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Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use

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Spatial variation in predation risk generates a 'landscape of fear', with prey animals modifying their distribution and behaviour in response to this variable predation risk. In systems comprising multiple predators and prey species, a key challenge is distinguishing the independent effects of different predator guilds on prey responses. We exploited the acoustically distinct alarm calls of samango monkeys, *Cercopithecus mitis erythrarchus*, to create a predator-specific landscape of fear from eagles to assess its impact on space use within mixed regressive–spatial regressive models incorporating data on resource distribution and structural characteristics of the environment. The landscape of fear from eagles was the most significant determinant of samango range use, with no effect of resource availability. The monkeys also selected areas of their range with higher canopies and higher understory visibility, behaviour consistent with further minimizing risk of predation. These results contrast with those of vervet monkeys, *Chlorocebus aethiops pygerythrus*, at the same site for which the landscapes of fear from leopards and baboons were the most significant determinants of space use. While highlighting that predation risk is a key driver of primate behaviour in this population, the landscapes of fear experienced by samango monkeys and vervet monkeys appear to differ despite exposure to identical predator guilds. This emphasizes the importance of distinguishing between the risk effects of different predators in understanding prey ecology, but also that closely related prey species may respond to these predator-specific risks in different ways.

Predation is a major selective force driving animal evolution (Dawkins & Krebs, 1979) with almost all animal species engaged in some form of predator–prey interaction (Abrams, 2000). Understanding how animals manage the risk of predation is thus a central issue in behavioural ecology (Quinn & Cresswell, 2004). Predation imposes two costs on prey individuals: the direct fitness costs of mortality resulting from successful predation and the indirect costs of employing behaviours to reduce mortality risks. These nonlethal effects of predators appear to affect almost every aspect of prey behaviour and ecology (Caro, 2005; Lima, 1998; Werner & Peacor, 2006). Nevertheless, these risk effects are among the most difficult to quantify (Creel & Christianson, 2008; Creel, Winnie, Christianson, & Liley, 2008; Hill & Dunbar, 1998).

Spatial variation in risk is a key driver of nonlethal predation effects (Cresswell & Quinn, 2013), primarily because of the constraints this places on foraging behaviour and the subsequent impact this has on competitive and trophic interactions (Creel, Christianson, Liley, & Winnie, 2007; Minderman, Lind, & Cresswell, 2006; Peckarsky & McIntosh, 1998; Willems & Hill, 2009). Spatial variation in perceived predation risk has often been conceptualized as a 'landscape of fear' (Brown & Kotler, 2004; Brown, Laundre, & Gurung, 1999; Laundré, Hernandez, & Altendorf, 2001), with approaches such as giving-up densities quantifying the trade-offs animals make between nutrient acquisition and the costs of predation (Brown, 1988). One of the challenges though is that these methods do not strictly measure perceived predation risk (Searle, Stokes, & Gordon, 2008) and in multipredator environments they do not convey information on the impact of different predators on the behavioural responses of prey species. This latter issue is critical, since when prey are subject to attack from several predators that present different types of risk, the appropriate antipredator responses differ between predator guilds (Cresswell & Quinn, 2013; Preisser, Orrock, & Schmitz, 2007; Shultz, Noe, McGraw, & Dunbar, 2004; Willems & Hill, 2009). As a consequence, to understand how prey manage the risk of predation within their environment, the risk of predation from each predator guild must be quantified independently. Nevertheless, there is a significant body of evidence to suggest that animals trade food availability against predation risk in habitat choice (Cowlishaw,

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1997; Fortin & Fortin, 2009; Willems & Hill, 2009). The landscape of fear is thus a powerful concept in animal ecology and has been suggested to be the key landscape within an animal's environment (Brown & Kotler, 2004). To test this assertion, however, methods are required that exclusively reflect perceived predation risk and distinguish between predator-specific predation risks in determining prey behaviour.

In a novel approach, Willems and Hill (2009) showed that predator-specific landscapes of fear could be constructed on the basis of vervet monkey, *Chlorocebus aethiops pygerythrus*, alarm calls. Vervet monkeys' predators at their South African field site included leopard, *Panthera pardus*, African crowned eagle, *Stephanoaetus coronatus*, chacma baboon, *Papio ursinus*, and African rock python, *Python sebae*. When predator-specific landscapes of fear were combined with data on resource distribution in a spatially explicit model, the ranging behaviour of the study group could be interpreted as an adaptive response to the spatial availability of resources and the perceived risk of predation by some, but not all, predators (Willems & Hill, 2009). The landscapes of fear for baboon and leopard were negatively associated with the group's utilization distribution indicating that the monkeys avoided areas of high perceived predation risk by these two predators. Furthermore, the effects of fear exceeded those of local resource availability in determining range use. In contrast, the spatial distribution and local frequency of alarm responses to eagles and snakes did not significantly affect range use. This highlighted the value of their framework in distinguishing between the effects of different predators in studies of predator–prey ecology in multipredator environments. Willems and Hill (2009) also noted the potential for integrating additional variables such as the structural characteristics of a habitat and the utilization distributions of predators and neighbouring groups into their modelling approach and advocated these as an avenue for future research.

