Behavioral Ecology

Multiple antipredator behaviors in red-tailed monkeys reveal spatially distinct landscapes of fear

Journal:	*Behavioral Ecology*
Manuscript ID	BEHECO-2022-0179.R1
Manuscript Type:	Original article
Keywords:	vigilance, aggregation, alarm-calling, Riparian forest, Issa Valley, Tanzania, perceived predation risk

LAY SUMMARY

Predation risk influences how prey use and respond to their environment. We show that locations where prey alarm-call, search, and group closely seldom overlap. The antipredator behaviors are also influenced by the type of vegetation and the degree to which their group members are alarm-calling, searching, or grouped closely. We indicate that antipredator behaviors are applied under different contexts, making one antipredator behavior alone an imperfect measure of a prey's perceived risk of predation.

MULTIPLE ANTIPREDATOR BEHAVIORS IN RED-TAILED MONKEYS REVEAL SPATIALLY DISTINCT LANDSCAPES OF FEAR

ABSTRACT

Foraging opportunity and predation risk act as opposing influences on an animal's habitat use. "Landscapes of fear" (LOF), whereby one predicts the spatial distribution of predators or perceived predator presence using prey responses, are an important tool for modeling this conflict. LOF models examining perceived predation risk are often generated using a single behavioral metric, even though individuals can respond to predation pressure with multiple potential behaviors. Here, we expanded traditional LOF approaches by measuring three antipredator behaviors in wild red-tailed monkeys (*Cercopithecus ascanius*): aggregation, alarm calling, and vigilance. We predicted that each behavior would reveal spatially explicit regions of high risk, as each behavior may attend to different aspects of perceived predation risk. The use of different behaviors may depend upon factors such as vegetation type, age/sex class of an individual, and which other antipredator behaviors are being exhibited by group members. We collected data on two troops of monkeys in the Issa Valley, Tanzania for over 19 months and conducted 3,189 group follows. We found that vegetation type varied in its effect on antipredator behavior. Monkeys conducted more antipredator behavior in more open vegetation types compared to more closed, riparian forests. The LOF models generated for each behavior mapped distinct and predominantly non-overlapping spatial regions of perceived predation risk, which was replicated across the two groups. This suggested that monkeys responded differently across their home range to specific perceived risks. Such spatially explicit behavior may indicate vegetation-specific predation risk or unique trade-offs in antipredator behavior throughout a heterogenous habitat.

KEYWORDS

Perceived predation risk; vigilance; aggregation; alarm-calling; Riparian forest; Issa Valley, Tanzania

INTRODUCTION

Predation pressure exerts a strong selective pressure on animal morphology, physiology, and behavior (Lima 1998b; Bidner 2014; Schmitz 2017). Although lethal effects of predation may drive the evolution of various traits, non-lethal effects can also impact prey responses (Lima 1998; Brown et al. 1999; Peacor et al. 2007; Peckarsky et al. 2008), including foraging costs associated with antipredator behaviors like vigilance (Lima 1998a; Cowlishaw et al. 2004). 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 informed by the prey’s perception of predator presence (Lima and Dill 1990; Laundré et al. 2001; Brown and Kotler 2004; Laundré et al. 2010; Campos and Fedigan 2014). This concept relies upon the hypothesis that an animal’s home range encompasses a gradient of risky areas, all of which can be mapped by measuring space use and anti-predator behaviors (Laundré et al. 2001; Laundré et al. 2010; Prugh et al. 2019).

Given the rarity of observing predation events, sufficient predation pressure data to build LOF models can be difficult to gather in many systems (Lima 1998b; Bleicher 2017). As a result, antipredator behavior is often used as a proxy, revealing perception of the predator landscape (Lima and Dill 1990; Brown and Kotler 2004). Prey species perceive predators using visual, auditory, and olfactory cues that are sometimes difficult for an observer to directly identify (Moll et al. 2017). The information on predation that prey use to inform their space use can be partial, imperfect, or context-specific (Blumstein et al. 2004; Prugh et al. 2019). Yet, the overestimation of risk may be the most beneficial strategy for prey species given the high-risk and high consequence of predator attacks (Bouskila and Blumstein 1992; Abrams 1994). Measurements of direct predation risk may therefore likely underestimate the risk that affects prey behavior.

There are numerous behaviors that reveal predation risk perception. Vigilance behavior and alarm calling are two of the most commonly studied (Brown 1999; Hirsch 2002; Willems and Hill 2009; Campos and Fedigan 2014; Coleman and Hill 2014). Alarm calls can serve two, non-mutually exclusive functions – either to alert group members of danger or deter an ambush predator by exposing it (Zuberbühler et al. 1997; Papworth et al. 2008; Isbell and Bidner 2016). The spatial organization of individuals may also respond to predation risk. Larger group sizes reduce predation risk by increasing group defense while diluting the risk of each individual (Hamilton 1971; Treves 2000). Further, group members may associate in close proximity to dilute any one individual's risk and increase predation detection ~~by~~ (Hirsch 2002; Morrell et al. 2011). Past work has modeled non-experimental LOFs using alarm calling behavior (Willems and Hill 2009; Campos and Fedigan 2014; Nowak et al. 2014; Coleman and Hill 2014; LaBarge et al. 2021), but other common antipredator behaviors have yet to be considered in LOF studies. We propose that vigilance, alarm-calling, and aggregation represent three important antipredator behaviors to model LOFs. This will be the first study to integrate aggregation behavior into an LOF model, despite its prevalence in antipredator behavior research (Kohl et al. 2018).

While multiple, independent behaviors reveal predation risk, the occurrence of any one antipredator behavior may influence the use of others. Alarm-calling, especially by multiple callers, is known to elicit more vigilance (Blumstein et al. 2004; Campos and Fedigan 2014). In numerous taxa, closer proximity to conspecifics correlated with decreased vigilance behavior, itself a frequently used metric of assessing predation risk (Allan and Hill 2018). Each behavior may also respond to different aspects of risk. For example, antipredator vigilance can be used both preemptively and reactively to predator presence, whereas alarm-calling is used typically only after predators are identified (Hirsch 2002; Boinski et al. 2003; Allan and Hill 2018). These differences highlight the way that LOF models are heavily dependent upon the antipredator behavior in question. What we lack to date are comparative LOF models from a single system to assess model variability resultant of any one behavior.

Predation and antipredator responses can also be context-dependent, influenced by predator type, habitat characteristics, age/sex class, group demography, and conspecific behaviors (Seyfarth et al. 1980; Isbell 1994; Treves 2000; Hirsch 2002; Verdolin 2006; Laundré et al. 2010; Campos and Fedigan 2014; Moll et al. 2017; Reyna-Hurtado et al. 2018). In Samango monkey (*Cercopithecus albogularis*) groups, fewer individuals responded with antipredator behavior to snake models compared to eagle and leopard models, demonstrating that the likelihood to respond to predation risk can depend upon the predator type (LaBarge et al. 2021). Another influence on responses to perceived predation risk is the vegetation type of the prey species. Arboreal primates are more vulnerable to predation in open forest or at forest edges, where they are more exposed and visible, compared to closed canopy forests (Jaffe and Isbell 2009). Meta-analysis has shown that studies measuring the effect of predation risk on foraging effort were better predicted by habitat characteristics, such as open vs. closed habitats, than predator observations or odors (Verdolin 2006). Furthermore, the age and sex of an individual may influence their vulnerability to predation risk and subsequently their production of antipredator behavior (i.e., yellow marmots: Lea and Blumstein 2011). ~~The~~ Any influence that these contexts may have ~~across groups, populations, or taxa is important to better understand the influence of predation~~on the production of antipredator behavior would then also shape a group's LOF.

Despite the fact that many LOF studies have used guenons as a model primate prey species (Willems and Hill 2009; Emerson et al. 2011; Makin et al. 2012; Jaatinen et al. 2014;

Nowak et al. 2014; Coleman and Hill 2014; LaBarge et al. 2021), these predominantly focus on samango monkeys. Comparisons of red-tailed monkey antipredator behavior demonstrate that red-tailed monkeys have species-specific behavioral responses to predation risk (Struhsaker 1980; Treves 1999; Teelen 2007). Yet, data are lacking on the landscape of fear of red-tailed monkeys (*C. ascanius*). Red-tailed monkeys in the Issa Valley live sympatrically with multiple predator types (carnivore, primate, and avian predators) and within a heterogeneous (mosaic-woodland) environment, providing an excellent opportunity for us to characterize the distinct, context-dependent patterns of antipredator behaviors and model LOFs. We investigated three antipredator behaviors: vigilance, aggregation, and alarm-calling, and in which vegetation types ~~of~~ these behaviors were most often produced.

Specifically, we hypothesized that each of the three antipredator behaviors 1) is uniquely context-dependent, 2) reveals spatially explicit risk-regions, and 3) ultimately constructs unique LOF models compared to one other. We tested ~~three~~ four predictions under the first hypothesis: 1) that each of two red-tailed monkey groups ~~would~~ will exhibit more antipredator behaviors in woodland (compared to riparian forest) vegetation; 2) that more individuals ~~would~~ will ~~show~~ be ~~increased vigilance~~ vigilant during an alarm call; 3) that there ~~would~~ will be fewer vigilant individuals during closer group aggregations; 4) that individuals of more vulnerable age/sex classes will aggregate more closely. For the second hypothesis, we constructed LOFs for each antipredator behavior to show risky and safe regions. Lastly, we predicted that similar context-dependent conditions, such as vegetation type, would impact the frequency of behavioral responses and thus produce variable LOFs with only partial overlap across the home range of each group.

METHODS

Study site and system

We collected data on two troops of red-tailed monkeys from the Issa valley, Tanzania that have been habituated since 2012 (McLester, Brown, et al. 2019). The Issa valley lies approximately 100 km east of Lake Tanganyika, inland between Gombe Stream and Mahale Mountains National Parks (Figure 1). The elevation ranges from 1050 to 1800 meters. Between August 2018-July 2019, mean daily temperatures ranged from 9.7 to 35.6 °C and the study area received 1,247 mm of rainfall. The Issa valley is a mosaic landscape, dominated by miombo woodland, and including riparian forest, thicket, and grassland. Riparian forest consisted of thin strips of forest along rivers and ~~and with~~ can be further categorized by regions of densely clustered trees that we termed closed forest and regions of ~~, or~~ more widely distributed trees, sometimes along rivers, that we termed open forest. ~~Miombo woodland consists predominantly of *Brachystegia* and *Julbernardia* (Fabaceae) with a previously estimated canopy cover of 63% (Hernandez-Aguilar 2009; Piel et al. 2017)~~. ~~Within the riparian forest, there~~There are also ~~are~~ patches of dense thicket that have a low canopy, considered the most closed vegetation type with estimated cover of 85.5% (Hernandez-Aguilar 2009). Miombo woodland, an open vegetation type, consists predominantly of *Brachystegia* and *Julbernardia* (Fabaceae) with a previously estimated canopy cover of 63% (Hernandez-Aguilar 2009; Piel et al. 2017). Issa is characterized by its faunal diversity (Bonnin et al. 2020), including bushbuck (*Tragelaphus scriptus*), roan antelope (*Hippotragus equinus*), eland (*Taurotragus oryx*), and numerous predators such as leopard (*Panthera pardus*), lion (*P. leo*), spotted hyena (*Crocuta crocuta*), wild dog (*Lycaon pictus*), crowned-hawk eagles (*Stephanoaetus coronatus*), and various small carnivores (Piel et al. 2019).

