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## ARTICLE

# Behavioral responses to spatial variation in perceived predation risk and resource availability in an arboreal primate

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**Abstract**

Prey species must often face a trade-off between acquiring resources and minimizing predation risk. The spatial variation in predation risk across a landscape, as perceived by prey across their foraging or home range, creates a “landscape of fear” by which individuals modify their behavior in response to the level of perceived risk. Here, we explored the influence of perceived predation risk, habitat features associated with risk, and fruit availability, on the spatial variation in behavior of the endangered forest-dwelling samango monkey (*Cercopithecus albogularis schwarzi*). We collected behavioral and location data on two habituated samango monkey groups in the Soutpansberg Mountains, South Africa, between 2012 and 2016. We further collected location data of the samango monkey’s acoustically distinct alarm call, which has an unambiguous association with aerial predators, to spatially map perceived risk across the landscape. Using generalized linear mixed models, we found that perceived risk from eagles significantly influenced the spatial distribution of critical life-functioning behaviors, with samango monkeys increasing feeding and foraging in high-risk areas. To mitigate this risk, samangos increased cohesion between group members, which subsequently reduced vigilance levels. Group cohesion further increased in high-risk areas with abundant fruit, relative to high-risk, fruit-poor areas, demonstrating the monkey’s foraging/risk trade-off. Feeding was also reduced in areas of low canopy height, while vigilance decreased with increasing understory visibility and distance from sleep site, showing the influence of landscape features on risk perception from other predator guilds. Thus, for arboreal species foraging in a 3-D landscape, risk perception may occur at multiple scales and in response to multiple predator guilds. Only moving was influenced by fruit availability, either due to moving between localized food patches or from escaping high-risk areas following feeding bouts. These findings highlight that risk-taking in samango monkeys is only associated with behaviors fundamental to survival at a given

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location and that increased cohesion between neighbors is the main anti-predator response in this species.

#### KEYWORDS

landscape of fear, predation risk, resource availability, samango monkey, spatial behavior

## INTRODUCTION

Understanding how animals utilize their environment over both space and time is one of the central issues in behavioral ecology (Lima, 1998) and has implications for directing conservation and wildlife management efforts. While the spatial and temporal distribution of resources (Pyke, 1984; Schoener, 1971) and competitors (Swanson et al., 2016) play a key role in how a species utilizes their environment (Pyke, 1984, Schoener, 1971), so too, does the presence of predators (Brown et al., 1999). Predators not only have a direct, lethal effect on prey individuals, but also impose an indirect effect through behaviorally mediated changes. These behavioral changes, which have consequences for individual physiology, population dynamics, and community interactions (Brown & Kotler, 2004), can be just as important, if not more so, than the direct lethal effects of predation (Brown et al., 1999; Creel & Christianson, 2008; Kuijper et al., 2013; Laundré et al., 2010; Lima & Dill, 1990; Peers et al., 2018). As predation risk varies spatially across heterogeneous landscapes, owing to the variability in visibility, detection, and movement of predators and prey alike (Gaynor et al., 2019), the perception of risk by prey individuals also varies spatially. This perceived risk is based on indirect (landscape associated) and direct (predator associated) cues across the prey individual's foraging or home range and manifests as a "landscape of fear" (Gaynor et al., 2019; Laundré et al., 2001).

In more cognitively advanced species, the landscape of fear may exist as a "mental map" but can also occur in real time as prey navigate heterogeneous landscapes with varying risk. Consequently, prey species frequently adopt two behavioral strategies in order to actively minimize risk; avoidance of areas perceived as high risk (Coleman & Hill, 2014a; Creel et al., 2005; Lima & Dill, 1990; Thaker et al., 2011; Valeix et al., 2009; Willems & Hill, 2009), or modification of behavior at a given location. Specifically, in areas perceived as high-risk prey species may actively increase vigilance levels (Campos & Fedigan, 2014; Laundré et al., 2001), alter movement patterns (Fischhoff et al., 2007; Fortin et al., 2005; Willems & Hill, 2009), shift activity patterns toward less risky times (Bonnot et al., 2013; Creel et al., 2008; Palmer et al., 2017; Valeix et al., 2009), or increase group size/cohesion (LaBarge

et al., 2020; Lima, 1995; Scott-Samuel et al., 2015). However, these behavioral strategies to minimize risk must often be balanced with other behaviors critical to survival, such as acquiring food, meaning nearly all antipredator behaviors involve some element of cost (Lima & Dill, 1990). Subsequently, prey species may either opt to forage in food-poor areas where the risk of predation is low (birds: Suhonen, 1993, Walther & Gosler, 2001; fish: Dill & Fraser, 1984; cetaceans: Heithaus & Dill, 2002; ungulates: Creel et al., 2005, Hernández & Laundré, 2005, Fortin & Fortin, 2009, Bonnot et al., 2013, Cappa et al., 2014; and primates: Cowlshaw, 1997), or, where resources are finite or clumped, forage in food-rich areas where predation risk is inherently greater (primates: Wright, 1998, Stone, 2007; ungulates: Valeix et al., 2009, Riginos, 2015, Schmidt & Kuijper, 2015).

In light of the importance of resource acquisition to survival, the majority of studies exploring the spatial variation in antipredator behavior have focused on the foraging/vigilance trade-off (Campos & Fedigan, 2014; Heithaus & Dill, 2002; Laundré et al., 2001) while largely ignoring other behavioral responses. However, in studies where other behavioral responses have been considered, animals typically reserve less intrinsic behaviors for areas where predation risk is lowest. For example, Cowlshaw (1997) found that desert baboons (*Papio ursinus*) in Namibia preferentially foraged in food-poor areas to minimize predation risk from leopards (*Panthera pardus*) and lions (*Panthera leo*), while they also preferred the safest habitats for other behaviors such as resting and grooming. Similarly, De Vos et al. (2015) found that Cape fur seals (*Arctocephalus pusillus pusillus*) in South Africa preferred safe, shallow waters when engaging in social and thermoregulatory behaviors, where risk from white shark (*Carcharodon carcharias*) predation was reduced. Furthermore, Palmer et al. (2017) found that both African buffalo (*Syncerus caffer*) and common wildebeest (*Connochaetes taurinus*) in Tanzania increased their levels of relaxed behaviors during the wet season in areas where encounter risk with lions was low. In contrast, relaxed behaviors were more common in plains zebra (*Equus quagga*) during low-risk periods in the dry season (Palmer et al., 2017).

One of the challenges with these types of studies, however, lies in quantifying risk from the perception of the prey (Gaynor et al., 2019; Peers et al., 2018). Common

proxies for measuring predation risk, such as prey vigilance or avoidance behaviors, predator hunting strategies or kill sites, or giving-up densities, are invariably influenced by habitat structural characteristics (Lima & Dill, 1990) and, in the case of giving-up densities, are also influenced by nutritional preferences (McMahon et al., 2018). Consequently, these methods do not explicitly measure perceived risk (Peers et al., 2018; Searle et al., 2008), leading to inconsistencies in quantifying the nonlinear relationship between risk and response (Gaynor et al., 2019). This is particularly relevant in multi-predator environments where the appropriate anti-predator response varies with each predator guild (Cresswell & Quinn, 2013; Shultz et al., 2004; Willems & Hill, 2009). Although quantifying predator-specific predation risk can be difficult for most species, primates are a notable exception in that predator-specific alarm responses of some primate species are easily recognizable and can be attributed to specific predators (Cheney & Seyfarth, 1981; Seyfarth et al., 1980), while also providing information on the location of predators (Murphy et al., 2013; Willems & Hill, 2009). However, although alarm calls are indicative of an individual or group's perception of risk, the habitat structural characteristics associated with risk are also likely to influence an individual's perception of risk, albeit at different spatial scales (Gaynor et al., 2019). This is particularly relevant in arboreal species, which experience 3-D landscapes of fear (Emerson et al., 2011; Makin et al., 2012). Despite this, studies exploring the influence of each respective measure of risk on prey behavior are almost entirely lacking (Coleman & Hill, 2014a; Willems & Hill, 2009).