In this study we applied the framework of Willems and Hill (2009) to a population of samango monkeys, *Cercopithecus mitis erythrarchus*, inhabiting the same multipredator environment as in the original vervet study. Initially we directly replicated the modelling approach and variable selection of Willems and Hill (2009) to facilitate a direct comparison of our results with the previous models on vervet monkeys. In doing so, we assessed the impact that substrate preferences (arboreal versus semiterrestrial) have on the exposure to different predator guilds and the implications of this for predator-specific landscapes of fear and range use. Samango monkeys, as an arboreal species, may experience different predation threats to more terrestrial species such as vervet monkeys (Lawes, 1991; McGraw, 2002), so influencing the relative importance of different predators in driving ranging behaviour.

We then extended the modelling framework of Willems and Hill (2009) in two ways. First, we replaced categorical habitat types with continuous spatial measures of resource availability and structural characteristics of habitats (e.g. canopy height, habitat visibility) to investigate the key drivers of habitat choice within the landscape of fear. Samango monkeys have been observed to spend most of their time high in the canopy (Thomas, 1991), with the ground perceived as higher risk (Emerson, Brown, & Linden, 2011), suggesting that areas of tall canopy will be preferred. Similarly, habitats with dense understory vegetation may provide cover for terrestrial ambush predators (du Bothma & Le Riche, 1986) while areas of high visibility may increase an individual's ability to monitor threats from predators or competitors (Cowlishaw, 1994; Hill & Weingrill, 2007; Jaffe & Isbell, 2009). For example, vervet monkeys have been shown to decrease vigilance in high-visibility areas (Chapman, 1985; Enstam & Isbell, 2002). Samango monkeys are thus predicted to prefer higher visibility habitats. Since canopy height and visibility will vary independently between habitat types, consideration of the spatial variation in these parameters should be more informative than broad habitat classifications. Second, we explored the impact of competition with neighbouring groups. Intraspecific competition and the active avoidance of neighbouring groups have long been recognized as significant factors shaping space use strategies and movement decisions in many species (Gibson & Koenig, 2012; Markham, Guttal, Alberts, & Altmann, 2013), and yet how intraspecific competition, predation risk and resource availability interact in determining spatial range use is largely unknown.

METHODS

Study Species and Field Site

Samango monkeys are medium-sized (adult females about 4.4 kg, adult males about 7.6 kg: Harvey, Martin, & Clutton-Brock, 1987) arboreal, diurnal guenons. They form single-male, multifemale groups (Henzi & Lawes, 1987; Rudran, 1978), with group sizes ranging from four to 65 (Beeson, Tame, Keeming, & Lea, 1996; Butynski, 1990; Houle, Chapman, & Vickery, 2010; Lawes, Cords, & Lehn, 2013; Smith, Link, & Cords, 2008). Samango monkeys are primarily frugivorous but supplement their diets with leaves, insects and flowers (Coleman, 2013; Lawes, 1991; Lawes, Henzi, & Perrin, 1990). Like vervet monkeys, samango monkeys have acoustically distinct alarm calls for different predator guilds which can be differentiated by human observers (Brown, 1989; Papworth, Bose, Barker, Schel, & Zuberbuhler, 2008).

Research was conducted at the Lajuma Research Centre, located in the Soutpansberg Mountains, Limpopo Province, South Africa (23°02′23″S, 29°26′05″E). Substantial local variation in abiotic factors such as elevation and water availability results in a variety of microclimates which are able to support a substantial diversity of both flora and fauna (Brock, Nortje, & Gaigher, 2003; Willems, 2007). The study area has natural fragments of tall forest (10–20 m height) occurring among areas of natural short forest (5–10 m height). Local climate is classified as temperate/mesothermal, with cool dry winters from April to September and warm to hot wet summers from October to March (Willems, 2007). Mean annual temperature on site averages 17.1 °C, with a mean annual rainfall of 724 mm (Willems, Barton, & Hill, 2009). On site, samango monkeys are sympatric with vervet monkeys, chacma baboon, thick-tailed galago, *Otolemur crassicaudatus*, and southern lesser bushbaby, *Galago moholi*. Potential predators include leopard, crowned eagle, African black eagle, *Aquila verreauxii*, and African rock python. Venomous snakes, including black mamba, *Dendroaspis polylepis*, puff adder, *Bitis arietans*, and Mozambique spitting cobra, *Naja mossambica*, while not actively preying on samango monkeys, still pose potential mortality threats and may affect range use.

Permission to conduct research in South Africa was provided by the Limpopo Province Department of Economic Development and Tourism, with the research receiving ethical approval from the Durham University's Life Sciences Ethical Review Process Committee.