The two groups of red-tailed monkeys, K1 and K2, were comprised of 35 and 15 individuals, respectively, at the beginning of the study (August 2018). Each group had around one adult male, but numbers likely fluctuated. K1's home range was 3.12 km^2 and K2 was 0.66 km^2 (Figure 1), of which only 4.27% was shared. ~~K1 and K2 overlapped in their home range by ~4.85% (Figure 2).~~ There -is known predation on *C. ascanius* by leopards (McLester, Sweeney, et al. 2019) and chimpanzees (*Pan troglodytes schweinfurthii*) (AP & FS, unpublished data) at Issa. At nearby Mahale Mountains National park, *C. a~~A~~scanius* accounts for the most frequent prey species for c~~C~~rowned-hawk eagles (Seike 2022). However, to date no observation of predation by hawks of monkeys has been made at Issa. We ascribed focal individuals to the following age/sex classes: adult males, subadults/juveniles, adult females, and mothers with infants, but were unable to identify individuals. Without individual identification, we could not reliably determine the age/sex class composition of the entire group.

Data Collection

We collected data from July 2018 to December 2019. Each monkey group was followed for ~ one week/month by experienced field assistants and researchers personally trained by LF for collection of these data and validated for interobserver reliability. Although observers changed across the study period, we found that data collected in group scans had a consistent spread across the collection period (Supplementary Figure S1). We collected data from sunrise (~7:00), around the point the group left their sleeping site, until they arrived at the next sleeping site (~19:00).

Red tails produce 'ka' and 'chirp' alarm calls, the former produced by males and louder than the latter, produced by females, subadults, and juveniles (Marler 1973). We recorded ~~data on calls using instantaneous focal sampling in which~~ all occurrences of alarm calls by any group member ~~were documented~~. We ~~distinguished~~ were able to distinguish alarm call types by age/sex class-specific alarm call types (male and female-subadult-juvenile types), however predator-specific alarm calls have yet to be identified in red-tailed monkeys. For age/sex class identification, individuals that were unidentifiable, difficult to see sufficiently, or between age/sex classes were recorded as unknown. They are not discussed for the age/sex class results. However, they were kept in the models so that we may consider these observations with the other response variables.

We used 10-minute interval group scan sampling to record vigilance behavior. During each observation period, we noted the number of vigilant individuals. Vigilance was defined as an individual looking at an area either above or below its line of sight ~~without~~ and not at another ~~individual~~ group member (Treves 2000; Allan and Hill 2018). 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 vigilant individuals, we also recorded the total number of individuals visible to the observer. We conducted 3,188 group scans on the vigilance patterns.

To measure aggregation behavior, we used a nearest neighbor protocol that was employed simultaneously to our group scans. We selected a random individual for focal observations and classified the distance to its three nearest neighbors in one of four distance bins (0-5 m, 5-10 m, 10-15 m, and greater than 15 m). If three neighbors were not all visible within 15 m, we recorded a value of greater than 15 m for those out of sight. To reduce the likelihood of resampling the same individual in consecutive scans, we did not collect individuals of the same age/sex class in consecutive scans. Dependent infants were not included as neighbors for mothers with infants. During group scans, we also collected observations of the nearest neighbors to a 'randomized' focal.

For all~~each~~ observations, ~~we also recorded~~ a GPS location ~~using~~ was automatically recorded by both Samsung tablets (Samsung, Galaxy Tab A) and hand-held Global Positioning System (GPS) units (Garmin Rhino 700, 2-way GPS radios). We also identified and recorded the vegetation type in which the group was present, classifying individuals as either in closed forest, open forest, woodland, or thicket. Each observation was measured at the group level (i.e., amount of vigilance in group). ~~When~~ Because of this, when group members were distributed across multiple vegetation types they were coded as either mixed forest (group spread between both open and closed forest) or edge (group spread between both forest and woodland). We classified ~~Vegetation~~ vegetation types ~~fall from most to least open~~ as follows (from most to least open): woodland, edge, open forest, mixed forest, closed forest, thicket.

To examine the occurrence of each antipredator behavior within a broader behavioral context, we matched the alarm calling behaviors to the group scan observations, recorded every 10 minutes. We paired alarm calls to the earliest group scan observation within 12 minutes following the alarm call. ~~For alarm-calling, we~~We were able to pair 174 alarm calls to group scan observations. When constructing LOFs with alarm call data, we considered all alarm call observations.

~~Predicting the frequency of antipredator behaviors~~ Hypothesis 1: Antipredator behavior is context-dependent.

To test *Hypothesis 1* concerning the influence of vegetation type, age/sex class (aggregation model only), and antipredator behaviors on each other, we generated generalized linear models (GLM) in R (Version 4.0.5, R Core Team 2021). For the vigilance model we looked at counts of the number of vigilant individuals and used a negative binomial distribution from the ‘glmmTMB’ package (Brooks et al. 2017). We quantified aggregation as the average distance to three nearest neighbors, then converted aggregation into a proportion out of 15 meters to allow us to run a gamma distribution using ‘glmmTMB’ (Brooks et al. 2017). Lastly, using the presence of alarm-calls during each scan, we constructed a binomial model using the ‘lme4’ package (Bates et al. 2015). We also included vegetation type and the two other antipredator behaviors as fixed effects. We controlled for the number of individuals visible as a fixed effect as counts of vigilance are limited by the number of monkeys in view to the researcher. In the aggregation model, we included the age/sex of the focal individual as a fixed effect. We ~~ran~~ were able to replicate each model ~~was twice, once for each~~ by using data from two groups of monkeys. The analysis of two groups allowed us to determine if some patterns ~~e~~were replicable. However, with only two groups, we had insufficient variation and statistical power to test the influence of any one factor that could contribute to group differences.

Using the ‘car’ package (Fox and Weisberg 2019), we conducted full null model comparisons and calculated model effect significance using type II Wald chi-square tests. We ran posterior predictive checks on all models using the ‘performance’ package to check the fit of the model to the data (Lüdecke et al. 2021). We completed Tukey’s HSD post-hoc analyses on the categorical variables, vegetation type and age/sex class, using the ‘multcomp’ package (Hothorn et al. 2008).

~~Perceived predation risk landscapes of fear~~Hypothesis 2: Multiple antipredator behaviors can construct spatially explicit regions of increased perceived predation risk

To test *Hypothesis 2*, we used relative risk modeling methods to determine if the behaviors collected would form distinct regions of increased risk relative to overall space use.

236 ~~We~~ We first calculated a 95% kernel density estimation and least-squares cross-validation (LSCV) using the package 'adehabitatHR' (Calenge 2006) to determine the home range of each group. A prominent statistical obstacle of using LSCV is that it often fails to converge when GPS points are overlapped, too close together, or there are simply too many points. Per package recommendations, we implemented a small amount of noise to our data, using the results of the LSCV itself to determine a minimal and sufficient amount of noise. To create LOF models using three different behavioral metrics of perceived predation risk, we calculated the relative risk based on the occurrence of each antipredator behavior. The spatial regions outputted indicated spatial areas of significantly greater occurrence of antipredator behavior relative to overall time spent in the region and were delineated at both the 0.05 and 0.01 alpha level. Relative risk models have been applied to previous LOF studies and maps the ratio of presence to absence of the behavior (Campos and Fedigan 2014; Davies et al. 2018). We dichotomized each behavior into presence/ absence to calculate the probability of its occurrence.

249 We scored all group scans without an alarm call as absence while all observations of alarm calls were coded as presence. To code aggregation, we defined neighbors within 10 meters as evidence of antipredator 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, we constructed asymptomatic tolerance contours using bootstrapping to define the limits of the polygons (Davies et al. 2018). Boundaries for these models were defined as 95% kernel density estimations of home range, using the 'adehabitatHR' package in R (Calenge 2006).

257 *Hypothesis 3: Different antipredator behaviors construct different landscapes of fear*

To test *Hypothesis 3*, we compared the contours produced in our LOF models to see how much they overlapped. We calculated the overlap of contours at the 0.05 alpha level using the packages 'spatstat.geom' (Baddeley et al. 2015). ~~Only contours within the group were compared and percentages were derived to indicate the amount of overlap.~~The exact area of regions and the subsequent exact percentages of overlap are sensitive to the estimation method, the bandwidth parameter, the smoothing regimen, and other parameters used in the model. Due to this sensitivity, our interpretation of overlap did not emphasize the exact percentages but considered them to be rough estimates of the underlying relationship between the antipredator behaviors or groups. We cannot know at what point such differences are meaningful to the monkeys themselves. Consequently, we discuss the more general trend of which behaviors had the most and least overlap to identify potentially important patterns in behavior.

RESULTS

~~*Predicting the frequency of antipredator behaviors*~~ *Hypothesis 1: Antipredator behavior is context-dependent*

We predicted that antipredator behavior would be conducted most in the open, woodland vegetation and the least in closed, riparian forest vegetation (*Prediction 1*). ~~The~~We found that frequency of two ~~all three~~ anti-predator behaviors, vigilance and aggregation, were predicted by ~~some, but not all the ecological and behavioral~~vegetation type, with a general trend of greater antipredator behavior in more open vegetation types ~~predictors~~. ~~Furthermore~~However, the relationships of specific vegetation types differed~~changed~~ between groups. ~~We conducted 3,188 group scans~~. Monkeys of both groups were the most vigilant when in forest edges (between woodland and forests), and the least vigilant in closed forest vegetation (χ^2= 14.34, df = 5, p =

0.014; Figure 2). In K1, the number of vigilant ~~individuals differed significantly between closed forests and edge vegetation, but~~individuals did not differ ~~not~~ amongst other vegetation types. In K2, monkeys in closed forest were significantly less vigilant than in all other vegetation types and they were more vigilant at the forest edge compared to the open forest (χ^2= 37.94, df = 4, p < 0.001; Figure 2). Vegetation type predicted aggregation behavior, though this relationship differed from that shown by vigilance behavior (K1: χ^2= 65.51, df = 5, p < 0.001; K2: χ^2= 90.15, df = 4, p < 0.001). Monkeys were the least aggregated in mixed forest and most aggregated in the woodland (~~Figure 3~~Figure 2). Vegetation type did not predict alarm calling behavior (K1: χ^2= 10.21, df = 5, p = 0.069; K2: χ^2= 1.78, df = 4, p = 0.78).

Secondly, we predicted that the group would have more vigilant members during alarm-calls (*Prediction 2*). However, we found that vigilance was not predicted by alarm-calling in either group (K1: χ^2= 0.18, df = 1, p = 0.67; K2: χ^2= 0.22, df = 1, p = 064). When considering alarm-calling as the dependent variable, it was not predicted by vigilance in K1 (χ^2= 0.14, df = 1, p = 0.71). In K2, alarm-calling was not predicted by any anti-predator behaviors (vigilance: χ^2= 0.26, df = 1, p = 0.61; aggregation: K1: χ^2= 0.06, df = 1, p = 0.81). However, closer aggregations correlated with a higher probability of alarm call production in K1 (χ^2= 6.42, df = 1, p = 0.011; Figure 3).

~~For K1, the number of vigilant monkeys observed and average distance to nearest neighbor were negatively correlated, as closer aggregations correlated with more vigilance behavior (χ^2= 18.28, df = 1, p < 0.001; Figure 5).~~ We predicted that there would be fewer vigilant individuals during closer group aggregations (*Prediction 3*). For K1, we found the opposite pattern as closer aggregations correlated with more vigilance behavior (vigilance as dependent variable: χ^2= 18.28, df = 1, p < 0.001; aggregation as dependent variable: χ^2= 9.60, df

= 1, $p < 0.001$; Figure 4). In K2, only the aggregation model, which controlled for age/sex class, showed a significant negative correlation between vigilance and aggregation (vigilance as dependent variable: $\chi^2 = 0.10$, df = 1, p = 0.75; aggregation as dependent variable: $\chi^2 = 4.13$, df = 1, p = 0.04).