In a classic example of predator-specific landscapes of fear, Willems and Hill (2009) found that vervet monkeys (*Chlorocebus pygerythrus*) at their South African field site avoided areas of high perceived risk from chacma baboons and leopards, regardless of the availability of food in these areas. In contrast, perceived risk from African crowned eagles (*Stephanoaetus coronatus*) and African rock pythons (*Python sebae*) did not influence range use. Similarly, Coleman and Hill (2014a) found that samango monkeys (*Cercopithecus albogularis schwarzi*) at the same field site avoided areas associated with high perceived risk from African crowned eagles and Verreaux's eagles (*Aquila verreauxii*), but also avoided areas of low visibility and canopy height, factors associated with risk from terrestrial predators (Cowlshaw, 1997; du Bothma & Le Richie, 1986; Valeix et al., 2009). Although many species have been observed to avoid areas perceived as high risk, these areas still offer some ecological value through forming part of a prey individual's foraging or home range. Yet, what individuals do when in these areas remains largely unknown.

The aim of this study, therefore, was to determine the influence of perceived predation risk and fruit availability on the spatial variation in behavior of the predominantly frugivorous, arboreal samango monkey (*Cercopithecus albogularis schwarzi*). Perceived predation risk in this study was largely attributed to the presence of aerial predators, owing to the samango monkey's predator-specific alarm call (Coleman & Hill, 2014a; Fuller, 2013). While the association of other alarm calls with different predator guilds is ambiguous (Fuller, 2013), these predators still pose significant risks and thus still contribute to the samango monkey's landscape of fear (Coleman & Hill, 2014a). We therefore additionally explored the influence of understory visibility, canopy height and distance from sleep site, and factors indirectly associated with predation risk (Albert et al., 2011; Anderson, 1998; Coleman & Hill, 2014a; Cowlshaw, 1997; Fortin et al., 2009; Shultz, 2001; Valeix et al., 2009), which have previously been shown to influence spatial utilization in this species (Coleman & Hill, 2014a). Finally, despite fruit availability having no influence on the intensity of space use in this species (Coleman & Hill, 2014a), we explored how samangos responded behaviorally to the availability of location-specific resources.

We predicted that groups would only enter high-risk areas to engage in behaviors intrinsic to survival, such as feeding (Pyke, 1984; Schoener, 1971). When in these areas, individuals should also adopt appropriate antipredator behaviors in order to mitigate the effects of increased risk, such as increasing vigilance and group cohesion (Campos & Fedigan, 2014; LaBarge et al., 2020; Lima, 1995; Teichroeb & Sicotte, 2012). As samango monkeys have previously been shown to avoid areas of low visibility and canopy height (Coleman & Hill, 2014a), we also expected feeding to increase in these areas corresponding to the associated risk. We further expected feeding would increase in fruit-rich areas (Whitten, 1988), in addition to moving, due to the finite and localized distribution of this resource at our field site (Coleman, 2013; Coleman & Hill, 2014a). Behaviors that do not depend on location-specific resources, such as grooming and resting, should be reserved for the safest habitats (Cowlshaw, 1997). Finally, we also predicted that behavior at any location would additionally be driven by an interaction between perceived risk and fruit availability (Riginos, 2015; Schmidt & Kuijper, 2015; Stone, 2007).

## MATERIALS AND METHODS

### Study species and study site

The samango monkey is South Africa's only exclusively forest-dwelling primate and is largely restricted to tall-

canopy indigenous forests across South Africa (Linden et al., 2016). Samango monkeys are primarily arboreal, diurnal guenons that live in single-male, multi-female groups (Henzi & Lawes, 1987) of around 40 individuals (Coleman & Hill, 2014b; Lawes et al., 2013; Linden et al., 2016). They are predominantly frugivorous but display considerable dietary flexibility, with leaves contributing significantly to the diet in some populations owing to the samango's gut morphology (Bruerton et al., 1991; Bruerton & Perrin, 1988, 1991; Coleman & Hill, 2014a; Lawes, 1991; Parker et al., 2020). This flexibility in feeding habits is responsible for the distribution of this genera throughout much of sub-Saharan Africa (Coleman & Hill, 2014b). Seeds (Linden et al., 2015), flowers, and insects (Butynski, 1990; Kaplin, 2001) are also consumed with varying regularity (Coleman & Hill, 2014b).

We conducted fieldwork at the Primate and Predator Project, Lajuma Research Centre, in the western Soutpansberg Mountains, South Africa (23°02'23"S, 29°26'05"E). Altitude at the field site ranged from 1150 to 1750 m. Climate is described as temperate, with highly seasonal conditions resulting in cool, dry winters from April to September and hot, wet summers from October to March (Willems, 2007). These conditions give rise to a variety of microclimates, which result in substantial variation in the diversity of both flora and fauna (Brock et al., 2003; Willems, 2007). This, in turn, creates a highly heterogeneous environment, with the south-facing cliffs of the mountain dominated by tall-canopy, indigenous mistbelt forest (Mucina & Rutherford, 2006), which exists in a mosaic of secondary shorter forests such as riparian forests, semi-deciduous woodlands, and thicket (Mostert, 2006). These forests are further fragmented by montane grasslands, farmland, and residential gardens.

At Lajuma, aerial predators such as the African crowned eagle and, to a lesser extent, the Verreaux's eagle, pose the greatest risk to samango monkeys largely owing to the samango's arboreal nature (Coleman & Hill, 2014a; Cordeiro, 2003) and the hunting strategies of this predator guild (Malan et al., 2016; Shultz, 2001). Terrestrial predators such as leopard and African rock python, however, are encountered much less frequently and so risk from these predator guilds is considered minimal (Coleman & Hill, 2014a). Venomous snakes such as the black mamba (*Dendroaspis polylepis*), puff adder (*Bitis arietans*), and Mozambique spitting cobra (*Naja mossambica*), while not directly preying on samangos, still present a significant mortality risk if encountered and may therefore influence antipredator behavior. However, as observed with other arboreal guenons, attacks by venomous snakes are rarely recorded (Foerster, 2008) and are almost always detected and avoided well before they become dangerous (Fuller, 2013; Smith et al., 2008).

As such, snakes were not assumed to have a significant influence on antipredator behavior of samango monkeys at Lajuma.

## Data collection

We collected behavioral data on two habituated groups of samango monkeys ("Barn Group," 30–40 individuals, and "House Group," 60–70 individuals) between February 2012 and December 2016, for an average of eight full days per month. Full days consisted of maintaining audio-visual contact with the group from morning sleep site to evening sleep site, without losing contact for more than 60 continuous minutes. We collected instantaneous group scan samples (Altmann, 1974) within a 5-min window on as many individuals as possible, using a handheld PDA (Psion Teklogix Workabout Pro 3). Scan samples occurred at 20-min intervals (e.g., 12:20, 12:40, 1:00 PM), with the group's location recorded with each scan sample using a GPS device (Garmin GPSmap 64S) and taken from a central position within each group. Information collected during each scan sample included date, time, group ID, and for each visible individual: age–sex class, general behavior (see below), vigilance, and number of conspecific neighbors within 5 m of the sampled individual, as a proxy for group cohesion. However, data on vigilance were only recorded from April 2014 meaning only 33 months of data were available for this behavior. General behavioral categories used in this study were feeding (feeding, foraging), grooming (given/received), resting (sitting, standing, huddled, lying, sleeping), moving (walking, running), and vigilance (scanning/visual search directed beyond an arm's reach [Treves, 1998] including looking up/down) (see Parker, 2019, for specific behavioral definitions).