Behavioural Data

A well-habituated group of approximately 40 samango monkeys was observed over a 16-month period (September 2009–December 2010). We restrict the data presented here to that collected during the final 12 months (January–December 2010) to confine the analyses to a single annual cycle. Behavioural data were collected over 8 full follow days per month (totalling 96 days), with a successful day defined as following the group from dawn to dusk without losing audiovisual contact for more than a total of 60 min. Study days ranged from approximately 11.5 to 14 h depending upon the season. Data were collected on a palmtop (Sony Clie SL-10) with behavioural data collection software (Pendragon Forms 4.0; Pendragon Software, Libertyville, IL, U.S.A.) and a GPS (Garmin GPS 60CSX; Garmin, Olathe, KS, U.S.A.) continually recording location. Additional data were collected in paper notebooks.

To determine perceived predation risk, the time, location and details of alarm calls were recorded on an all-occurrence basis. There were a total of 131 alarm calls across the study (eagle = 59, snake = 3, other = 7, unknown = 62) with no confirmed leopard-specific alarm vocalizations. Since a minimum of 10 observations is required for the statistical techniques used here (Borger et al., 2006), only eagle alarm calls were further investigated. Eleven of the 59 eagle alarm calls were accompanied by an eagle sighting, leaving 48 potentially 'false' alarm calls; these calls still express the monkeys' perception of eagle risk, however, and are equally as informative as when a predator sighting was confirmed (Willems & Hill, 2009).

Intergroup encounters were defined as the study group being within visual range of another samango group, with the time, location and details of all such encounters recorded on an all-occurrence basis. There were a total of 41 intergroup encounters of varying antagonism over the course of the study.

Environmental Data

The study area was separated into eight distinct habitat types: tall forest, short forest, riverine forest, wetland, open/closed mountain bushveld and open/closed rocky mountain bushveld (based on criteria in Mucina and Rutherford (2006); Fig. 1a). All water sources available for a minimum of 1 month during the study were recorded using GPS. The locations of sleeping sites were recorded using the final GPS location of the day from the behavioural data.

Food availability was calculated from phenological transects and random quadrat sampling; these methods are the most efficient for determining all types of density-related features (Southwood & Henderson, 2000). We established a series of phenological transects, with 10 mature trees from 24 potential food species then selected and tagged to ensure an even coverage of each species throughout the monkeys' home range as well as a range of tree sizes. All trees were monitored monthly for height, crown diameter at the widest point, number of leaves, percentage mature leaves, number of flowers, number of fruits and percentage ripeness (unripe/ripe/overripe). Where there were too many items to count, estimates were made for a single branch or section and then scaled up to the size of the tree. For the purposes of this analysis, food availability estimates focused on fruit availability owing to samango monkeys' mainly frugivorous diet (Lawes, 1991), with eight tree species, accounting for more than 67.1% of the total fruit intake (Coleman, 2013) extracted from the phenological data set. For each species, linear regression analysis was used to derive equations that expressed annual food availability for each species as a function of tree height and/or crown diameter. These equations were then used to estimate food availability for trees of known height and crown diameter from the quadrat sampling (below). Further details of the equations used are given in Coleman (2013).

We used quadrat sampling to calculate food availability and habitat structure within habitat types and across the home range. Each month, a minimum of 100 5 m × 5 m quadrats were randomly selected throughout the monkeys' home range using the ArcGIS add-on Hawth's Tools (Beyer, 2004), with a total of 1268 quadrats sampled across the study. Within each quadrat, all trees with a diameter greater than 10 cm at 1 m were identified and measured for height and crown diameter. Estimated total fruits per tree were then calculated on the basis of the species-specific equations derived from the transects and converted to fruit volume based on average fruit size for each species (based on measurements in Coates-Palgrave (1996); acacia pods were given a nominal thickness of 1 mm). Total fruit volume per 25 m^2 quadrat was then calculated for the 1268 quadrats within the home range.

Mean tree height per quadrat was used to determine canopy height for each of the 1268 quadrats sampled. To estimate habitat visibility, percentage understory visibility was measured for 632 quadrats using a 0.8 m × 0.8 m chequerboard (divided into 10 cm squares). An observer was located at the northwest corner of the quadrat, and a field assistant then held the chequerboard at a height of 2 m and a distance of 5 m in each of the four cardinal point directions. The observer recorded the proportion of the grid visible in each direction and understory visibility was calculated for each quadrat as the mean of these four measurements.

Spatial Landscapes

All data were imported into ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA, U.S.A.), with data projected into the Universal Transverse Mercator coordinate system (datum, WGS 1984; zone, 35 S) and the cell size of all output rasters set to 3 m, consistent with GPS accuracy in the field. A series of layers were then computed to characterize the spatial distribution of the different parameters.