~~Vigilance was not predicted by aggregation or alarm-calling in K2 ($\chi^2 = 0.10$, df = 1, p = 0.75).Closer aggregations correlated with a higher probability of alarm call production in K1 ($\chi^2 = 6.42$, df = 1, p = 0.012; Figure 6). Alarm-calling was not predicted by any other anti-predator behaviors in K2 (vigilance: $\chi^2 = 1.26$, df = 1, p = 0.61; aggregation: K1: $\chi^2 = 0.06$, df = 1, p = 0.081).~~

We predicted that individuals of age/sex classes previously identified in other guenon species to face greater predation risk will aggregate more closely and alarm-call more often (*Prediction 4*).

~~Vegetation type predicted aggregation behavior, though this relationship differed from that shown by vigilance behavior (K1: $\chi^2 = 65.51$, df = 5, $p < 0.001$; K2: $\chi^2 = 90.15$, df = 4, $p < 0.001$). Monkeys were the least aggregated in mixed forest and most aggregated in the woodland (Figure 3).~~ The age/sex class of the focal and presence of infants ~~also~~ predicted aggregation behavior (K1: $\chi^2 = 98.09$, df = 5, $p < 0.001$; K2: $\chi^2 = 115.17$, df = 5, $p < 0.001$; ~~Figure 4~~Figure 2). In both K1 and K2, mothers with infants had the furthest average distance to neighbors and subadults the closest aggregations. In K2, juveniles and sub-adults exhibited the closest aggregations, whereas adult males were closer to neighbors compared to mothers with infants, but not other adult females. In both groups adult females without infants were more closely aggregated than those with infants. ~~The only significant relationship among the antipredator behaviors observed in K2 was that vigilance predicted aggregation ($\chi^2 = 9.60$, df = 1, p =~~

~~0.0019).~~Considering raw counts of alarm-calls, we found that m~~M~~ales produced 34 (K1) and 26 (K2) alarm calls. Females, subadults, or juveniles produced 34 (K1) and 52 (K2) alarm calls.

~~For alarm-calling, we were able to pair 174 alarm calls to group scan observations. Vegetation type did not predict alarm calling behavior (K1: χ^2= 10.21, df = 5, p = 0.069; K2: χ^2= 1.78, df = 4, p = 0.78). Males produced 34 (K1) and 26 (K2) alarm calls. Females, subadults, or juveniles produced 34 (K1) and 52 (K2) alarm calls. Closer aggregations correlated with a higher probability of alarm call production in K1 (χ^2= 6.42, df = 1, p = 0.012; Figure 6). Alarm-calling was not predicted by any other anti-predator behaviors in K2 (vigilance: χ^2= 1.26, df = 1, p = 0.61; aggregation: K1: χ^2= 0.06, df = 1, p = 0.081).~~

~~Perceived predation risk landscapes of fear~~Hypothesis 2: Multiple antipredator behaviors can construct spatially explicit regions of increased perceived predation risk

~~K1's home range was 3.12 km^2 and K2 was 0.66 km^2 (Figure 1), of which only 4.27% was shared.~~ Using the home range estimation as boundaries, we created relative risk models of each behavior for each group (~~Figure 7~~Figure 5). In these models, the contours, or regions of significantly increased risk at the p = 0.05 alpha level, reflect the distinct regions of increased perceived predation risk.~~ For eachwe were~~. Despite having a smaller group size and home-range, K2 exhibited a larger ~~the~~ total area of relative risk for each anti-predator behavior ~~was larger for the smaller K2 group~~ compared to K1. K2 contour areas were 1.07 times larger for alarm-calling, 1.27 times larger for aggregation, and 1.08 times larger for vigilance. For both groups, vigilance contours had the most area with 3.01 (K1) and 2.62 (K2) times the area of the aggregation contours.

Hypothesis 3: Different antipredator behaviors construct different landscapes of fear

~~The~~ Which behaviors shared ~~LOF models with~~ the greatest overlap in their LOF models~~between~~ differed for each group. For K1, the greatest overlap of 5.59% was between aggregation and alarm-calling (Table 1). For K2, the greatest overlap of 5.53 % was between alarm-calling and vigilance. Relative risk models, like many spatial models, are sensitive to the parameters utilized. Though we present the exact numbers in our results, only the general trends of importance are used for interpretation, specifically which behaviors have the most or least overlap. Nevertheless, these models reveal that each behavior maps distinct (spatial) regions of perceived predation risk. ~~-~~Relative to the sum of each group's contours, there was the greatest percent overlap in K1 and K2's alarm-calling regions, with 4.50% overlap. Less than 0.04% of the area of K1 and K2's vigilance contours overlapped. Therefore, for each behavior, each group appears to be creating over 95% of the behavioral response contours in unique regions from the other group. ~~Despite having a smaller home-range, the total area of relative risk for each anti-predator behavior was larger for the smaller K2 group compared to K1. K2 contour areas were 1.07 times larger for alarm-calling, 1.27 times larger for aggregation, and 1.08 times larger for vigilance. For both groups, vigilance contours had the most area with 3.01 (K1) and 2.62 (K2) times the area of the aggregation contours. The LOF between two red-tail monkey groups of different sizes with little overlapping home range were variable in their size and patterns between the anti-predator behaviors.~~

DISCUSSION

We investigated three different antipredator behaviors in ~~two~~ groups of wild red-tailed monkeys to determine how ~~they~~ antipredator behaviors differ in their use and spatial distribution. We found support for our hypothesis that antipredator behaviors are context-specific, as each behavior demonstrated ~~distinct~~ different relationships to vegetation types and the other antipredator behaviors. We found that vegetation type was associated with antipredator behaviors in both K1 and K2, with individuals more vigilant and closely aggregated in open vegetation types compared to closed types. Additionally, aggregations were closer during instances of high vigilance or alarm calling. Furthermore, age/sex class predicted aggregations while alarm-calling occurred nearly as often in single adult males as between all other callers. For each antipredator behavior, the LOF models had ~~distinct~~ non-overlapping, contours, or spatial regions ~~of greater perceived predation risk, or distinct spatial regions~~ of significant occurrences of antipredator behavior relative to overall use. The regions themselves were dependent upon the antipredator behavior metric used and the group affiliated with the behavior. The antipredator behaviors with the greatest overlap for K1 had the least overlap for K2 and vice versa. The smaller K2 group had larger areas of relative risk and more variation in size between antipredator behaviors compared to K1. No antipredator behavior metric (alarm calling, aggregation, or vigilance) overlapped with all, or even more than 6%, of the contours of the other metrics or group, thus there is no evidence that any single antipredator behavior reflects a complete landscape of the prey's perceived predation risk.

The aim of this study was to develop a more complete representation of the red-tailed monkey's LOF as well as highlight the context-dependency of anti-predator behaviors with both linear and spatial modeling techniques. Most non-experimental LOF studies in primates measure alarm calls as a metric for perceived predation risk (Willems and Hill 2009; Campos and Fedigan 2014; Nowak et al. 2014; Coleman and Hill 2014; LaBarge et al. 2021). Yet, alarm calls are just one of multiple strategies that individuals employ when they perceive risk. The usage of any one anti-predator behavior is influenced by the context, ultimately influencing which behavior is exhibited. One context that we considered was vegetation type. We found that vegetation type had different relationships to each antipredator behavior, which could drive diverse behavioral reaction to perceived predation risk and consequently produce different LOFs for each antipredator behavior. Consistent with past work on the red-tailed monkeys of Kakamenga (Kenya) (Cords 1990), we found monkey groups to be more vigilant in open vegetation types. Specifically, in both groups, the edge between woodland and forest appeared to have the highest rates of vigilance in the group. Open habitat vegetation increases predator (and prey) visibility and thus may increase prey vulnerability; however, it may also influence the effectiveness of vigilance behavior (Isbell 1994) as monkeys can see further with less foliage (Jaffe and Isbell 2009). ~~The spacing of trees may also shape inter-individual distance. Greater inter-tree distance in woodlands may force monkeys to increase group spread to effectively exploit foraging trees, which in turn could leave individuals more vulnerable to attack. As a counterstrategy, they may increase vigilance.~~ The edge vegetation may be especially effective for vigilance. It is more open than the forest vegetation types and can allow individuals to scan woodlands (where they are more vulnerable) before entering them. As for the other antipredator behavior, we found that both groups were more closely aggregated in the woodland and edge vegetations compared to mixed and open forests. Differences in canopy across vegetation types ~~may also influence risk perception~~may also explain higher vigilance and closer aggregations in open vegetation types. Samango monkeys were found to demonstrate greater perceived predation risk when lower in the canopy (Nowak et al. 2014). The Issa woodland has canopy heights ranging 5-20 m, with most averaging 10-12 m. In comparison, riparian forest ranges from heights of 7-40 m (Hernandez-Aguilar 2009), which could further impact whether prey are more vulnerable to terrestrial predators when in the canopy. If a vegetation type increases the vulnerability of prey, predators may preferentially hunt in those locations. The vulnerability allotted by different predator types has been a significant predictor of predation activity and density in other prey taxa (e.g., Northern bobwhites in USA: Atuo and O'Connell 2017; livestock in S. Africa: Minnie et al. 2015). Future work could determine whether the open vegetation types that predict increased antipredator behavior also predict increased predator distribution.

We also examined the associations among antipredator behaviors themselves. ~~The final relationships that we examined were the associations between antipredator behaviors themselves.~~ During instances of alarm-calling or high vigilance, K1 monkeys were more closely aggregated. Close aggregations may allow for the social transmission of information on predation risk, driving more vigilance or alarm-calling (Treves 1998; LaBarge et al. 2021). Positive relationships between aggregation and vigilance may also be due to a contagion effect, where individuals that are more closely aggregated and visible to neighbors may copy the vigilance of nearby individuals (Pays et al. 2007). Yet, we did find more closer aggregations correspond to lower ~~amounts~~rates of vigilance in K2. One potential explanation for this is that more individuals nearby promote more reliable predator detection and greater risk dilution akin to the influence of larger group sizes (Hamilton 1971; Treves 2000). Another potential explanation is that ~~the smaller, K2 group has a different kinship structure than K1, with more related individuals compared to the larger group~~the K2 group could be more closely related than those individuals in K1. In Japanese macaques (*M. fuscata*), individuals that were more closely aggregated were less vigilant only when those neighbors were kin (Iki and Kutsukake 2021). It is possible that K2 exhibits a closer kinship structure than K1, which would influence our aggregation results. ~~When sampling the three nearest neighbors to K2 individuals, any random three neighbors are more likely to be related to the focal than the K1 group due to the smaller group size.~~ This ~~may~~would also drive K2 individuals to benefit more from close aggregations if they are more likely to contain kin. To resolve this uncertainty, we ~~will need to~~can in the future assess genetic relatedness amongst the members of each group.

