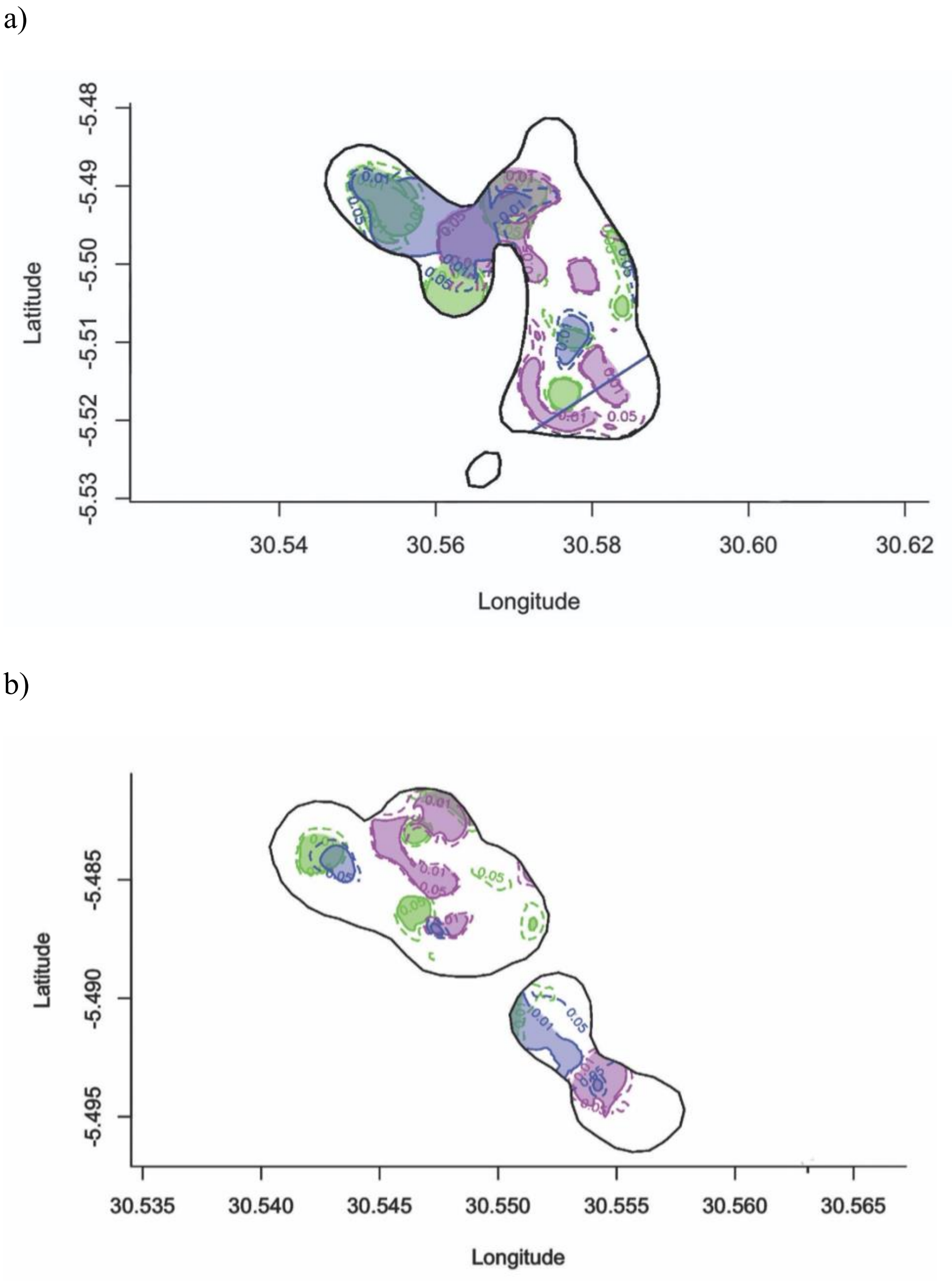


Figure 8: For a) K1 and b) K2, the overlay of regions of increased relative risk for each behavior, alarm calling (blue), vigilance (purple), and aggregation (green). Contours reflect significantly increased predation risk at the p= 0.05 alpha-level (dashed line) and the p = 0.01 alpha-level (solid line and shaded in). The models were confined to a polygon representing a 95% kernel density estimation of the group's home range.