To specify spatial variation in perceived predation risk, we followed the approach of Coleman and Hill (2014a) using the samango monkeys' acoustically distinct alarm calls, particularly the ka and katrain calls, which have an unambiguous association with aerial predators (Fuller, 2013). Samango monkey calls such as the boom and pyow, although being attributed to predators in some contexts, appear to have multiple functions and so we did not consider them reliable indicators of perceived risk here (Fuller, 2013; Papworth et al., 2008). The location and details of all kas, katrains, and group-wide alarm calls were recorded on an all-occurrence basis, resulting in a total of 1110 alarm calls across both groups over the study period, with the context known for 210 calls (eagle: 198, snake: 12). A further 323 calls were associated with antipredator behavior in response to raptors (e.g., jumping into trees, moving down from canopy, scanning sky), meaning 47% of calls could be attributed

to the presence of aerial predators. While no context could be established for the remaining 577 calls, these calls are still informative as they indicate the monkeys' perception of risk (Campos & Fedigan, 2014; Willems & Hill, 2009) and, as such, all alarm calls were used to create spatial maps of perceived predation risk. While this resulted in landscapes indicating overall perceived risk, likely comprised of multiple predator guilds, the large proportion of calls associated with raptors meant the landscapes of fear were predominantly focused on this predator guild.

Fruit availability data were collected using a combination of phenological transects and random quadrat sampling to effectively determine all types of density-related features (Southwood & Henderson, 2000). Phenological transects were established across each group's home range and included 20 individually marked trees from 24 species (480 trees in total, see Parker, 2019). Tree species were selected due to the relative importance of each species to the diet of the samango monkey (Coleman, 2013; Linden et al., 2015), while also giving a representation of various habitat types across the study area and accounting for trees of various sizes. All trees were monitored monthly for the number of leaves, fruit, seed pods, and flowers on individually marked branches. This value was then multiplied by the estimated number of branches for that tree to give a total food availability estimate per tree. Where there were no items on the marked branches but items on the tree, estimates were made for the whole tree. We restricted our monthly estimates of food availability to that of fruit species ( $n = 20$ ), owing to the predominantly frugivorous diet of the samango monkey (Coleman & Hill, 2014b; Lawes, 1991; Linden et al., 2016), and the likelihood of behavior varying spatially in response to this finite and clumped resource over more readily available food items.

To calculate fruit availability, habitat visibility, and canopy height throughout each group's home range, we randomly generated  $5\text{ m} \times 5\text{ m}$  quadrats ( $n = 702$ ), using the ArcGIS add-on Hawth's Tools (Beyer, 2004). Within each plot, we recorded the height (in meters) of all identifiable trees with a diameter  $>10\text{ cm}$  at a height of 1 m. We then took the average height across all trees sampled in each plot to give an estimate of mean canopy height per plot. To estimate understory visibility, we counted the number of squares on a  $0.8\text{ m}^2$  checkerboard with  $0.1\text{ m}^2$  cells at a distance of 5 m and 10 m, and at a height of 0 m and 1.25 m, for each of the four cardinal point directions from the northwest corner of each vegetation plot. This resulted in 16 checkerboard measurements per plot, which we averaged to get an estimate of understory visibility per plot.

## Data processing

We imported all data into QGIS 3.0 (QGIS Development Team, 2017) with the cell size of all output rasters set to  $5\text{ m} \times 5\text{ m}$  to be consistent with GPS accuracy in the field. We then created utilization distributions, landscapes of fear, and monthly fruit availability maps to spatially map these various landscapes across each group's home range. In addition, we also imported behavioral data into QGIS for visualization.

We created annual home ranges delineating the utilization distribution of each group using adaptive localized convex hulls (a-LoCoH) analysis (Getz et al., 2007; Getz & Wilmers, 2004). This home range estimation method is particularly useful for small ranging species living in fragmented landscapes, as it has a superior ability of identifying hard boundaries and parts of the range which are avoided (Ryan et al., 2006), while also dealing with temporally close data points (Coleman & Hill, 2014a; Getz et al., 2007; Getz & Wilmers, 2004; Ryan et al., 2006). We calculated home ranges using the "t-LoCoH" package (Lyons et al., 2013) in R 3.5 (R Core Team, 2018), using the distance between the widest points within each groups' respective annual home range as the  $\alpha$ -value to allow for the correct construction of isopleths (Getz et al., 2007).

We created annual landscapes of fear for each group by initially using the "Kernel Density Estimation" tool in QGIS to create density distributions of GPS points for all alarm calls recorded for each year for each group, resulting in five alarm calls layers for each group. A PLUG-IN bandwidth was used for the nearest neighbor search distance due to its reduced variability and increased performance when compared to least-squares cross validation (Gitzen et al., 2006) and its ability to operate with small sample sizes, which was evident in some of our sample years. We then calculated each annual landscape of fear by dividing the alarm call layer by the utilization distribution (Coleman & Hill, 2014a; Willems & Hill, 2009) using the Raster Calculator, to account for the time spent in certain areas of the home range and ensure that more frequently visited areas were not erroneously weighted as being riskier than less frequently visited areas. This process also bound the annual landscape of fear by each groups' respective home range.

To estimate mean monthly fruit availability at a given location, we averaged the availability of fruit across the 20 individuals sampled for each of the 20 fruiting tree species, for each month across the five sample years. We then applied these monthly estimates to each vegetation plot based on the number of fruit species identified within each plot, giving a mean monthly fruit availability estimate across all species for each plot. We then

imported all vegetation plots into QGIS and used Inversed Distance Weighted (IDW) interpolation, with a distance coefficient of 5, to create mean monthly fruit availability maps. A distance coefficient of 5 was used in all IDW calculations to maintain the influence of clumped resources in subsequent food availability maps. We also used IDW interpolation in the same way to create understory visibility and canopy height maps across each group's home range using these mean measurements estimated from the vegetation plots. To calculate the distance from morning sleep site for each scan sample, we used the "Distance Matrix" tool in QGIS to calculate the distance (in meters) of each scan sample from the corresponding first sample collected each day. Finally, we used the GPS point associated with each scan sample to extract values for the landscape of fear, fruit availability, understory visibility, canopy height, and distance from sleep site, using the "Point Sampling Tool" in QGIS.

## Statistical analysis

We calculated the number of individuals displaying a particular behavior (feeding, grooming, resting, moving, and vigilant) as a proportion of the total number of individuals recorded within each 5-min scan sample, using the group by, summarize and mutate functions in the "dplyr" package (Wickham et al., 2017) in R. We confined all analyses to data on adult females to remove any bias in age–sex class and owing to the fact that samango monkey groups comprise mainly of adult females (Henzi & Lawes, 1987). Restricting analyses in this way also reduces the possible error from variability in age–sex classes sampled in each scan sample, while also reducing potential bias from including a single adult male who was easily identifiable and regularly sampled. We used a minimum threshold of five individuals per scan sample to remove biases resulting from scan samples comprising of few individuals. We also calculated the mean number of conspecific neighbors within a 5 m radius of the scanned individual, taken across all individuals sampled within the 5-min scan window, using the aforementioned functions within the "dplyr" package. This was used as an additional predictor variable in our vigilance analysis, but also as our response variable in our near neighbors analysis.