Utilization distribution

Local convex hulls (LoCoH) analysis (Getz et al., 2007; Getz & Wilmers, 2004) was used to determine utilization distribution. This method was chosen over kernel density estimation owing to its superior convergence properties and ability to cope better with hard boundaries such as cliffs and rivers and clumped data points (Getz et al., 2007; Hemson et al., 2005; Ryan, Knechtel, & Getz, 2006; Silverman, 1986; Steury, McCarthy, Roth, Lima, & Murray, 2010). Ranging data were filtered to give a location point every 10 min, providing 6912 points for analysis. An adaptive LoCoH utilization distribution (Getz & Wilmers, 2004) was created using R version 2.13 (R Core Development Team, 2011). The adaptive LoCoH method is one of three variations of LoCoH analysis, and enables smaller convex hulls to arise in higher usage areas, allowing more detailed information in areas of clumped data (Getz et al., 2007), such as around sleeping sites or key food resources that are used repeatedly or for long periods of time. For adaptive LoCoH analysis it is suggested that the widest point between two locations is used as the value a to ensure the correct formation of the 100% isopleth (Getz et al., 2007); here a was set to 1329 m with the utilization distribution calculated in 1% isopleths (Fig. 2).

Resource availability and habitat structure

Initially, estimates of mean food availability, canopy height and visibility were computed from the quadrats sampled for each of the eight habitat types (Table 1) and linked to the habitat layer within GIS. To investigate the effect of the spatial variation in environmental parameters more precisely, we then constructed landscapes of fruit availability, canopy height and understory visibility. Quadrat data for each of these variables were interpolated using kriging (Cressie, 1990) to generate the landscapes (Fig. 1b, c, d). The search radii for kriging were calculated based on the number of points achieving minimum root mean squared error (food resources: 45; canopy height: 45; visibility: 60; Salih, Petterson, Sivertun, & Lund, 2002). Finally, access to water and sleeping sites was expressed as the shortest Euclidean distances to the nearest water source and confirmed sleeping tree taken from the behavioural data (Fig. 1e, f). All layers were clipped to the utilization distribution.

Predation risk and intergroup encounter risk

We used a fixed kernel density estimation (Silverman, 1986) to create a density distribution of eagle alarm vocalizations and intergroup encounters. A PLUGIN bandwidth parameterization was used since on smaller samples it has been shown to have less variability and outperform least-squares cross validation (Gitzen, Millspaugh, & Kernohan, 2006; Lichti & Swihart, 2011). Following Willems and Hill (2009), measures of the probability of an alarm