Individuals of different age/sex classes may experience different trade-offs in their behavioral responses to perceived predation risk, such as greater benefits in protecting group members or increased vulnerability to actualized predation. We were only able to examine age/sex class in the aggregation model. We found that adult male red-tailed monkeys aggregated more closely than mothers with infants, though not other adult females. ~~Mothers with infants~~ The “infant safety hypothesis” proposes that mothers may avoid grouping near males to decrease vulnerability to threats like infanticide, which has been observed in red-tailed monkeys (Struhsaker 1977; Otali and Gilchrist 2006). Another potential explanation is that mothers with dependent offspring may move slower due to the energetic and physical demands of raising and carrying their dependent young, which affects their presence and positioning within the social group (Wrangham 2000).

Juveniles and subadults aggregated more closely than adult males, which may be explained by increased vulnerability to predation of this group. Juveniles or subadults are generally most vulnerable to predation and therefore invest more into vigilance than adults (Oversluijs Vasquez and Heymann 2001; Lledo-Ferrer et al. 2009; Lea and Blumstein 2011). We were able to compare raw counts of alarm calls by adult males versus females, subadults, or juveniles. Though each group tended to have a single adult male, adult male calls were nearly as prevalent as calls produced by any of the other many females, subadults or juveniles. This suggests that any single male may produce more calls than any single female, subadult, or juvenile would. However, we would still need to confirm this by identifying individuals and then determining the number of calls produced by each individual.

In numerous cercopithecine species, males produce more alarm calls than females, vary less in their distance to conspecifics, and are more vigilant than females (Smuts et al. 1987; Baldellou and Peter Henzi 1992; Treves 1998; van Schaik et al. 2022). Males may ~~also~~ be more incentivized to alarm-call to protect future mates and/or ~~their~~ sired offspring. As ~~one of the~~there are typically few adult males in ~~the~~ any one group, ~~we would expect t~~these ~~males~~ individuals ~~to~~ ~~likely~~ have high reproductive skew and sire many of the offspring in their social group (Altmann 1962; Kutsukake and Nunn 2006). Identifying individual callers and constructing the genealogy of each group could confirm whether the relatedness of an individual to its group members predicts the propensity to alarm-call. ~~In numerous cercopithecine species, males produce more alarm calls than females, vary less in their distance to conspecifics, and are more vigilant than females (Smuts et al. 1987; Baldellou and Peter Henzi 1992; Treves 1998; van Schaik et al. 2022)~~. ~~We were only able to examine age/sex class in the aggregation model, yet we found that adult male red-tailed monkeys aggregated more closely than mothers with infants, though not other adult females. Lastly, at Issa, juveniles and subadults aggregated more closely than adult males, which may be explained by increased vulnerability to predation of this group. Juveniles or subadults are generally most vulnerable to predation and therefore invest more into vigilance than adults, like that observed in other prey mammals (Oversluijs Vasquez and Heymann 2001; Lledo-Ferrer et al. 2009; Lea and Blumstein 2011).~~ One takeaway of age/sex class investigation into aggregation and the categorization of counts of alarm-calls is that ~~Alarm-call LOFs may reflect more of a male's behavior while other behavioral responses, like~~ aggregation~~,~~ may reflect the ~~behaviors~~ behavioral response of females without infants, subadults, or juveniles, while alarm-calling could potentially bias a male's antipredator responses. Since ~~demographics~~ demography differed across the groups, ~~one should be~~we are cautious of ~~generalizations at the population or species level on~~relying upon the frequency and concentration of a single antipredator behavior~~s~~ to indicate an entire group's perceived predation risk.

~~The final relationships that we examined were the associations between antipredator behaviors themselves. During instances of alarm-calling or high vigilance, K1 monkeys were more closely aggregated. Close aggregations may allow for the social transmission of information on predation risk, driving more vigilance or alarm-calling (Treves 1998; LaBarge et al. 2021). Positive relationships between aggregation and vigilance may also be due to a contagion effect, where individuals that are more closely aggregated and visible to neighbors may copy the vigilance of nearby individuals (Pays et al. 2007). Yet, we did find more closer aggregations correspond to lower amounts of vigilance in K2. One potential explanation is that the smaller, K2 group has a different kinship structure than K1, with more related individuals compared to the larger group. In Japanese macaques (*M. fuscata*), individuals that were more closely aggregated were less vigilant only when those neighbors were kin (Iki and Kutsukake 2021). It is possible that K2 exhibits a closer kinship structure than K1, which would influence our aggregation results. When sampling the three nearest neighbors to K2 individuals, any random three neighbors are more likely to be related to the focal than the K1 group due to the smaller group size. This may also drive K2 individuals to benefit more from close aggregations if they are more likely to contain kin. To resolve this uncertainty, we will need to assess genetic relatedness amongst the members of each group.~~

If the use of any one antipredator behavior influences the likelihood of other behaviors, then any LOF model that uses a single behavioral response (spatially) under-estimates perceived predation risk. We did not find vigilance and alarm-calls to be associated, even after we controlled for vegetation type. Considering this in combination with the lack of overlap in each LOF model, we suggest that each antipredator behavior is responding to different aspects of predation risk, e.g., predator type, predator attack mode (ambush, etc.), or escape routes. These aspects may be relative to the prevalence of other antipredator behaviors. The use of one behavior in a given context could decrease the need of other antipredator behaviors, e.g., alarm calls can prompt group movement away from a perceived threat~~,~~ which may nullify the need for further antipredator ~~behavior~~responses (Seyfarth et al. 1980; Zuberbühler et al. 1997). Subsequent analysis into pre- and post-calling movement patterns could test this hypothesis. Lastly, animals may be vigilant preemptively, before a predator is visually detected, which would suggest the behavior may be used before others (Boinski et al. 2003).

Other factors that we did not measure directly may explain the variation that we found in our results. Antipredator strategies may also be used relative to predator types, which would explain the lack of relationship between antipredator behaviors and lack of overlap in the LOF models. Experimental work has demonstrated that vervet monkeys (e.g., *Chlorocebus pygerythrus*) increased vigilance after raptor and snake (playback) alarm calls but fled into the trees following (playback) leopard alarm calls (Seyfarth et al. 1980). Samango monkeys are known to elicit different degrees of antipredator response to different predator models (LaBarge et al. 2021). At Issa, red-tailed monkeys are most vulnerable to attack by leopards, chimpanzees, and potentially crowned hawk eagles (McLester et al., 2019, AP & FS~~,~~ unpublished data). In an observed leopard predation event on K1 in the Issa Valley, the leopard attacked from the woodland (McLester, Sweeney, et al. 2019). Leopards in woodland savanna hunt most in intermediate vegetation coverage despite prey being most abundant in dense vegetation (Balme et al. 2007). Leopards that predate livestock were observed to concentrate kills at specific vegetation types and the borders of the prey's habitat (Minnie et al. 2015). Most observed hunting events by chimpanzees at Issa occurred in woodlands (AP, FS unpublished data). If certain predators are more common in certain vegetation types and monkeys demonstrate predator-specific behavioral responses to risk, we would expect predator type to partially explain the trend that we see between behavior and vegetation as well as differences in the LOF models of each behavior. To further test the relationship of predator and vegetation types, we could construct predator occupancy models and relate them to monkey movement and behavior. Using the LOF as a guide, we could also more effectively target areas of high perceived risk for camera trap sampling.

Different cues of potential predation risk may be more likely to elicit different antipredator behaviors in response. In theory, alarm calling may only reflect urgency given the high risk it incurs on callers (Charnov and Krebs 1975). However, if alarm-calling is applied in only high-urgency contexts, we would expect higher frequencies of all antipredator behaviors (Lima 1998a). We do not find this to be the case as alarm-calling was not associated with increased vigilance. Rather, alarm-calling may be applied in context-dependent scenarios, such as in the presence of more direct cues of predators, e.g., direct observation or predator vocalization. Olfactory and less direct auditory cues of predation may elicit vigilance and aggregation of prey before they directly observe the predator. Data from Samango monkeys suggest that aggregation may be a preemptive rather than a reactive strategy in regions of high predation risk (LaBarge et al. 2020). Monkeys may also use cues from their environment to determine their risk. We found that open vegetation types correlated with increased vigilance and closer aggregations. It has previously been suggested that open vegetation may serve as a cue for increased vulnerability to predation (Jaffe and Isbell 2009). Monkeys may use specific behavioral responses for specific cues of potential risk, allowing them to forgo more costly responses when possible.

Lastly, we ~~We also~~ found that some patterns of antipredator behavior were only seen in one group. Though our intention of this study was not to compare the groups, our failure to replicate findings may provide insight into other factors that influence the use and distribution of antipredator behaviors. ~~Furthermore, the~~We also found that the LOF models varied between groups in their overlap and size. ~~These~~ The differences between the two groups could be due multiple, unmeasured factors such as ~~to~~ differences in predator densities/distribution, monkey kinship relationships, group size, vegetation proportions, or home range between the two groups. Our small sample size of only two groups prevented~~s~~ us from making ~~any~~ comparisons to test what influences these differences. However, we ~~will~~ suggest differences in the group that may identify potential factors for future studies comparing across a larger sample of groups. ~~For example, K2's use of their range did not contain thicket vegetation unlike K1.~~ The relationship between proximity to conspecifics and alarm calling that we observed in K1 c~~w~~ould indicate that alarm calling in *C. ascanius* is influenced by the behavior of conspecifics. It~~'~~s absence in K2 may~~ke~~ be indicative of a potential interaction with ~~n effect of~~ group size that influences the relationships between antipredator behaviors. A smaller group size would (theoretically) face higher risk ~~in K2~~and may ~~result in~~drive generally ~~fewer kin surrounding the caller, and indirectly more spread individuals~~closer aggregations irrespective of the alarm ~~and less frequent~~ calls. Our findings also demonstrate that the smaller group had larger areas of high perceived predation risk than the larger group. This corroborates theory that proposes that large group sizes decrease predation risk (Hamilton 1971; Treves 2000). Though it may not reflect increased predator presence, small group size may drive the prey to use anti-predator behaviors more commonly throughout their habitat. Future investigation into predator presence across the Issa Valley could corroborate whether groups perceive greater vulnerability to predators or predator presence. ~~A possible effect, like~~However, to test group size as an effect itself, we~~,~~ would ~~also be measurable using~~need to study more than two- habituated, single species monkey groups ideally living under similar environmental and predation conditions. ~~a multi-group study possibly across populations.ed OedOverall, the two groups, whose home ranges only overlap 4.27%, provide further insight into how group size and environmental differences shape a prey species' landscape of fear.~~ Yet, the variation we see serves as an important caveat to behavioral ecologists on overgeneralizing any one pattern of antipredator behavior observed in a single group to the entire population or species.

CONCLUSION

In summary, we found that groups of mosaic habitat dwelling red-tailed monkey antipredator behavior varied with vegetation, the other behaviors conducted, and the age/sex class. The LOF models of each behavior demonstrated distinct contours from one another~~, and home range, and different antipredator behaviors created distinct LOFs~~. These differences suggest that each behavioral response may inform a different aspect of perceived predation risk. Antipredator behavior in red-tailed monkeys may respond to not just the physical environment– as we have shown here – but also the social environment, with individuals responding to each other's behavior. Monkey groups of different sizes and predominantly different home ranges appear to also differ in patterns of antipredator behaviors and their LOFs. Future LOF studies will benefit from using multiple antipredator response metrics and especially across multiple groups (with known individuals) to help identify causative influences on these key behaviors.

REFERENCES

Abrams PA. 1994. Should Prey Overestimate the Risk of Predation? Am Nat. 144(2):317–328. doi:10.1086/285677. https://doi.org/10.1086/285677.

Allan ATL, Hill RA. 2018. What have we been looking at? A call for consistency in studies of primate vigilance. Am J Phys Anthropol. doi:10.1002/ajpa.23381.