We used generalized linear mixed models (GLMMs) with a beta error structure and logit link to model the proportion of individuals per scan sample that were feeding, grooming, resting, moving, and vigilant for each samango monkey group across the study period. In addition, we used a GLMM with a Gamma error structure

and log link to model the mean number of near neighbors per sample window. We included perceived predation risk, fruit availability, understory visibility, canopy height, and distance from morning sleep site as predictor variables. As behavior at a given location may be influenced by both perceived predation risk and fruit availability (Riginos, 2015; Schmidt & Kuijper, 2015; Stone, 2007), we additionally included an interaction term between these variables in our models. In our vigilance model, we further included the mean number of near neighbors as an additional predictor variable, owing to the relationship between group cohesion and vigilance (Lima, 1995; Treves, 1998, 1999). Group ID was also included in each model to control for behavioral differences between groups and group size. Month and year were included as crossed random effects. All models were fitted in R using the glmmTMB function in the "glmmTMB" package (Brooks et al., 2017). No collinearity between fixed effects was evident as Variance Inflation Factors (VIF), using the vif function within the "car" package, all indicated values below 1.5 (Hair et al., 2014). Significance for  $p$  values of the individual effects was inferred at the 5% level. Due to the spatial nature of the response variable in all our models, we examined the residuals of each model for evidence of autocorrelation. Visual inspection of correlograms using the spline.correlog function in the "nfc" package (Bjornstad, 2016) and semivariograms using the variogram function in the "gstat" package (Pebesma, 2004) in R indicated no spatial autocorrelation between the residuals and lagged distance. However, Moran's  $I$  tests using the "spdep" package (Bivand & Wong, 2018) on the residuals of each model indicated autocorrelation was present, albeit only at very short distances. We therefore additionally crossed both month and year with a spatial random effect, based on a Euclidean distance matrix of each scan sample's coordinates, to account for this nonindependence between points located closely together (Brooks et al., 2017). However, we excluded the spatial random effect from our grooming model due to the variance of this random effect equaling 0 (Pasch et al., 2013).

## RESULTS

Samango monkey landscapes of fear were relatively consistent for both groups across the study period (Figure 1), with the areas perceived as higher risk predominantly associated with the nest location of a breeding pair of African crowned eagles. Similarly, another area of high perceived risk, particularly with regards to Barn group, corresponded to the location of a Verreaux's eagle nest. Perceived predation risk also influenced the spatial