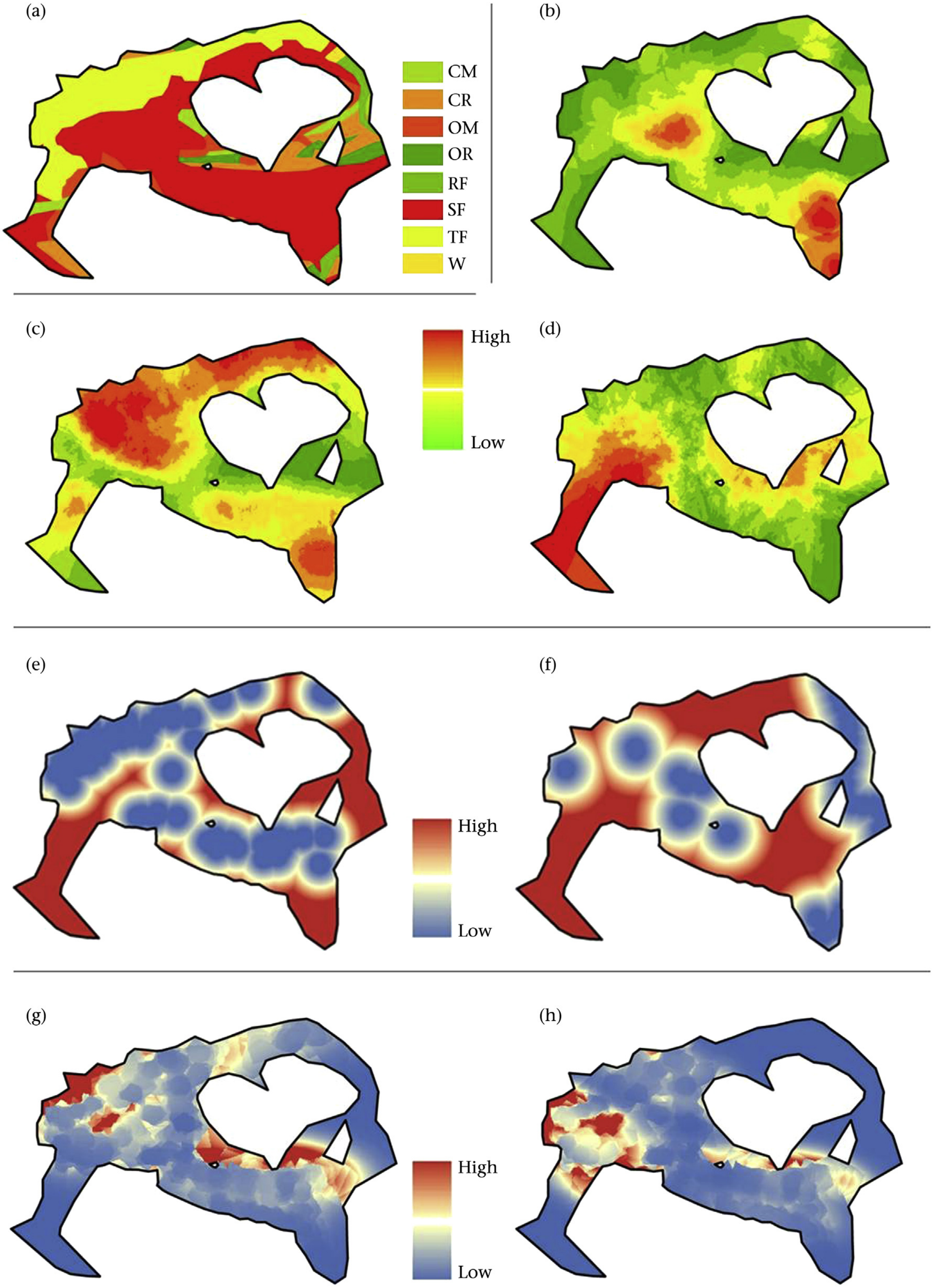

Figure 1. Spatial distribution of (a) habitat types with colours denoting food availability (CM: closed mountain; CR: closed rocky; OM: open mountain; OR: open rocky; RF: riverine forest SF: short forest; TF: tall forest; W: wetland), (b) fruit availability, (c) canopy height, (d) understory visibility, (e) Euclidean distance to sleeping sites, (f) Euclidean distance to water sources, (g) landscape of fear from eagles, and (h) landscape of intergroup encounter risk in the samango monkey home range.

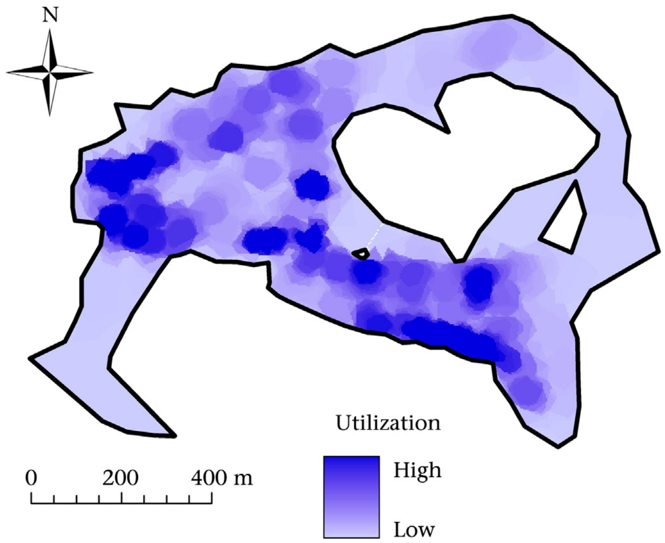

Figure 2. Home range and utilization distribution of the study group (54.7 ha) constructed using adaptive LoCoH analysis. The black outline indicates the edges of the home range with dark blue indicating areas of high utilization.

response or group encounter occurring at each point per unit of time the monkeys spent there were then calculated by dividing the kernel density estimations by the utilization distribution within ArcGIS to create the landscapes of fear from eagles and intergroup competition (Fig. 1g, h).

Statistical Analysis

Following Willems and Hill (2009), a random set of 1000 points from within the home range was selected using the Geospatial Modelling Environment (Version 0.5.5 Beta: Beyer, 2011) and parameter values were extracted. The spatial patterns within these data were assessed by inspection of correlograms and Moran's I values calculated in ArcGIS 10.0 (Fig. 3). Two mixed regressive–spatial regressive (or lagged predictor) models were conducted to determine the combined effect of the predictor variables on the intensity of space while also accounting for spatial autocorrelation (Willems & Hill, 2009). Model A incorporated habitat types (recoded into seven dummy variables) and included perceived eagle predation risk, distance from water and sleeping sites as separate predictor variables. Model B replaced habitat types with fruit availability, canopy height and understory visibility and included perceived eagle predation risk, distance from water and sleeping sites and intergroup encounter risk as separate predictor variables. Models were selected based on the AIC selection method suggested by Richards (2008). Initially all models with a Δ value ≤ 6 were selected with a more complex model chosen only if its AIC value was less than the AIC value of all the simpler models within which it was nested. Visual inspection of the residuals from the models confirmed the data were close to normally distributed (Appendix Fig. A1). Spatial analyses were conducted using the package Spatial Analysis in Macroecology 4.0 (Rangel, Diniz-Filho, & Bini, 2010).