Altmann SA. 1962. A field study of the sociobiology of rhesus monkeys, Macaca mulatta. Ann N Y Acad Sci. 102:338–435. doi:10.1111/j.1749-6632.1962.tb13650.x. http://europepmc.org/abstract/MED/14012344.

Atuo FA, O'Connell TJ. 2017. The landscape of fear as an emergent property of heterogeneity: Contrasting patterns of predation risk in grassland ecosystems. Ecol Evol. 7(13):4782–4793. doi:https://doi.org/10.1002/ece3.3021. https://doi.org/10.1002/ece3.3021.

Baddeley A, Rubak E, Turner R. 2015. Spatial Point Patterns.

Baldellou M, Peter Henzi S. 1992. Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. Anim Behav. 43(3):451–461. doi:10.1016/S0003-3472(05)80104-6.

Balme G, Hunter L, Slotow R. 2007. Feeding habitat selection by hunting leopards Panthera pardus in a woodland savanna: prey catchability versus abundance. Anim Behav. doi:10.1016/j.anbehav.2006.12.014.

Bates D, Mächler M, Bolker BM, Walker SC. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw. 67(1). doi:10.18637/jss.v067.i01.

Bidner LR. 2014. Primates on the Menu: Direct and Indirect Effects of Predation on Primate Communities. Int J Primatol. doi:10.1007/s10764-014-9797-x.

Bleicher SS. 2017. The landscape of fear conceptual framework: definition and review of current applications and misuses. PeerJ. 5:e3772. doi:10.7717/peerj.3772. https://peerj.com/articles/3772.

Blumstein DT, Verneyre L, Daniel JC. 2004. Reliability and the adaptive utility of discrimination among alarm callers. Proc R Soc B Biol Sci. doi:10.1098/rspb.2004.2808.

Boinski S, Kauffman L, Westoll A, Stickler CM, Cropp S, Ehmke E. 2003. Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (Saimiri oerstedii, S. boliviensis, and S. sciureus). Behaviour. 140(11–12):1421–1467. doi:10.1163/156853903771980666. [accessed 2021 May 22]. https://brill.com/view/journals/beh/140/11-12/article-p1421_5.xml.

Bonnin N, Stewart FA, Wich SA, Pintea L, Jantz SM, Dickson R, Bellis J, Chitayat A, Ingram R, Moore RJ, et al. 2020. Modelling landscape connectivity change for chimpanzee conservation in Tanzania. Biol Conserv. 252. doi:10.1016/j.biocon.2020.108816.

Bouskila A, Blumstein DT. 1992. Rules of Thumb for Predation Hazard Assessment: Predictions from a Dynamic Model. Am Nat. doi:10.1086/285318.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. doi:10.32614/rj-2017-066.

Brown JS. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behav Ecol Sociobiol. 22(1):37–47. doi:10.1007/BF00395696.

Brown JS. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. Evol Ecol Res.

Brown JS, Kotler BP. 2004. Hazardous duty pay and the foraging cost of predation. Ecol Lett. doi:10.1111/j.1461-0248.2004.00661.x.

Brown JS, Laundre JW, Gurung M. 1999. The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. J Mammal. 80(2):385–399. doi:10.2307/1383287. https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1383287.

Calenge C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecol Modell. doi:10.1016/j.ecolmodel.2006.03.017.

Campos FA, Fedigan LM. 2014. Spatial ecology of perceived predation risk and vigilance behavior in white-faced capuchins. Behav Ecol. 25(3):477–486. doi:10.1093/beheco/aru005.

Charnov EL, Krebs JR. 1975. The Evolution of Alarm Calls: Altruism or Manipulation? Am Nat. doi:10.1086/282979.

Coleman BT, Hill RA. 2014. Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. Anim Behav. doi:10.1016/j.anbehav.2013.11.027.

Cords M. 1990. Vigilance and mixed-species association of some East African forest monkeys. Behav Ecol Sociobiol. doi:10.1007/BF00178323.

Cowlishaw G, Lawes MJ, Lightbody M, Martin A, Pettifor R, Rowcliffe JM. 2004. A simple rule for the costs of vigilance: Empirical evidence from a social forager. Proc R Soc B Biol Sci. doi:10.1098/rspb.2003.2522.

Davies TM, Marshall JC, Hazelton ML. 2018. Tutorial on kernel estimation of continuous spatial and spatiotemporal relative risk. Stat Med. doi:10.1002/sim.7577.

Emerson SE, Brown JS, Linden JD. 2011. Identifying Sykes’ monkeys’, Cercopithecus albogularis erythrarchus, axes of fear through patch use. Anim Behav. 81(2):455–462. doi:10.1016/j.anbehav.2010.11.018.

Fox J, Weisberg S. 2019. An {R} Companion to Applied Regression, Third Edition. Sage.

673 https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

674 Hamilton WD. 1971. Geometry for the selfish herd. J Theor Biol. 31(2):295–311.

675 doi:10.1016/0022-5193(71)90189-5.

676 Hernandez-Aguilar RA. 2009. Chimpanzee nest distribution and site reuse in a dry habitat:

677 implications for early hominin ranging. J Hum Evol. 57(4):350–364.

678 doi:https://doi.org/10.1016/j.jhevol.2009.03.007.

679 https://www.sciencedirect.com/science/article/pii/S0047248409001316.

680 Hirsch BT. 2002. Social monitoring and vigilance behavior in brown capuchin monkeys (Cebus

681 apella). Behav Ecol Sociobiol. 52(6):458–464. doi:10.1007/s00265-002-0536-5.

682 Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models.

683 Biometrical J. doi:10.1002/bimj.200810425.

684 Iki S, Kutsukake N. 2021. Japanese macaques relax vigilance when surrounded by kin. Anim

685 Behav. 179:173–181. doi:https://doi.org/10.1016/j.anbehav.2021.07.001.

686 https://www.sciencedirect.com/science/article/pii/S0003347221002153.

687 Isbell LA. 1994. Predation on primates: Ecological patterns and evolutionary consequences. Evol

688 Anthropol Issues, News, Rev. doi:10.1002/evan.1360030207.

689 Isbell LA, Bidner LR. 2016. Vervet monkey (Chlorocebus pygerythrus) alarm calls to leopards

690 (Panthera pardus) function as a predator deterrent. Behaviour. doi:10.1163/1568539X-00003365.

691 Jaatinen K, Seltmann MW, Öst M. 2014. Context-dependent stress responses and their

692 connections to fitness in a landscape of fear. J Zool. 294(3):147–153. doi:10.1111/jzo.12169.

693 Jaffe KE, Isbell LA. 2009. After the fire: Benefits of reduced ground cover for vervet monkeys

694 (Cercopithecus aethiops). Am J Primatol. doi:10.1002/ajp.20644.

695 Kohl MT, Stahler DR, Metz MC, Forester JD, Kauffman MJ, Varley N, White PJ, Smith DW,

MacNulty DR. 2018. Diel predator activity drives a dynamic landscape of fear. Ecol Monogr. doi:10.1002/ecm.1313.

Kutsukake N, Nunn CL. 2006. Comparative tests of reproductive skew in male primates: The roles of demographic factors and incomplete control. Behav Ecol Sociobiol. 60(5). doi:10.1007/s00265-006-0213-1.

LaBarge LR, Allan ATL, Berman CM, Hill RA, Margulis SW. 2021. Extent of threat detection depends on predator type and behavioral context in wild samango monkey groups. Behav Ecol Sociobiol. 75(1):1–12. doi:10.1007/s00265-020-02959-1. [accessed 2021 May 22]. https://doi.org/10.1007/s00265-020-02959-1.

LaBarge LR, Allan ATL, Berman CM, Margulis SW, Hill RA. 2020. Reactive and pre-emptive spatial cohesion in a social primate. Anim Behav. 163:115–126. doi:https://doi.org/10.1016/j.anbehav.2020.03.005. https://www.sciencedirect.com/science/article/pii/S0003347220300658.

Laundré JW, Hernández L, Altendorf KB. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. Can J Zool. 79(8):1401–1409. doi:10.1139/cjz-79-8-1401. http://www.nrc.ca/cgi-bin/cisti/journals/rp/rp2_abst_e?cjz_z01-094_79_ns_nf_cjz79-01.

Laundré JW, Hernández L, Ripple WJ. 2010. The landscape of fear: Ecological implications of being afraid. Open Ecol J. doi:10.2174/1874213001003030001.

Lea AJ, Blumstein DT. 2011. Age and sex influence marmot antipredator behavior during periods of heightened risk. Behav Ecol Sociobiol. 65(8):1525–1533. doi:10.1007/s00265-011-1162-x. https://doi.org/10.1007/s00265-011-1162-x.

Lima Steven L. 1998. Stress and Decision Making under the Risk of Predation: Recent

Developments from Behavioral, Reproductive, and Ecological Perspectives. In: Advances in the Study of Behavior. Vol. 27. p. 215–290.

Lima Steven L. 1998. Nonlethal Effects in the Ecology of Predator-Prey Interactions. Bioscience. doi:10.2307/1313225.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool. doi:10.1139/z90-092.

Lledo-Ferrer Y, Hidalgo A, Heymann EW, Peláez F. 2009. Field Observation of Predation of a Slate-Colored Hawk, *Leucopternis schistacea*, On a Juvenile Saddle-Back Tamarin, *Saguinus fuscicollis*. Neotrop Primates. 16(2):82–84. doi:10.1896/044.016.0212. https://doi.org/10.1896/044.016.0212.

Lüdecke D, Ben-Shachar M, Patil I, Waggoner P, Makowski D. 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. J Open Source Softw. 6(60). doi:10.21105/joss.03139.

Makin DF, Payne HFP, Kerley GIH, Shrader AM. 2012. Foraging in a 3-D world: how does predation risk affect space use of vervet monkeys? J Mammal. doi:10.1644/11-mamm-a-115.1.

Marler P. 1973. A Comparison of Vocalizations of Red-tailed Monkeys and Blue Monkeys, Cercopithecus ascanius and C. mitis, in Uganda. Z Tierpsychol. 33(3–4):223–247. doi:10.1111/j.1439-0310.1973.tb02093.x.

McLester E, Brown M, Stewart FA, Piel AK. 2019. Food abundance and weather influence habitat-specific ranging patterns in forest- and savanna mosaic-dwelling red-tailed monkeys (Cercopithecus ascanius). Am J Phys Anthropol. doi:10.1002/ajpa.23920.

McLester E, Sweeney K, Stewart FA, Piel AK. 2019. Leopard (Panthera pardus) predation on a red-tailed monkey (Cercopithecus ascanius) in the Issa Valley, western Tanzania. Primates.

doi:10.1007/s10329-018-0700-9.

Minnie L, Boshoff AF, Kerley GIH. 2015. Vegetation Type Influences Livestock Predation by Leopards: Implications for Conservation in Agro-Ecosystems. African J Wildl Res. 45(2):204–214. doi:10.3957/056.045.0204. https://doi.org/10.3957/056.045.0204.

Moll RJ, Redilla KM, Mudumba T, Muneza AB, Gray SM, Abade L, Hayward MW, Millspaugh JJ, Montgomery RA. 2017. The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. J Anim Ecol. doi:10.1111/1365-2656.12680.

Morrell LJ, Ruxton GD, James R. 2011. Spatial positioning in the selfish herd. Behav Ecol. 22(1):16–22. doi:10.1093/beheco/arq157. https://doi.org/10.1093/beheco/arq157.