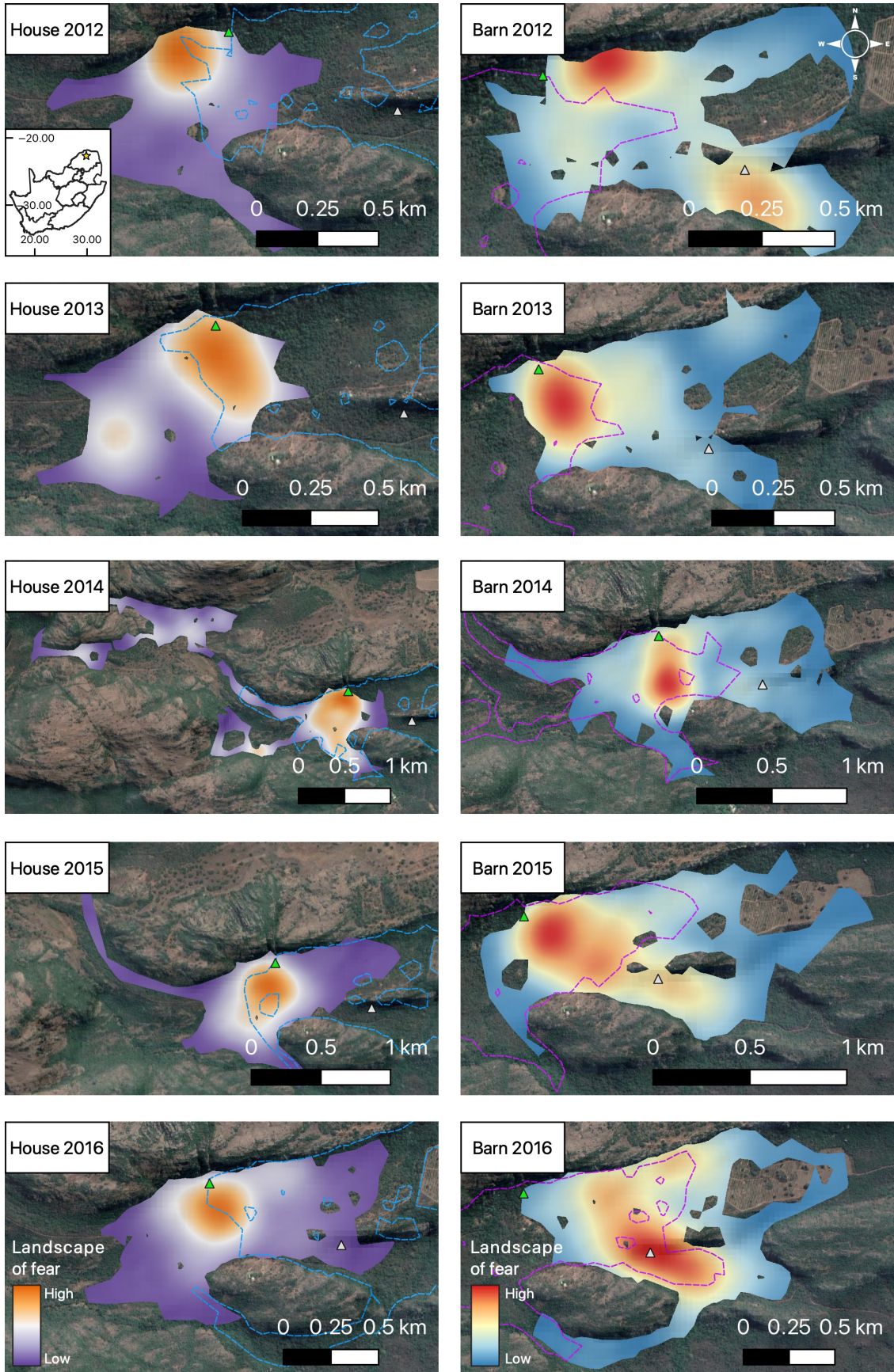


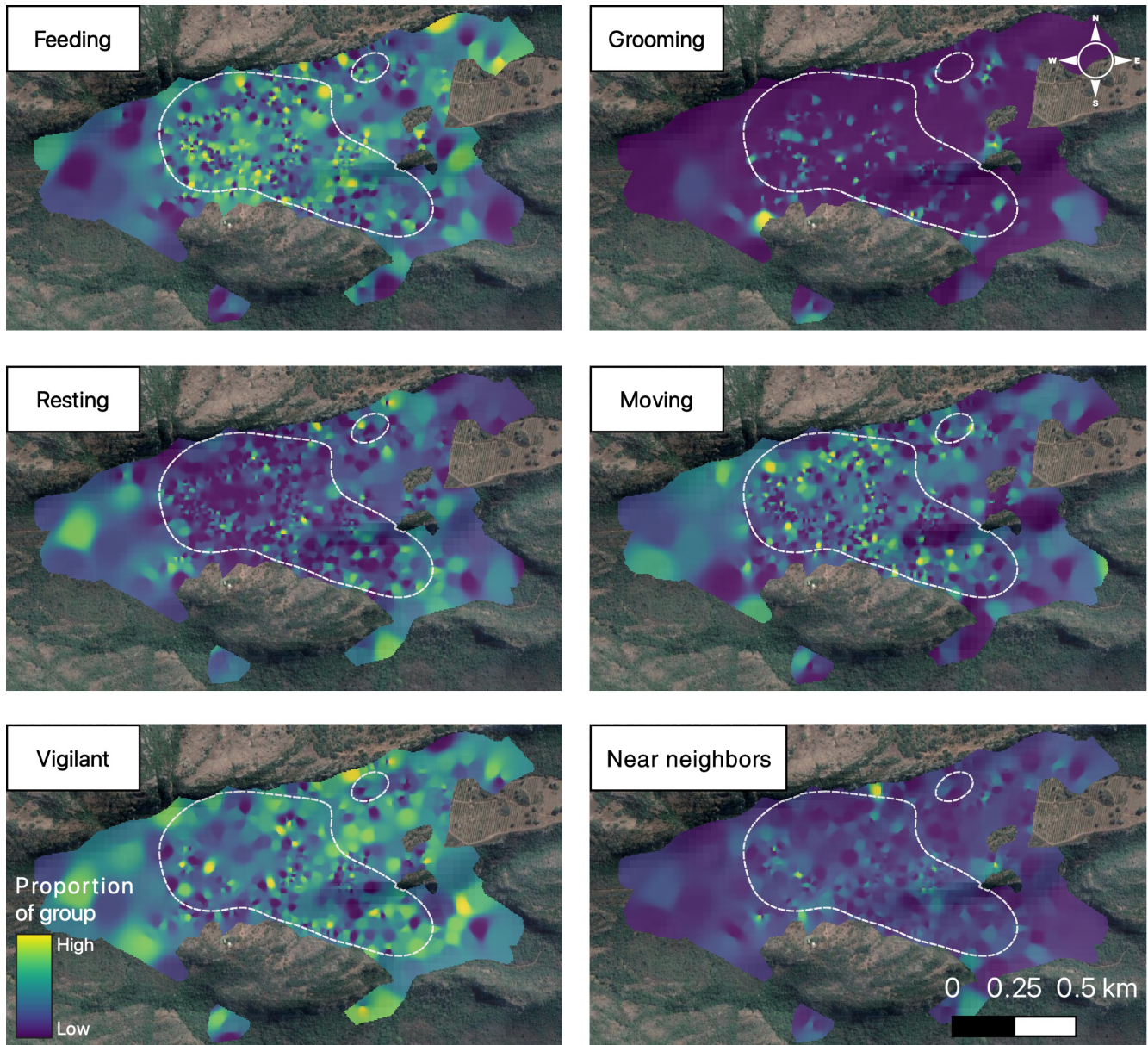
FIGURE 1 Legend on next page.



variation in behavior across each group's home range across the study period, with the mean proportion of the group engaging in certain behaviors showing distinct spatial patterns of higher and lower intensity (Figure 2).

The landscape of fear significantly influenced the intensity of feeding behaviors across the landscape, with

the proportion of samango monkeys feeding and foraging increasing in areas perceived as high risk (Table 1, Figure 3). Feeding behaviors also significantly increased when in areas of reduced canopy height. However, monthly fruit availability, understory visibility, and distance from sleep site had no effect on the proportion of



**FIGURE 2** Comparison between the mean proportion of “Barn” group feeding, grooming, resting, moving, and vigilant, and the number of nearby conspecific neighbors, across the study period (2012–2016) at Lajuma Research Centre, Soutpansberg Mountains, South Africa. White dashed line indicates 50% landscape of fear isopleth for “Barn” group across the study period

**FIGURE 1** Spatial distributions of annual landscapes of fear for both “House” and “Barn” group at Lajuma Research Centre, Soutpansberg Mountains, South Africa, from 2012 to 2016. Approximate location of African crowned eagle's nest (green) and Verreaux's eagle's nest (white) shown for reference. Inset: Location of study site within South Africa. For each year, each group's respective landscape of fear is also shown for reference (“Barn”: Blue dashed line, “House”: Purple dashed line)

**TABLE 1** Parameter estimates and key statistics of spatial GLMMs for proportion of individuals feeding, grooming, resting, moving and vigilant, as a function of landscape of fear, monthly fruit availability, understory visibility, canopy height, and distance from sleep sites

<b>Coefficient</b>	<b>B</b>	<b>SE</b>	<b>z</b>	<b>Lower</b>	<b>Higher</b>	<b>Sig</b>
<i>Feeding</i>						
(Intercept)	-0.484	0.175	-2.771	-0.827	-0.142	(1)
Landscape of fear	0.118	0.042	2.793	0.035	0.201	0.005
Fruit availability	-0.042	0.035	-1.198	-0.112	0.027	0.231
Understory visibility	-0.058	0.047	-1.234	-0.149	0.034	0.217
Canopy height	-0.096	0.044	-2.203	-0.182	-0.011	0.028
Distance from sleep site	-0.016	0.038	-0.421	-0.092	0.059	0.674
Group (House)	0.098	0.082	1.200	-0.062	0.258	0.230
Fear × fruit	0.029	0.042	0.689	-0.054	0.112	0.491
<i>Grooming</i>						
(Intercept)	-2.476	0.060	-40.940	-2.594	-2.357	(1)
Landscape of fear	-0.012	0.024	-0.510	-0.058	0.034	0.608
Fruit availability	-0.015	0.023	-0.630	-0.060	0.031	0.532
Understory visibility	0.017	0.028	0.620	-0.037	0.072	0.532
Canopy height	0.023	0.026	0.870	-0.029	0.075	0.382
Distance from sleep site	0.022	0.025	0.870	-0.027	0.070	0.383
Group (House)	0.096	0.052	1.840	-0.006	0.198	0.065
Fear × fruit	-0.003	0.027	-0.100	-0.056	0.051	0.922
<i>Resting</i>						
(Intercept)	-1.568	0.231	-6.799	-2.020	-1.116	(1)
Landscape of fear	-0.019	0.035	-0.546	-0.088	0.050	0.585
Fruit availability	-0.002	0.028	-0.069	-0.057	0.053	0.945
Understory visibility	-0.003	0.046	-0.070	-0.093	0.086	0.944
Canopy height	0.006	0.045	0.122	-0.083	0.094	0.903
Distance from sleep site	-0.023	0.032	-0.731	-0.086	0.039	0.465
Group (House)	0.226	0.087	2.609	0.056	0.396	0.009
Fear × fruit	-0.018	0.032	-0.544	-0.081	0.046	0.587
<i>Moving</i>						
(Intercept)	-1.211	0.143	-8.491	-1.490	-0.931	(1)
Landscape of fear	-0.066	0.044	-1.512	-0.151	0.020	0.131
Fruit availability	0.131	0.032	4.058	0.068	0.194	<0.001
Understory visibility	-0.039	0.044	-0.895	-0.125	0.047	0.371
Canopy height	-0.039	0.041	-0.931	-0.120	0.043	0.352
Distance from sleep site	-0.053	0.034	-1.543	-0.119	0.014	0.123
Group (House)	-0.207	0.076	-2.739	-0.355	-0.059	0.006
Fear × fruit	-0.045	0.038	-1.172	-0.119	0.030	0.241
<i>Vigilance</i>						
(Intercept)	-0.589	0.316	-1.865	-1.208	0.030	(1)
Landscape of fear	-0.109	0.050	-2.197	-0.207	-0.012	0.028
Fruit availability	-0.076	0.047	-1.619	-0.167	0.016	0.106
Understory visibility	-0.121	0.053	-2.275	-0.224	-0.017	0.023
Canopy height	-0.090	0.049	-1.833	-0.187	0.006	0.067

(Continues)

TABLE 1 (Continued)

Coefficient	B	SE	z	Lower	Higher	Sig
Distance from sleep site	-0.152	0.049	-3.132	-0.248	-0.057	0.002
Mean near neighbors	-0.303	0.056	-5.390	-0.413	-0.193	<0.001
Group (House)	-0.328	0.099	-3.322	-0.521	-0.134	0.001
Fear × fruit	-0.070	0.050	-1.381	-0.168	0.029	0.167

Note: Fear × fruit, interaction between the landscape of fear and fruit availability. (1) Not shown because of having no meaningful interpretation.