Table 1
Mean fruit volume per 25 m^2, canopy height and understory visibility in the eight habitat types in the samango monkeys' home range

Habitat	Mean fruit volume (cm^3)	Mean canopy height (m)	Mean visibility (%)
Short forest	14 977	5.01	56.41
Open mountain	13 358	3.72	63.22
Closed rocky	12 677	3.77	58.68
Wetland	12 675	3.91	56.31
Tall forest	10 350	5.58	58.45
Closed mountain	10 072	4.96	66.70
Riverine forest	6.261	5.82	59.65
Open rocky	3.680	3.95	49.94

RESULTS

Two mixed regressive–spatial regressive models were used to determine the extent to which the variation in intensity of space use could be ascribed to the simultaneous effects of all investigated parameters. In Model A, containing the different habitat types, the full model included a nonsignificant effect of distance to water (Appendix Table A1) and water availability was dropped following AIC selection. The final model indicated significant negative relationships between intensity of range use and both perceived eagle predation and distance to sleeping sites (Table 2), with the standardized regression parameters and t values identifying eagle risk as the most important variable in the model. Significant relationships were also revealed with six of the seven habitat variables; range use intensity increased in tall forest, with highly significant negative relationships for riverine forest, open and closed mountain bushveld and open and closed rocky mountain bushveld. No significant relationship existed for short forest despite this habitat containing the highest food availability within the monkeys' home range (Table 1). The one preferred habitat, tall forest, contained the second-highest mean canopy height of the habitats available within the home range.

For Model B, the habitat types were replaced with separate landscapes of food availability, understory visibility and canopy height, and intergroup encounter risk was also incorporated into the analysis. The full model contained nonsignificant effects of intergroup encounter risk and food availability (Appendix Table A2) and these were dropped following AIC selection. The best model contained four parameters (Table 3). As for Model A, range use intensity was significantly negatively related to perceived eagle predation risk and distance to sleeping sites, with the standardized regression parameters and t values indicating that the landscape of fear from eagles had the strongest effect. Canopy height and understory visibility were positively related to the utilization distribution with the monkeys preferring areas of tall trees and high visibility.

DISCUSSION

The nonlethal effects of predators are increasingly recognized as one of the most significant constraints on prey behaviour and yet these effects are among the most difficult to quantify. Here we extended the spatially explicit models of Willems and Hill (2009) in order to explore the significance of arboreal substrate use and fine-grained environmental variables for understanding primate ranging behaviour. The key driver of samango monkey range use was spatial variation in the risk of predation from eagles in both models. In our initial model based on habitat types, strong relationships were found with almost every habitat type, although the relationships were not consistent with habitat selection based on food availability or canopy structure. Strikingly, food availability was also not a significant parameter in our model based on continuous environmental landscapes, with canopy height and understory visibility identified as significant parameters. Nevertheless, given that selection for tall trees and the avoidance of areas with low understory visibility are consistent with a predator avoidance strategy (Emerson et al., 2011; Jaffe & Isbell, 2009), these results highlight the significance of the landscape of fear as a key determinant of animal space use and behaviour.