Nowak K, Le Roux A, Richards SA, Scheijen CPJ, Hill RA. 2014. Human observers impact habituated samango monkeys' perceived landscape of fear. Behav Ecol. 25(5). doi:10.1093/beheco/aru110.

Otali E, Gilchrist JS. 2006. Why chimpanzee (Pan troglodytes schweinfurthii) mothers are less gregarious than nonmothers and males: the infant safety hypothesis. Behav Ecol Sociobiol. 59(4):561–570. doi:10.1007/s00265-005-0081-0. https://doi.org/10.1007/s00265-005-0081-0.

Oversluijs Vasquez MR, Heymann EW. 2001. Crested Eagle (*Morphnus guianensis*) Predation on Infant Tamarins (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichinae). Folia Primatol. 72(5):301–303. doi:10.1159/000049952. https://www.karger.com/DOI/10.1159/000049952.

Papworth S, Böse AS, Barker J, Schel AM, Zuberbühler K. 2008. Male blue monkeys alarm call in response to danger experienced by others. Biol Lett. 4(5):472–475. doi:10.1098/rsbl.2008.0299.

Pays O, Renaud PC, Loisel P, Petit M, Gerard JF, Jarman PJ. 2007. Prey synchronize their vigilant behaviour with other group members. Proc R Soc B Biol Sci.

doi:10.1098/rspb.2006.0204.

Peacor SD, Schiesari L, Werner EE. 2007. Mechanisms of nonlethal predator effect on cohort size variation: Ecological and evolutionary implications. Ecology. doi:10.1890/06-1066.

Peckarsky BL, Abrams PA, Bolnick DI, Dill LM, Grabowski JH, Luttbeg B, Orrock JL, Peacor SD, Preisser EL, Schmitz OJ, et al. 2008. Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator prey Interactions. Ecology. doi:10.1890/07-1131.1.

Piel AK, Bonnin N, RamirezAmaya S, Wondra E, Stewart FA. 2019. Chimpanzees and their mammalian sympatriates in the Issa Valley, Tanzania. Afr J Ecol. 57(1). doi:10.1111/aje.12570.

Piel AK, Strampelli P, Greathead E, Hernandez-Aguilar RA, Moore J, Stewart FA. 2017. The diet of open-habitat chimpanzees (Pan troglodytes schweinfurthii) in the Issa valley, western Tanzania. J Hum Evol. 112:57–69. doi:https://doi.org/10.1016/j.jhevol.2017.08.016. https://www.sciencedirect.com/science/article/pii/S0047248417303603.

Prugh LR, Sivy KJ, Mahoney PJ, Ganz TR, Ditmer MA, van de Kerk M, Gilbert SL, Montgomery RA. 2019. Designing studies of predation risk for improved inference in carnivore-ungulate systems. Biol Conserv. doi:10.1016/j.biocon.2019.02.011.

R Core Team. 2021. R Core Team (2021). R: A language and environment for statistical computing. R Found Stat Comput Vienna, Austria URL http//wwwR-project.org/.

Reyna-Hurtado R, Teichroeb JA, Bonnell TR, Hernández-Sarabia RU, Vickers SM, Serio-Silva JC, Sicotte P, Chapman CA. 2018. Primates adjust movement strategies due to changing food availability. Behav Ecol. doi:10.1093/beheco/arx176.

van Schaik CP, Bshary R, Wagner G, Cunha F. 2022. Male anti-predation services in primates as costly signalling? A comparative analysis and review. Ethology. 128(1):1–14. doi:https://doi.org/10.1111/eth.13233. https://doi.org/10.1111/eth.13233.

788 Schmitz O. 2017. Predator and prey functional traits: Understanding the adaptive machinery driving predator-prey interactions. F1000Research. doi:10.12688/f1000research.11813.1.

790 Seike T. 2022. Frequent predation on primates by crowned eagles (Stephanoaetus coronatus) in Mahale Mountains National Park, Tanzania. Primates. doi:10.1007/s10329-022-00990-6. https://doi.org/10.1007/s10329-022-00990-6.

793 Seyfarth RM, Cheney DL, Marler P. 1980. Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. Science (80-). doi:10.1126/science.7433999.

796 Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. 1987. Primate societies. Primate Soc.:xi, 578–xi, 578.

798 Stephens DW. 2018. Optimal foraging theory. In: Encyclopedia of Ecology.

799 Struhsaker TT. 1977. Infanticide and Social Organization in the Redtail Monkey (Ceraopithecus ascanius schmidti) in the Kibale Forest, Uganda. Z Tierpsychol. 45(1):75–84. doi:https://doi.org/10.1111/j.1439-0310.1977.tb01009.x. https://doi.org/10.1111/j.1439-0310.1977.tb01009.x.

803 Struhsaker TT. 1980. Comparison of the behaviour and ecology of red colobus and redtail monkeys in the Kibale Forest, Uganda. Afr J Ecol. 18(1):33–51.

805 Teelen S. 2007. Influence of chimpanzee predation on associations between red colobus and red-tailed monkeys at Ngogo, Kibale National Park, Uganda. In: International Journal of Primatology. Vol. 28. p. 593–606.

808 Treves A. 1998. The influence of group size and neighbors on vigilance in two species of arboreal monkeys. Behaviour. doi:10.1163/156853998793066168.

810 Treves A. 1999. Has Predation Shaped the Social Systems of Arboreal Primates ? Int J Primatol.

811 20(1):35–67. doi:10.1023/A:1020532216737.

812 Treves A. 2000. Theory and method in studies of vigilance and aggregation. Anim Behav. 813 60(6):711–722. doi:10.1006/anbe.2000.1528.

814 Verdolin JL. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. 815 Behav Ecol Sociobiol. doi:10.1007/s00265-006-0172-6.

816 Willems EP, Hill RA. 2009. Predator-specific landscapes of fear and resource distribution: 817 Effects on spatial range use. Ecology. 90(2):546–555. doi:10.1890/08-0765.1.

818 Wrangham RW. 2000. Why are male chimpanzees more gregarious than mothers? A scramble 819 competition hypothesis. Primate males Causes consequences Var Gr Compos.:248–258.

820 Zuberbühler K, Noë R, Seyfarth RM. 1997. Diana monkey long-distance calls: Messages for 821 conspecifics and predators. Anim Behav. doi:10.1006/anbe.1996.0334.

822

823

TABLES

Table 1: Percentage of overlap between LOF models of different antipredator behaviors for each group. Contours were significant at the 0.05 p-value.

Group compared	**K1**			**K2**		
Anti-predator behaviors	*Vigilance*	*Aggregation*	*Alarm-calling*	*Vigilance*	*Aggregation*	*Alarm-calling*
Vigilance	-	4.03 %	0.19 %	-	2.11 %	5.53 %
Aggregation	4.03 %	-	1.99 %	2.11 %	-	1.99 %
Alarm-calling	0.19 %	1.99 %	-	5.53 %	1.99 %	-

FIGURE LEGENDS

Figure 1: Map of western Tanzania with the Issa Valley Research area indicated by the box in the center of the map. The 95 % kernel density estimation of habitat utilization from July 2018-December 2019 of group K1 (orange) and group K2 (green).

Figure 2: Heatmap demonstrating the pairwise comparisons, pulled from a Tukey's HSD. The box on the left shows results ~~,~~ between habitat types as predictors of vigilance behavior ~~by group a) K1 and b) K2~~. The right-hand box indicates results from the aggregation model, showing comparisons between habitat types (middle column) and age/sex classes (righthand column). Results separated by a dashed line indicating group K1 (top) and K2 (bottom). 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 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 4: Heatmap demonstrating the pairwise comparisons, pulled from Tukey's HSD, between age/sex class 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 3: Closer aggregations of conspecifics (meters) predict greater probability of alarm-calling in K1 only. Visualization contains +/- standard error as gray bands around the estimate line, rendered from GLM.

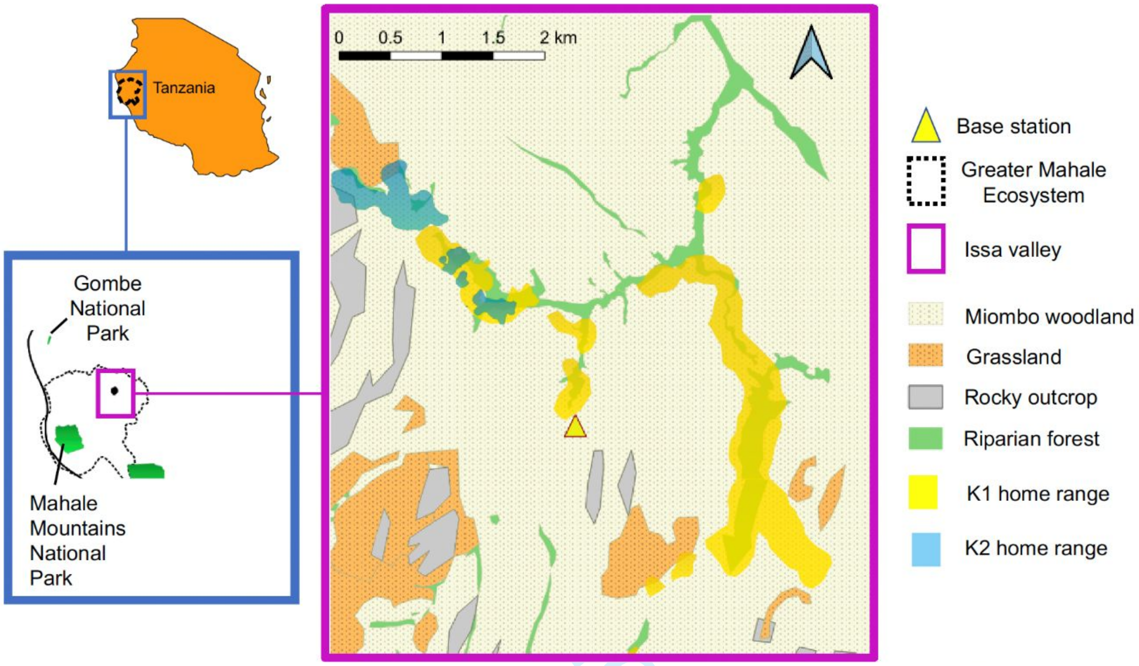
Figure 4~~5~~: Closer aggregations of conspecifics (meters) is predicted by observations of more vigilant individuals in a) K1 but not in b) K2. Visualization contains +/- standard error as gray bands around the estimate line, rendered from GLM. This model differs qualitatively from the model with vigilance as a response variable given the additional control of age/sex class, however both models show the same direction of the relationship between vigilance and aggregation behavior for K1. K2 shows the opposite trend, with greater vigilance in more spaced aggregations.