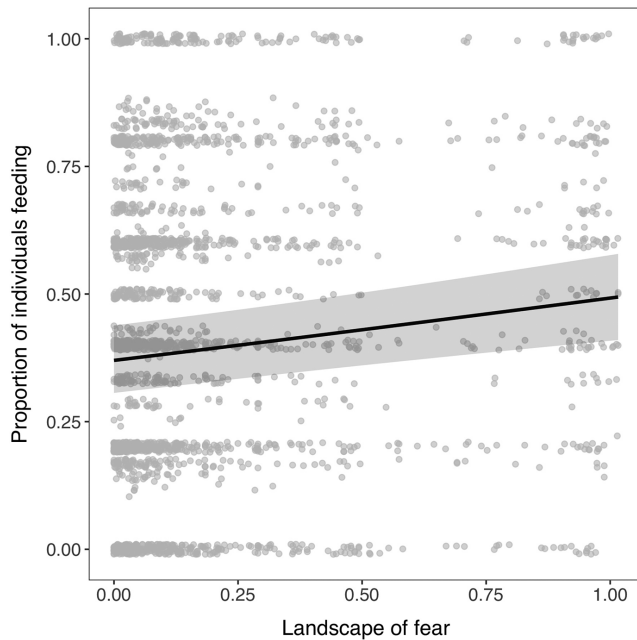


FIGURE 3 Effect of landscape of fear on the proportion of individuals feeding

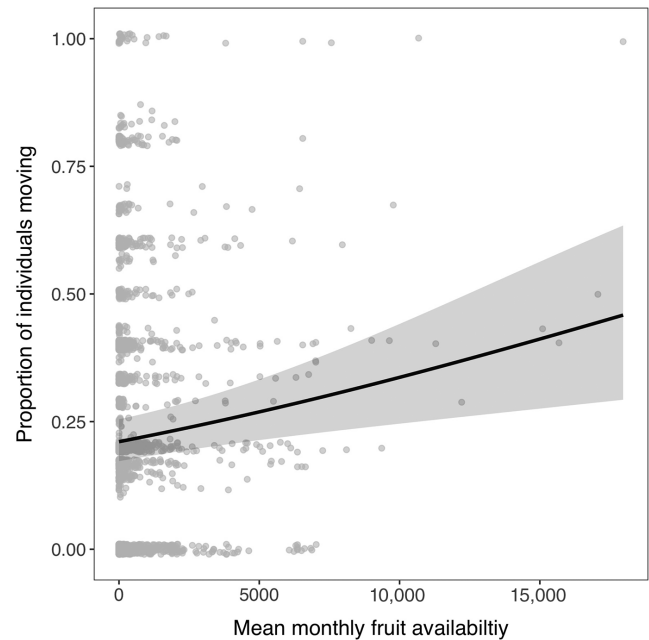


FIGURE 4 Effect of monthly fruit availability on the proportion of individuals moving

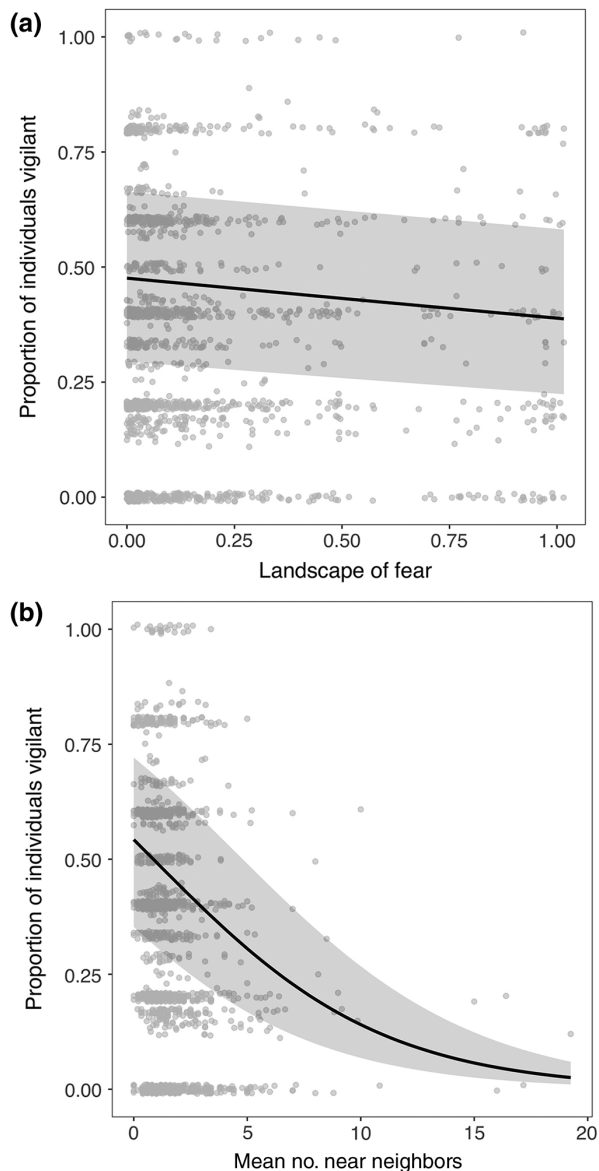
samango monkeys feeding, nor did an interaction between perceived risk and fruit availability. We found no effect of landscape of fear, habitat features associated with risk or monthly fruit availability on the spatial distribution of grooming or resting behaviors (Table 1). Movement (walking and running) significantly increased in areas where fruit was more abundant (Table 1, Figure 4), relative to the surrounding areas, but was not influenced by any measure of risk. The proportion of vigilant individuals was significantly negatively associated with the landscape of fear (Table 1, Figure 5a), understory visibility, distance from sleep site, and the number of nearby conspecific neighbors (Figure 5b). However, both perceived risk and fruit availability, nor an interaction between the two, had any influence on vigilance intensity across the landscape.

Finally, the number of nearby neighbors significantly increased in areas perceived as high risk and as distance from sleep site increased (Table 2, Figure 6a). Furthermore, group cohesion in high-risk areas was also

influenced by fruit availability, with neighbor distance decreasing in high-risk areas with high fruit availability, relative to high-risk low fruit availability areas (Figure 6b). In contrast, understory visibility, canopy height, and fruit availability had no influence on the number of near neighbors.

## DISCUSSION

There is growing recognition that the fear of being eaten can have a greater influence on prey populations than the consumptive effects of killing prey (Brown et al., 1999; Laundré et al., 2010; Lima & Dill, 1990; Peers et al., 2018; Wirsing et al., 2021). However, exploring the non-consumptive effects of predation on prey populations can be difficult to quantify. Previous studies have focused on the behavioral responses to variation in predation risk either in terms of space use (Coleman & Hill, 2014a; Heithaus & Dill, 2002; Laundré et al., 2001; Valeix



**FIGURE 5** Effect of landscape of fear (a) and mean number of near neighbors (b) on the proportion of individuals vigilant

**TABLE 2** Parameter estimates and key statistics of spatial LMM for mean near neighbors as a function of landscape of fear, fruit availability, understory visibility, canopy height, and distance to sleep sites