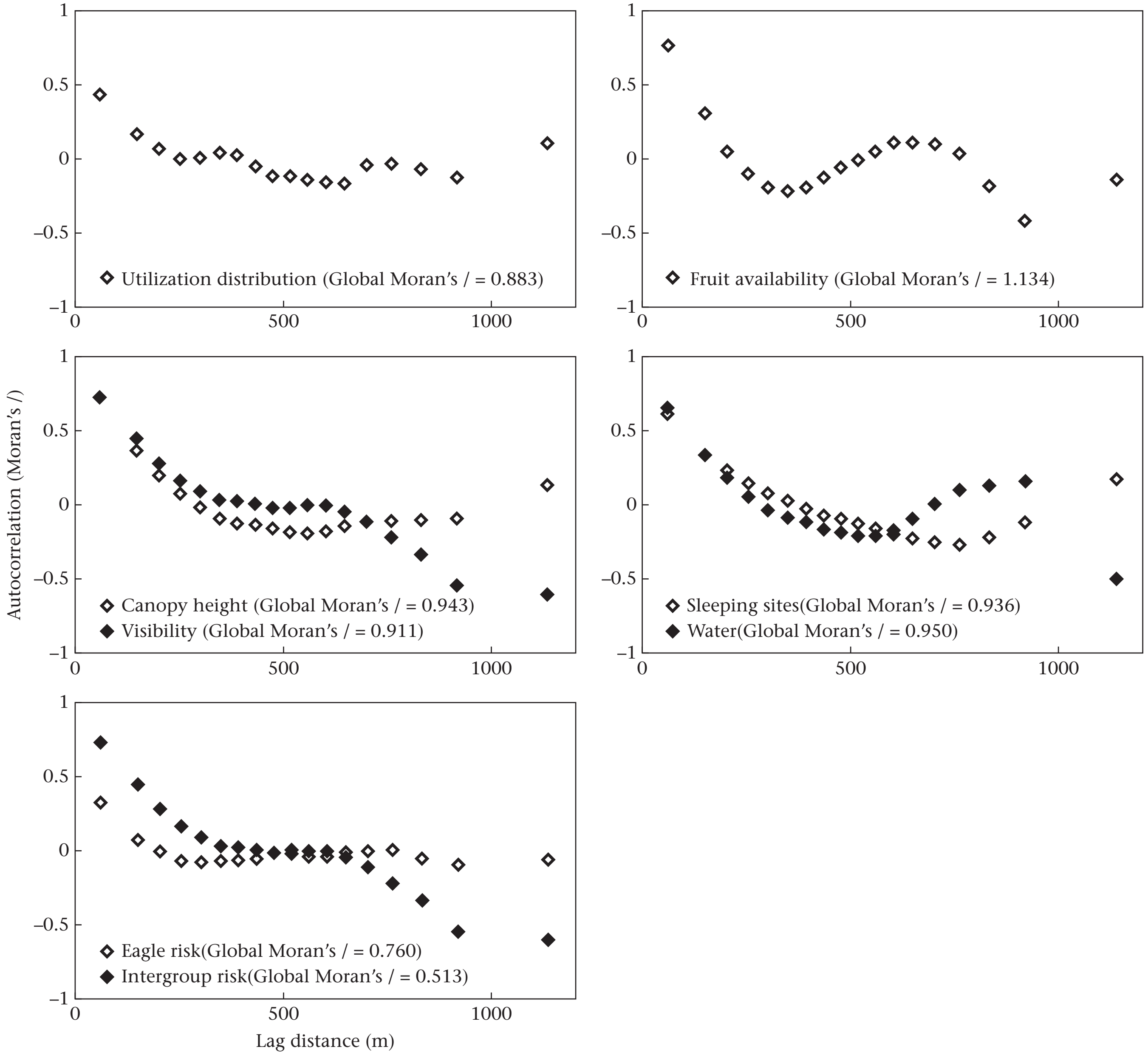

Figure 3. Correlograms and global Moran's *I* values for all parameters. Moran's *I* figures around ±1 signify strong positive/negative autocorrelation; a figure close to 0 means no autocorrelation.

Eagle predation risk was the strongest predictor of samango monkey space use in both models, with the strong negative effects suggesting that the eagles posed enough danger that samangos avoided areas considered high risk. While supporting the significance of predation as the principal parameter driving range use decisions, the significance of eagle risk in our study does contrast with Willems and Hill (2009) who found no significant relationship between an eagle landscape of fear and vervet ranging behaviour in the same habitat. Willems and Hill (2009) suggested that the eagles' ability to range over large hunting areas resulted in a relatively even distribution of predation risk across a primate's home range, such that adjustments in vertical space use by prey were a more effective antipredator strategy for this predator guild. Although we cannot rule out the fact that the differences in our results could emerge from our not formally incorporating landscapes of fear from leopards and snakes in our models, our results do suggest that predation risk from eagles does indeed produce a horizontal landscape of fear.

The two highest areas of perceived eagle risk in our study were close to two known nesting sites of breeding pairs of eagles: in the northwest a crowned eagle nest and in the east a black eagle pair (Fig. 1g). As a consequence, direct encounters in these areas may have been more frequent. Many eagles prefer to hunt from a perched position high in the canopy, especially in areas of relatively dense vegetation or high density of prey species (Garrett, Watson, & Anthony, 1993; Shultz, 2001; Valdez & Osborn, 2004). Since samangos select areas of tall continuous forest canopy this is likely to increase their risk of encounter with eagles, particularly in comparison to vervet monkeys. As a consequence samango monkeys may be exposed to greater risk of predation from raptors in comparison to semiterrestrial vervet monkeys, potentially accounting for the differences in response to this predator guild

Table 2
Parameter estimates and key statistics of Model A, expressing utilization distribution as a function of perceived eagle predation risk, habitat type and distance to sleeping sites

Predictor	β	*B*	SE *B*	SE γ	*t*	*P*
Landscape of fear						
Eagle	−0.329	−0.338	0.028	0.192	−11.583	<0.001
Habitat types						
Short forest	0.018	0.018	0.038	0.171	0.476	0.635
Open mountain	−0.092	−0.121	0.022	0.518	−4.158	<0.001
Closed rocky	−0.233	−0.289	0.024	0.408	−9.796	<0.001
Tall forest	0.091	0.083	0.046	0.118	1.998	0.046
Closed mountain	−0.095	−0.138	0.019	0.758	−4.989	<0.001
Riverine forest	−0.162	−0.211	0.022	0.495	−7.369	<0.001
Open rocky	−0.132	−0.190	0.020	0.736	−6.538	<0.001
Environmental factors						
Sleeping sites	−0.353	−0.154	0.063	0.006	−5.582	<0.001

Habitat types are presented in descending order of fruit availability. Model statistics: $N = 1000$; $R^2 = 0.312$; $\rho = 0.992 \pm 0.172$; $\gamma = 0.992$; $\mathrm{AIC_c} = 8046.844$. Terms: ρ, spatial autoregressive parameter; γ, spatial cross-regressive parameter; β, unstandardized regression parameter; *B*, standardized regression parameter.

between the two species and the existence of a strong eagle landscape of fear in the arboreal species.