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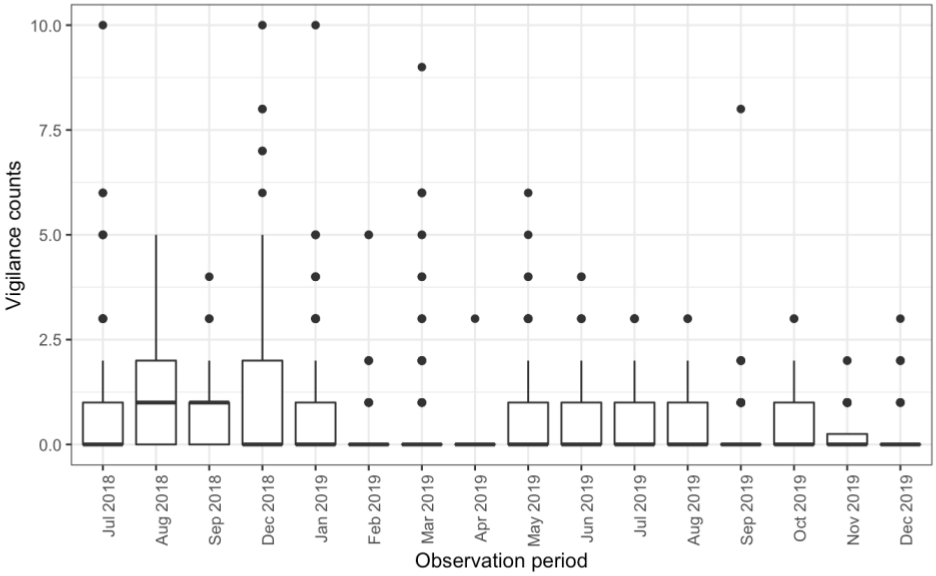
SUPPLEMENTARY MATERIALS

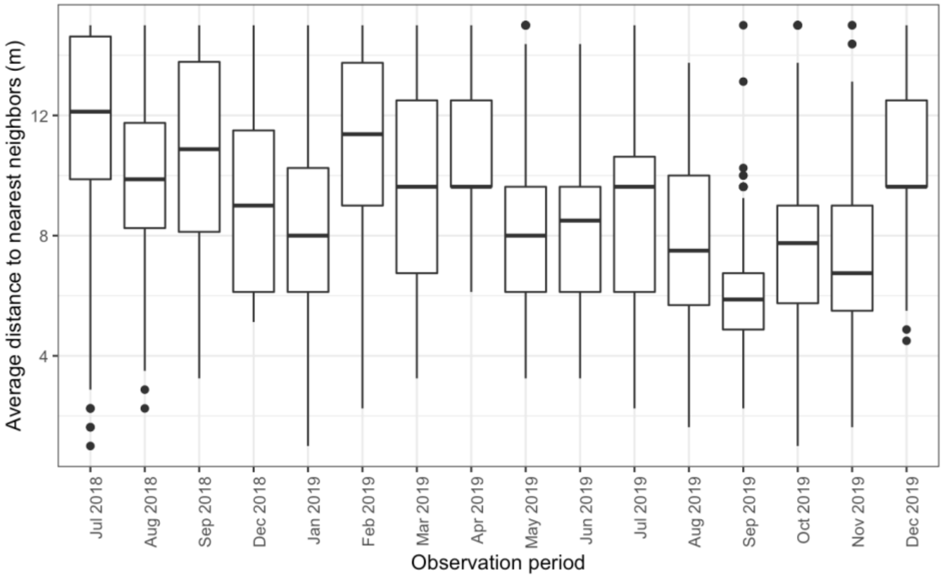
Binarizing the aggregation variables

One major obstacle in this work was in determining a way to binarize aggregation which was collected as a continuous variable of distance. Aggregation was simplified to a case/control structure to accommodate for the relative risk model. Previous aggregation studies suggested anti-predatory aggregations to persist at distances in which there is food competition (Janson 1996, Hirsch 2002). Past research on *C. ascanius* shows that they would forage and consume 86% of seeds within 10 m of the base of the trees (Lambert 1999). I then concluded that foraging of a single arboreal resource, which could be competed for by neighbors, would occur within 10 m of that source. Therefore, I concluded that a 10 m radius would serve as an informative cut-off for anti-predatory aggregation behavior. This is further supported by past work on capuchins that used the same cut-off (Hirsch 2002). With this justification, all nearest neighbors that were within 10 meters or less were considered to be a part of the anti-predatory aggregation and assigned as cases. Neighbors outside of this range were assigned as controls.

a)



b)



Supplementary Figure 1: The spread of observations of a) vigilance counts and b) average aggregation distance (m) across each month of the data collection period from July 2018-December 2019.