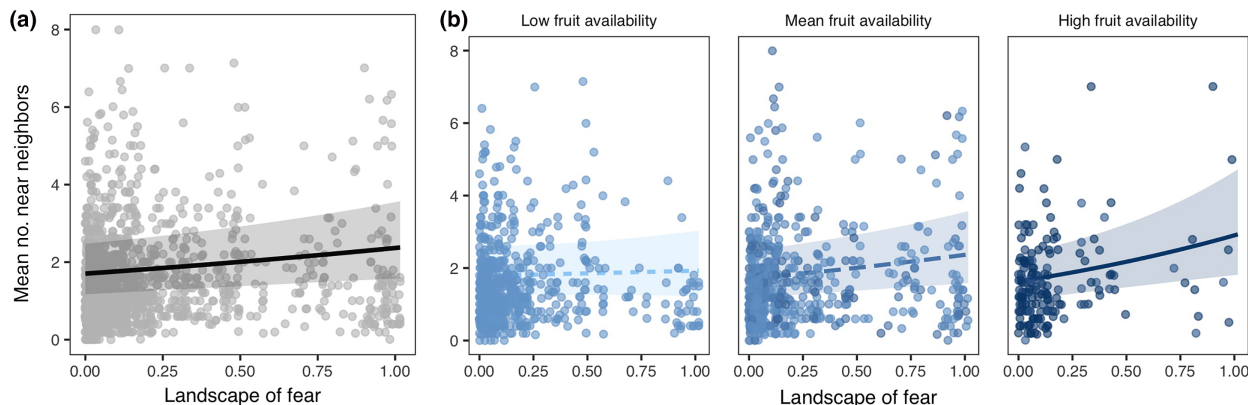
Coefficient	B	SE	z	Lower	Higher	Sig
<i>Neighbors</i>						
(Intercept)	0.293	0.268	1.093	-0.233	0.819	(1)
Landscape of fear	0.089	0.033	2.718	0.025	0.153	0.007
Fruit availability	0.017	0.027	0.637	-0.036	0.071	0.524
Understory visibility	0.000	0.041	0.005	-0.080	0.081	0.996
Canopy height	-0.002	0.043	-0.038	-0.085	0.082	0.970
Distance from sleep site	0.078	0.031	2.559	0.018	0.138	0.011
Group (House)	-0.028	0.084	-0.329	-0.193	0.138	0.742
Fear × fruit	0.069	0.034	2.013	0.002	0.136	0.044

Note: Fear × fruit, interaction between the landscape of fear and fruit availability. (1) Not shown because of having no meaningful interpretation.

et al., 2009; Willems & Hill, 2009), or the foraging/vigilance trade-off (Dill & Fraser, 1984; Heithaus & Dill, 2002; Hernández & Laundré, 2005; Suhonen, 1993) and thus have largely ignored other behavioral responses (Cowlshaw, 1997; De Vos et al., 2015; Palmer et al., 2017). Previous work at our field site showed that samango monkeys avoid areas perceived as high risk from African crowned eagles (Coleman & Hill, 2014a). We show here, however, that when samango monkeys enter these high-risk areas, they do so to engage in behaviors which significantly enhance fitness relative to other areas.

When entering high-risk areas, we found that samango monkeys increased the levels of feeding and foraging relative to other behaviors. Acquiring food is fundamental to an individual's survival (Pyke, 1984; Schoener, 1971) and, therefore, it stands to reason that individual's will only enter high-risk areas to engage in behaviors that significantly enhance fitness relative to other locations. For example, common squirrel monkeys (*Saimiri sciureus*) increased time spent feeding on artificial high-reward food platforms where predation risk was high, when availability of natural fruit was low during the dry season (Stone, 2007). Similarly, Milne-Edwards' sifakas (*Propithecus diadema edwardsi*) in the Madagascan rainforest spent more time feeding in the fruit-rich but high-risk canopy where risk from raptors was greatest (Wright, 1998). Furthermore, Grant's gazelle (*Gazella granti*) and hartebeest (*Alcelaphus buselaphus* sp.) in Kenya preferred food-rich areas during the drought season, despite the increased risk of predation from multiple predators in these areas (Riginos, 2015).

However, foraging in high-risk areas in these examples is largely motivated by food availability (Schmidt & Kuijper, 2015; Valeix et al., 2009), as hungry animals may view risky areas as lower cost according to the asset protection hypothesis (Clark, 1994). A similar scenario does



**FIGURE 6** Effect of landscape of fear (a) and interaction between landscape of fear and fruit availability (b) on the mean number of near neighbors

not appear to be the case here however, judging by the lack of a significant interaction between the landscape of fear and fruit availability, suggesting that feeding levels increase in high-risk areas irrespective of fruit availability across the landscape. An important consideration of our methodology, however, was that our feeding response variable comprised of feeding and foraging behaviors on a range of food items, owing to the samango monkey's pronounced dietary flexibility (Coleman & Hill, 2014b; Lawes, 1991; Lawes et al., 1990; Linden et al., 2015; Parker et al., 2020). These high-risk areas then, although avoided as part of the monkeys' home range (Coleman & Hill, 2014a), may include important food items in order to facilitate the risk/reward trade-off observed here. Indeed, high-risk areas are associated with the tall-canopy, indigenous mistbelt forest at our study site (Coleman & Hill, 2014a), which, as numerous studies on samangos have shown, are also the location of essential indigenous food items (Coleman & Hill, 2014a; Nowak et al., 2017; Parker et al., 2020; Wimberger et al., 2017). Indeed, samangos preferentially selected indigenous food items even when more calorie-dense alternative items are available (Nowak et al., 2017; Wimberger et al., 2017). In light of this, samango monkeys clearly integrate high-risk areas into their foraging range in order to maximize net energy gain, according to optimal foraging theory, while also balancing predation risk by adopting antipredator strategies (Sih, 1980).

Previous research has also shown that samango monkeys avoid areas of low canopy height within their home range (Coleman & Hill, 2014a), due to the associated risk from ambush predators (du Bothma & Le Richie, 1986; Murphy et al., 2013). Here, we show that when entering these risky habitats, samangos do so to engage in fitness-enhancing behaviors at that location, such as feeding, relative to other locations. Arboreal species have frequently been shown to display a

vertical axis of fear owing to their 3-D foraging landscape (Campos & Fedigan, 2014; Emerson et al., 2011; Makin et al., 2012; Nowak et al., 2014). Areas closer to the ground offer increased ambush opportunities from terrestrial predators, which therefore inherently influence the monkey's perception of risk due to reduced ease of escape (Hart et al., 1996; Lima, 1992). When entering areas of their range with habitat characteristics that enhance perceptions of risk, therefore, samango monkeys concentrate predominately on behaviors that significantly enhance fitness at that location.

We found no relationship between local fruit availability and feeding intensity. While we would expect the predominantly frugivorous samango monkey to feed more in high fruit availability areas, the lack of any relationship likely reflects the samango monkeys' foraging/risk trade-off (Lima & Dill, 1990). Coleman and Hill (2014a) similarly found no influence of fruit availability (albeit on an annual scale) on range use intensity in samangos, with the monkeys able to exploit a rich habitat matrix and consume large amounts of leaves (Coleman & Hill, 2014b; Parker et al., 2020) in order to meet their nutritional needs while avoiding the risk of predation. Furthermore, in areas of high fruit availability but lower perceived risk, there are no constraints to engaging in other activities in these areas.

In contrast to feeding, we found that movement increased in areas of high fruit availability. The observed relationship may be a result of increased movement between clumped patches of fruit, such as large fruiting trees, which are common across Lajuma (Coleman, 2013; Linden et al., 2015), and is a trend frequently observed in frugivorous species (Clutton-Brock, 1975; Stevenson et al., 2000). However, as movement in this case comprised of both walking and running behaviors, increased movement in fruit-rich areas may equally be a consequence of quickly retreating from these areas following feeding

bouts, particularly as fruit-rich areas are associated with increased risk at Lajuma (Coleman & Hill, 2014a).

We found no effect of landscape of fear, habitat characteristics associated with risk, fruit availability or distance from sleep site on the proportion of individuals grooming or resting across the home range. While one might expect these maintenance behaviors to increase in safer areas (Cowlshaw, 1997, De Vos et al., 2015, Palmer et al., 2017), one might also expect feeding and moving to be equally expressed in these areas (Cowlshaw, 1997; Creel et al., 2005; Dill & Fraser, 1984; Heithaus & Dill, 2002; Hernández & Laundré, 2005; Suhonen, 1993). Thus, the spatial distribution of both grooming and resting behaviors may be influenced by other factors not explored here. For example, grooming may vary both spatially, according to both intra- and inter-group encounters (Henzi & Barrett, 1999; Koyama et al., 2006; Terry, 1970), and temporally in response to environmental factors (Dunbar et al., 2009). Similarly, resting may also be influenced by ecological constraints (Korstjens et al., 2010), which vary both spatially and temporally.