~~Figure 6: Closer aggregations of conspecifics (meters) predict greater probability of alarm-calling in K1 only. Visualization contains +/- standard error as gray bands around the estimate line, rendered from GLM.~~

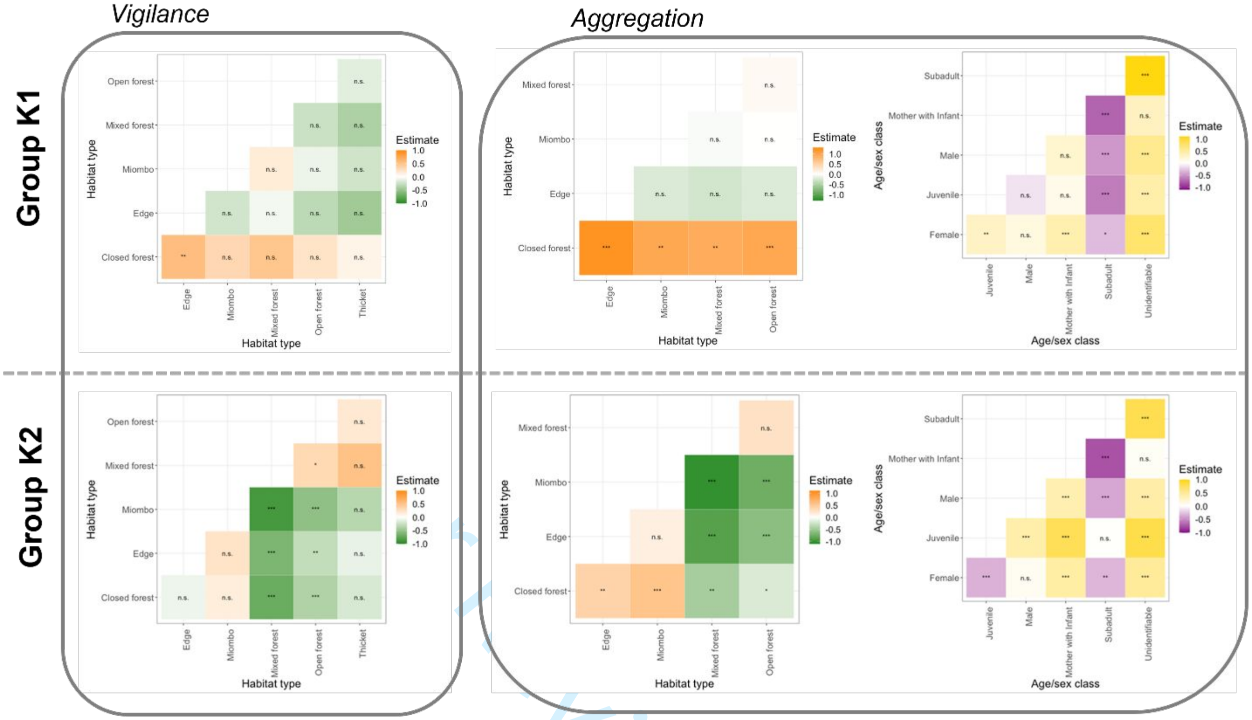
~~Figure 7~~Figure 5: Relative risk models of the occurrences of antipredator behavior relative to the monkey's home range. Contours reflect significantly increased predation risk at the p= 0.05 alpha-level (dashed line) and the p = 0.01 alpha-level (solid line). The models were mapped using a log-scale and confined to a polygon representing a 95% kernel density estimation of the group's home range.

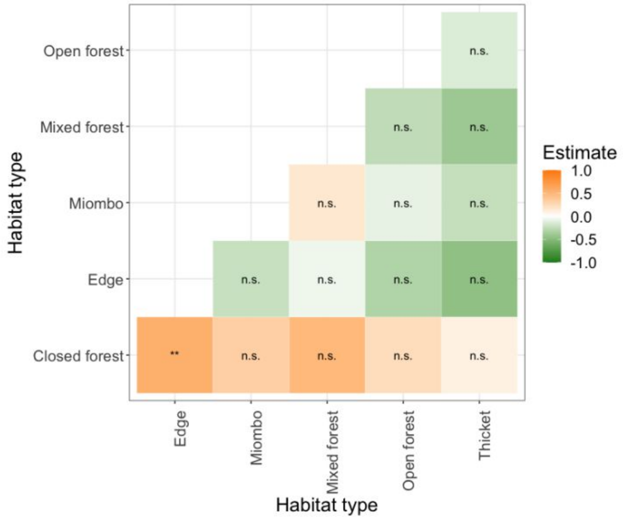
FIGURES

1)

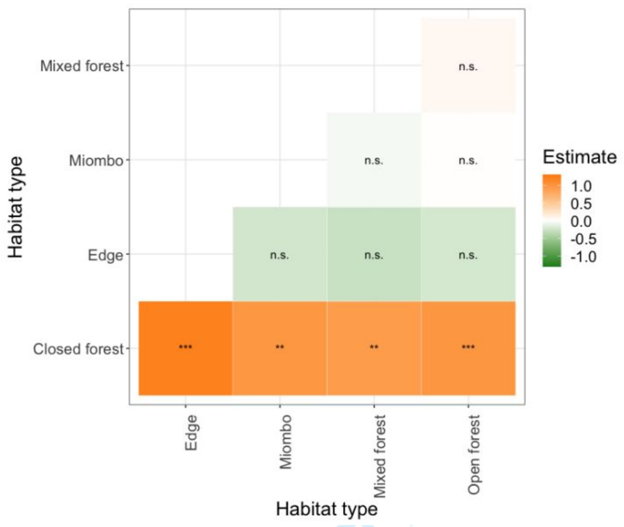

Tanzania
Gombe National Park
Mahale Mountains National Park
0 0.5 1 1.5 2 km
Base station
Greater Mahale Ecosystem
Issa valley
Miombo woodland
Grassland
Rocky outcrop
Riparian forest
K1 home range
K2 home range

2~~a~~)

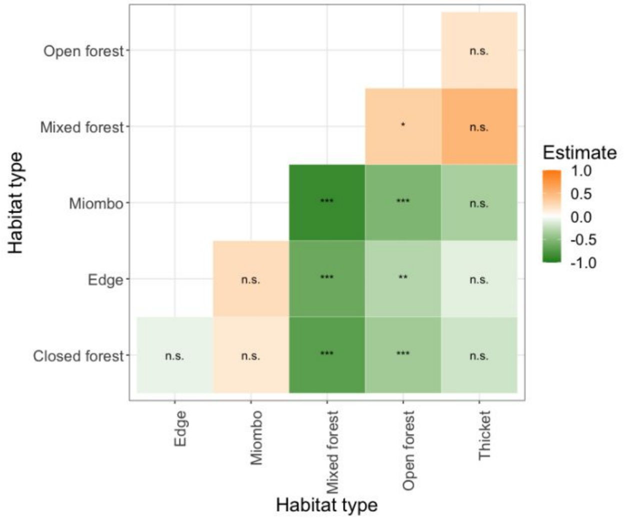

Vigilance
Aggregation
Group K1
Group K2
Habitat type
Open forest
Mixed forest
Miombo
Edge
Closed forest
Thicket
Estimate
1.0
0.5
0.0
-0.5
-1.0
Age/sex class
Subadult
Mother with Infant
Male
Juvenile
Female
Unidentifiable
n.s.


Open forest
Mixed forest
Miombo
Edge
Closed forest
Habitat type
Edge
Miombo
Mixed forest
Open forest
Thicket
Habitat type
Estimate
1.0
0.5
0.0
-0.5
-1.0
n.s.
**

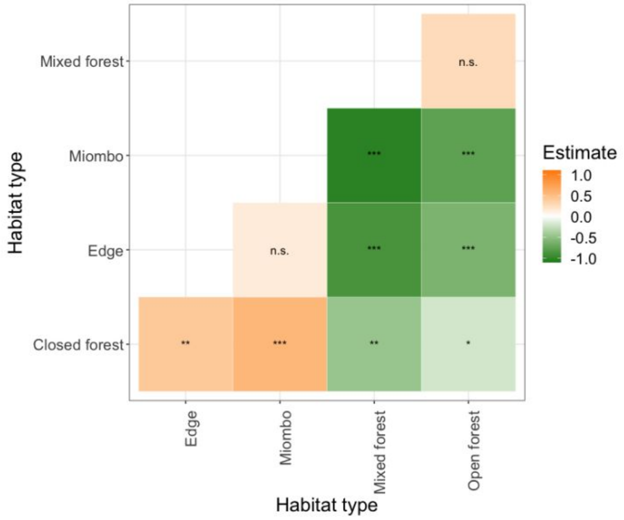
~~2b)~~


Mixed forest
Miombo
Edge
Closed forest
Habitat type
n.s.
n.s.
n.s.
n.s.
n.s.
n.s.
***
**
**
***
Edge
Miombo
Mixed forest
Open forest
Habitat type
Estimate
1.0
0.5
0.0
-0.5
-1.0

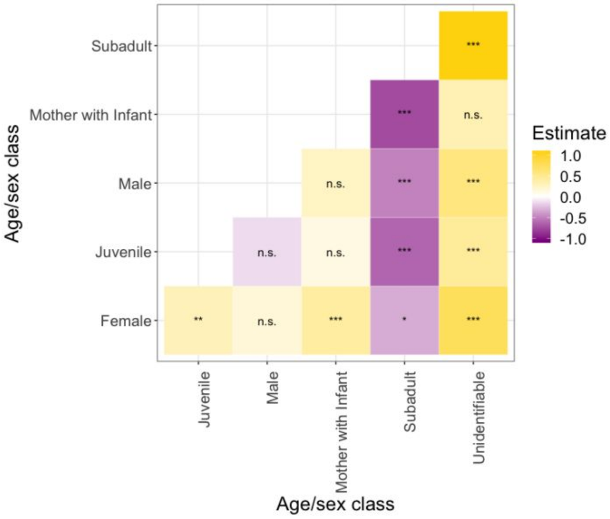
~~3a)~~


Open forest
Mixed forest
Miombo
Edge
Closed forest
Habitat type
n.s.
*
n.s.
***
***
n.s.
n.s.
***
**
n.s.
n.s.
n.s.
***
***
n.s.
Edge
Miombo
Mixed forest
Open forest
Thicket
Habitat type
Estimate
1.0
0.5
0.0
-0.5
-1.0

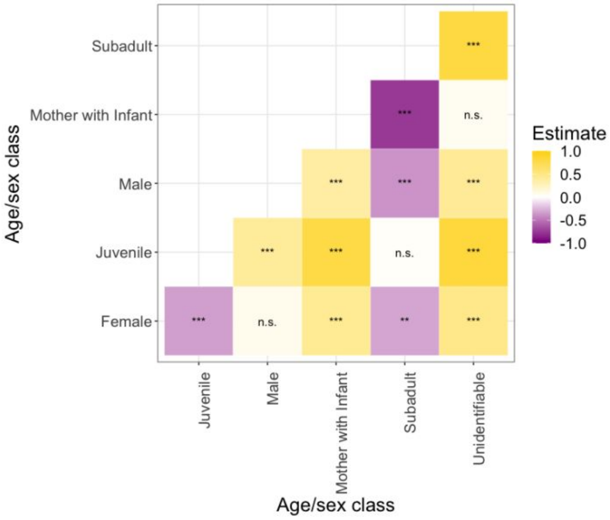
~~3b)~~


Mixed forest
Miombo
Edge
Closed forest
Habitat type
n.s.
***
***
n.s.
***
***
**
***
**
*
Edge
Miombo
Mixed forest
Open forest
Habitat type
Estimate
1.0
0.5
0.0
-0.5
-1.0