Contrary to our predictions, group vigilance declined in areas of high perceived risk from eagles. Despite increasing vigilance levels being a common antipredator response (Brown, 1999; Laundré et al., 2001), one possible explanation for the observed relationship here involves the foraging/vigilance trade-off; in that as individuals feed more in high-risk areas, less time is available for vigilance (Brown, 1999). However, feeding and vigilance are not incompatible in primates (Cowlshaw et al., 2004) and searching for food items may not be incompatible with detecting predators (Allan & Hill, 2018). Furthermore, vigilance may actually be lower in riskier areas, as safe places are made so by heightened vigilance (Brown, 1999), while the benefits of vigilance may also be reduced in high-risk areas where escape routes are lacking (Brown, 1999). Thus, a more parsimonious explanation may be that samango monkeys mitigate the potential costs of this trade-off by reducing the distance between conspecific neighbors (Cowlshaw, 1998; LaBarge et al., 2020; Roberts, 1996; Teichroeb & Sicotte, 2012; Treves, 1998), thereby allowing vigilance to be shared among group members (McNamara & Houston, 1992). Our findings would support this affirmation, given that group vigilance decreased with increasing number of near neighbors (Figure 5b). Vigilance also decreased in areas of greater understory visibility, reduced canopy height, and increasing distance from morning sleep site, all factors, which are indirectly associated with risk from other predator guilds (Coleman & Hill, 2014a; Hill & Weingrill, 2007; Jaffe & Isbell, 2009; Makin et al., 2012; Nowak et al., 2017).

Neighbor distance also decreased in high-risk areas, implying that group cohesion may also be a response to predation risk by deterring predators (Maisels et al., 1993; Scott-Samuel et al., 2015). In addition, neighbor distance also decreased in areas further away from morning sleep site, suggesting this may be a response to entering unfamiliar areas where ambush risk is elevated (Isbell, 1994). Although group size has frequently been cited as an effective antipredator strategy, owing to the “many eyes” hypothesis (Lima, 1995; Roberts, 1996), more recent evidence indicates that group cohesion may be a more effective strategy via the “confusion effect,” which causes a bottleneck in predator information processing (Krause & Ruxton, 2002; Scott-Samuel et al., 2015). The result is the inability of predators to single out and attack individual prey within a group (Krause & Ruxton, 2002), which scales with the size of the targeted prey group (Krakauer, 1995). As our groups represent some of the largest samango monkey groups recorded (Coleman & Hill, 2014b; Linden et al., 2016), the “confusion effect” may be the most effective antipredator strategy in this species, more so than increased vigilance.

We further found that reducing neighbor distance in response to eagle risk was weakly exaggerated by fruit availability in high-risk areas. In high-risk, fruit-rich areas, samango monkeys further reduce neighbor distance relative to high-risk, fruit-poor areas. Although fruit availability did not appear to motivate risk-taking behavior in this study, the modification of antipredator behavior in response to the combined effects of perceived risk and fruit availability demonstrates the samango monkey’s foraging/risk trade-off (Schmidt & Kuijper, 2015; Stone, 2007; Valeix et al., 2009). Nevertheless, our findings suggest that neighbor distance is the main response to perceived predation risk for our samango monkey population.

Interestingly, the areas perceived as high risk were relatively consistent for both groups across the study period and mapped almost perfectly on to the nest location of two breeding pairs of eagles (Figure 1). In particular, the observed consistency may particularly be attributed to the presence of an African crowned eagle’s nest located in the tall indigenous forest on the northernmost edges of both groups’ home ranges (Nowak et al., 2014). In addition, Barn group displayed high perceived risk to the southeast of its home range where, in some years, a Verreaux’s nest was present (Coleman, 2013). Nest location may therefore be a reliable indicator of actual predation risk in this instance, and although a slight mismatch between with perceived risk was observed here, this may be due to the activity patterns of predators (Dröge et al., 2017; Lima &

Bednekoff, 1999) or, perhaps more likely, the function of alarm calling in response to distant, particularly aerial, predators (Murphy et al., 2013). Nevertheless, the consistency between nest location and areas perceived as high risk between years, despite variation in breeding cycles and activity on the nest, is a striking outcome of this research and may indicate that the landscape of fear exists as a “mental map” in this species. Samango monkeys may therefore modify their behavior at a given location based on the spatial memory of previous encounters. A recent study from our field site by LaBarge et al. (2020) would appear to support this hypothesis, as they found that samangos pre-emptively increased spatial cohesion in response to eagle encounter risk. Our findings corroborate those of LaBarge et al. (2020), albeit over a longer study period, and suggest that samango monkeys may overestimate risk in areas perceived as high risk and opt to “play it safe” by reducing neighbor distance in these areas (Bouskila & Blumstein, 1992). Given the large fitness costs of predation, the low cost of this response likely outweighs that of being overly cautious in these areas (Abrams, 1994).

Evidence of spatial memory in response to predation risk, particularly in primates, has been found in other studies (Cunningham & Janson, 2007; de Guinea et al., 2021; Fagan et al., 2013; Garber, 1989; LaBarge et al., 2020) but remains an understudied area of behavioral ecology. In addition, while we observed an association between landscapes of fear and nest location over the study period, future research would benefit from measuring actual predation risk more explicitly, in order to better understand the nonlinear relationship between risk and response (Gaynor et al., 2019). Nevertheless, while perceived risk may over- or underestimate actual risk in some scenarios (such as false alarms), the purpose of this study was to explore behavioral responses to the samango monkeys’ perception of risk, and therefore, any misinterpretation of actual risk is still informative.

One potential limitation of our study lies in our estimates of fruit availability. Our broad proxy for fruit availability showed a weak association with neighbor distance when taking into account perceived predation risk at a given location. However, this association may be more pronounced, or may even influence other behaviors, when taking into consideration fruit size, ripeness, and nutritional value for example. While refining estimates of fruit availability to include additional information on fruit may shed more light on how behavior varies spatially according to resource availability, one would still make the assumption that all species are equally preferred which is unlikely (Johnson, 1980; Lubchenco, 1978; Wasserman & Chapman, 2003; Yeager, 1989).

Furthermore, even if fruit volume, nutritional value, and distribution across the home range were known perfectly, this still ignores other equally influential variables such as secondary components, fiber, and processing time (Wasserman & Chapman, 2003). Thus, regardless of the measure used to estimate fruit availability, most studies effectively end up with a proxy for this variable.

In conclusion, the nonconsumptive effects of predation can have consequences for prey physiology, population dynamics, and community interactions through behaviorally mediated changes. While samango monkeys have previously been shown to avoid areas perceived as high risk (Coleman & Hill, 2014a), we show here that samango monkeys only utilize risky areas to engage in behaviors critical to survival at that location, such as feeding. To mitigate the increased risk associated with these areas, samangos increase group cohesion as a means to “confuse” predators (Krause & Ruxton, 2002; Scott-Samuel et al., 2015), which may be a particularly effective antipredator strategy given the large size of our groups (Krakauer, 1995). The consistency in areas perceived as high risk across the study period, by both our groups, also presents the possibility that the spatial variation in risk may manifest as a mental map in samangos based on previous encounters, and future studies might explore this relationship more explicitly to gain a more comprehensive understanding of how risk is perceived by prey.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Parker et al., 2019) are available from Figshare: <https://doi.org/10.6084/m9.figshare.8868410.v2>.

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