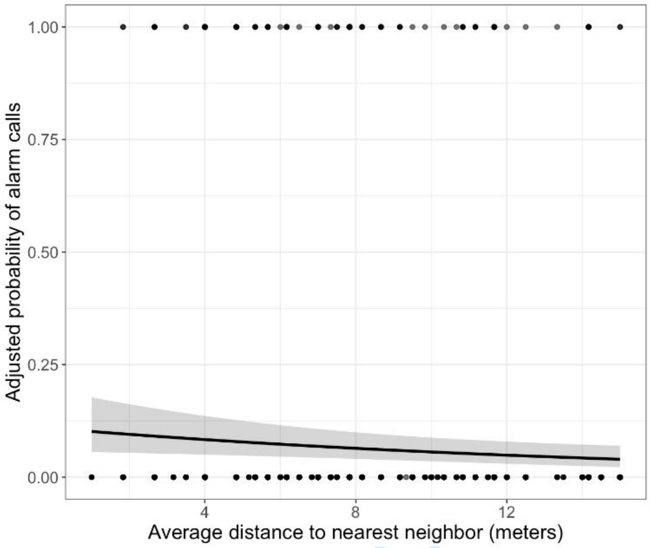
~~4a)~~


Subadult
Mother with Infant
Male
Juvenile
Female
Age/sex class
***
***
n.s.
n.s.
***
***
n.s.
n.s.
***
***
**
n.s.
***
*
***
Juvenile
Male
Mother with Infant
Subadult
Unidentifiable
Age/sex class
Estimate
1.0
0.5
0.0
-0.5
-1.0

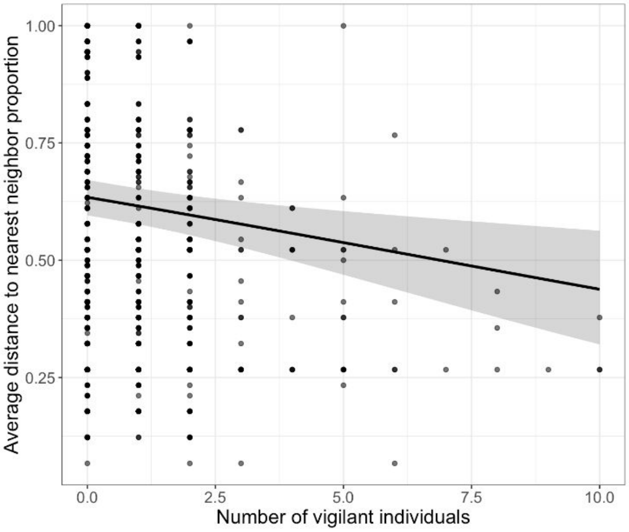
~~4b)~~

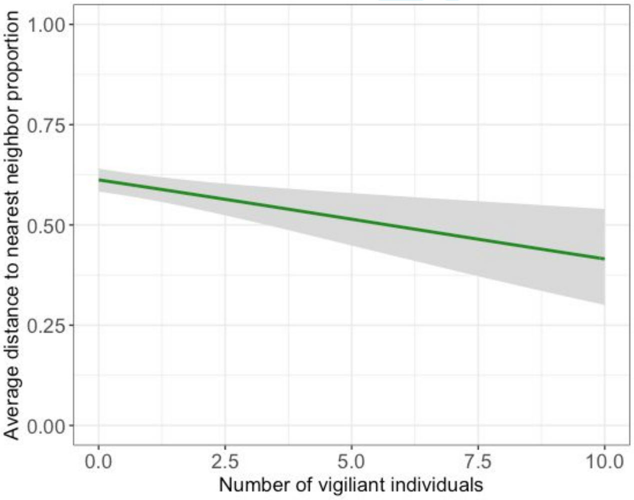

Subadult
Mother with Infant
Male
Juvenile
Female
Age/sex class
***
***
n.s.
***
***
***
***
***
n.s.
***
***
n.s.
***
**
***
Juvenile
Male
Mother with Infant
Subadult
Unidentifiable
Age/sex class
Estimate
1.0
0.5
0.0
-0.5
-1.0

3)

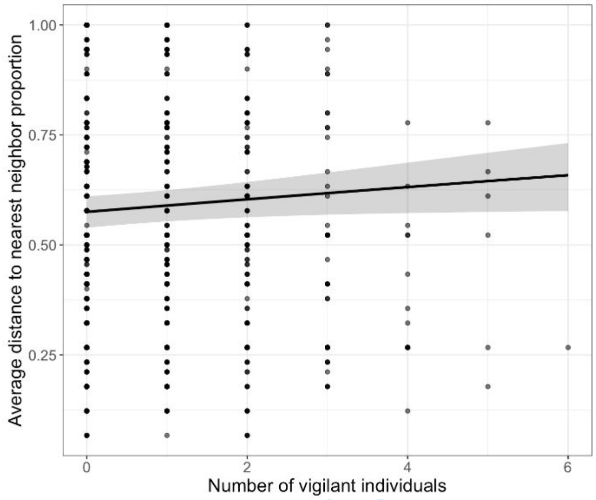

Adjusted probability of alarm calls
1.00
0.75
0.50
0.25
0.00
4
8
12
Average distance to nearest neighbor (meters)

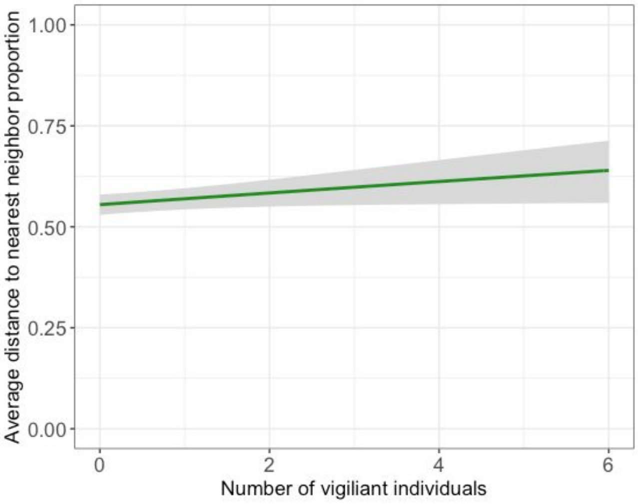
4~~5~~a)


Average distance to nearest neighbor proportion
1.00
0.75
0.50
0.25
0.0
2.5
5.0
7.5
10.0
Number of vigilant individuals

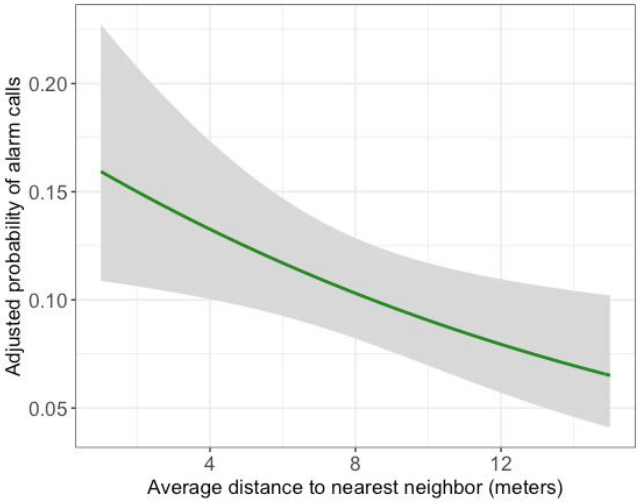

Average distance to nearest neighbor proportion
1.00
0.75
0.50
0.25
0.00
0.0
2.5
5.0
7.5
10.0
Number of vigiliant individuals

4~~5~~b)

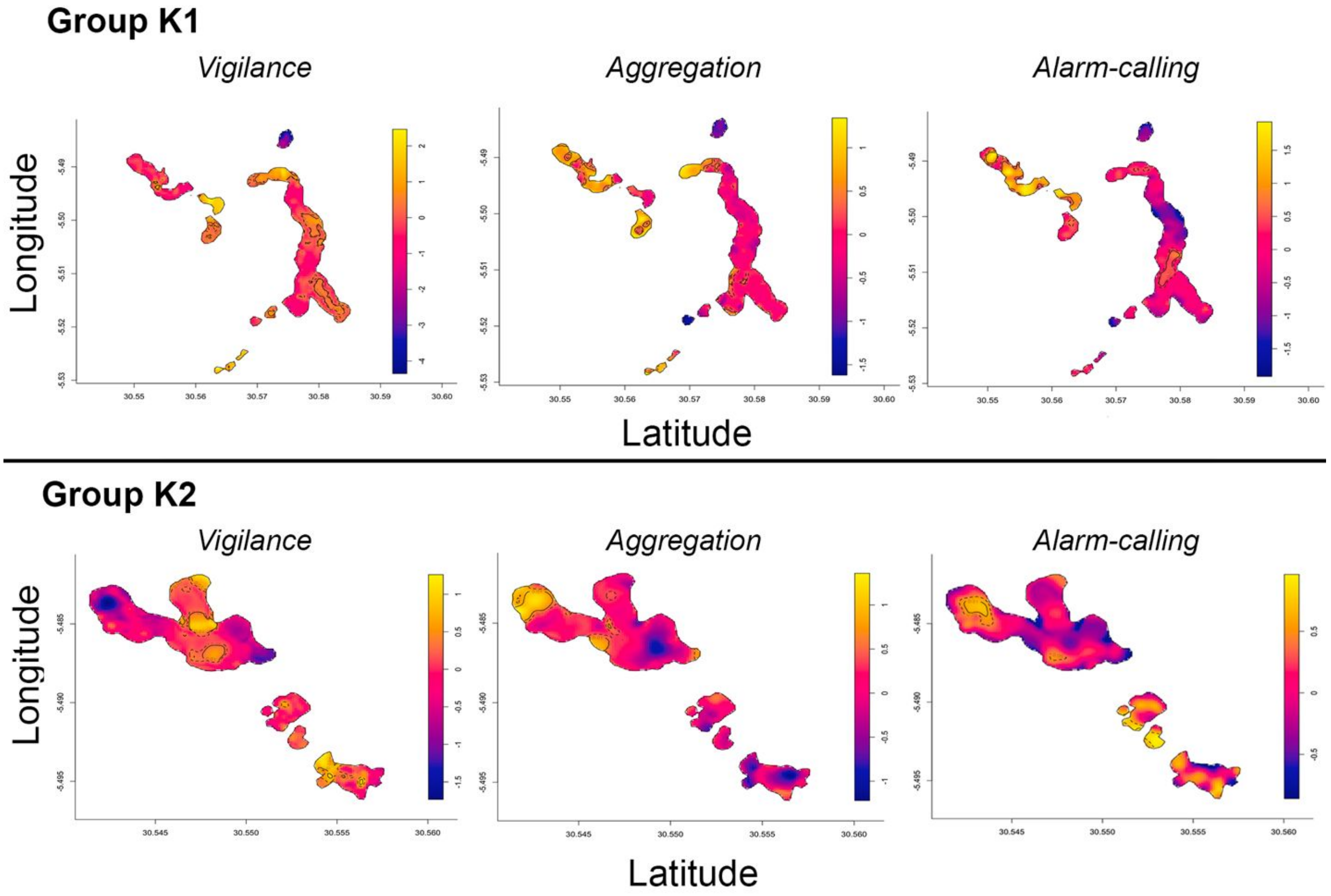

1.00
0.75
0.50
0.25
Average distance to nearest neighbor proportion
0
2
4
6
Number of vigilant individuals


1.00
0.75
0.50
0.25
0.00
Average distance to nearest neighbor proportion
0
2
4
6
Number of vigilant individuals

~~6)~~


Adjusted probability of alarm calls
0.20
0.15
0.10
0.05
4
8
12
Average distance to nearest neighbor (meters)

5~~7~~)


Group K1
Vigilance
Aggregation
Alarm-calling
Longitude
Latitude
-5.49
-5.50
-5.51
-5.52
-5.53
30.55
30.56
30.57
30.58
30.59
30.60
Group K2
Vigilance
Aggregation
Alarm-calling
Longitude
Latitude
-5.485
-5.490
-5.495
30.545
30.550
30.555
30.560