We recorded no evidence of leopard-specific alarm calls by samango moneys, despite the landscape of fear from leopards being the strongest predictor of vervet monkey space use on site (Willems & Hill, 2009). Papworth et al. (2008) identified a leopard-specific alarm vocalization in a population of samango monkeys in Uganda, although the male 'pyow' call has also been suggested to be a territory call (Cords, 1987; Marler, 1973) or having the characteristics of a general alarm call (Brown, 1989). Further work is therefore required to determine the validity of acoustically distinct calls for different predator guilds in samango monkeys. Nevertheless, dietary data from the high-density leopard population at Lajuma (10.73 leopards per 100 km^2: Chase-Grey, Kent, & Hill, 2013) indicate that samangos are less frequent prey than vervet monkeys (vervets 12.2%; samangos 2.1%: Chase-Grey, 2011). This suggests that the samango monkeys are successful in avoiding predation from this species at our site. Nevertheless, further work is clearly needed to determine the extent to which fear of terrestrial predators affects space use in samango monkeys. Similarly, while the small number of snake alarm calls probably reflects the fact that most on-site species of snake were not true predators, additional data are needed to explore the landscape of fear from snakes further.

In combination with the results of Willems and Hill (2009), the current study suggests that predation risk is a key driver of ranging behaviour for both samango monkeys and vervet monkeys. Nevertheless, the landscapes of fear experienced by the two species differ markedly in this population, despite exposure to identical predator guilds. The landscape of fear from eagles was the most significant influence on range use for samango monkeys, while fear of leopards and baboons was the key driver for the sympatric vervet monkeys (Willems & Hill, 2009). Although further work is needed to assess the importance of leopards and snakes to samangos, the current findings highlight the importance of distinguishing between the risk effects of different predators in understanding prey ecology (Cresswell & Quinn, 2013; Morosinotto, Thomson, & Korpimaki, 2010; Preisser et al., 2007), since differences in the antipredator responses of species may be apparent only when risk is assessed on a predator-specific basis.

Table 3
Parameter estimates and key statistics of Model B, expressing utilization distribution as a function of perceived eagle predation risk, understory visibility, height of trees and sleeping site location

Predictor	β	*B*	SE *B*	SE γ	*t*	*P*
Landscapes of fear						
Eagle	−0.271	−0.278	0.029	0.192	−9.322	<0.001
Environmental factors						
Understory visibility	0.173	0.109	0.048	0.027	3.561	<0.001
Height of trees	0.398	0.277	0.045	0.041	8.838	<0.001
Sleeping sites	−0.334	−0.146	0.071	0.006	−4.720	<0.001

Model statistics: $N = 1000$; $R^2 = 0.169$; $\rho = 0.992 \pm 0.172$; $\gamma = 0.992$; $\mathrm{AIC_c} = 8215.277$. Terms as for Table 3.

Food availability had no significant effect on samango monkey space use, either at the level of habitat type or when food availability was quantified as a spatial landscape. In contrast, canopy height was the most significant habitat parameter in the second model, with areas of high understory visibility also significantly preferred. Such relationships were obscured in Model A, however, where habitat classifications integrated information on food availability and vegetation structure into a single metric. This highlights the value of replacing categorical habitat types with continuous landscapes of environmental variables since in Model A it was difficult to infer the underlying habitat characteristics driving selection for particular habitat types. Although the methods employed in our second analysis are more labour intensive, and so may not be appropriate in all situations, future studies should adopt approaches that ensure environmental parameters are recorded at spatial scales appropriate to the ranging data and utilization distribution.

Preference for tall forest is unsurprising for an arboreal species, but Model B highlights that areas of relatively taller canopy were being selected within the forest habitats with the monkeys showing a strong preference for tree height. The findings are consistent with previous observations that samango monkeys spend most of their time high in the canopy (Thomas, 1991), behaviour that has previously been reported to decrease predation risk from terrestrial predators (Hart, Katembo, & Punga, 1996). An experimental study based on giving-up densities highlighted that the ground was perceived as higher risk by samangos in this population (Emerson et al., 2011) suggesting that terrestrial predators may be an important driver of habitat selection for the monkeys even if this is not reflected in the distribution of alarm vocalizations. The avoidance of areas with low visibility and dense understory vegetation that may conceal terrestrial ambush predators (du Bothma & Le Riche, 1986) is consistent with this interpretation, but further research is needed to determine the importance of terrestrial predators in shaping the range use of these arboreal primates.

The selection of habitats on the basis of canopy height and understory visibility appears to account for the lack of independent effects of food availability within our models. Although food availability correlates positively with canopy height within the study area, low-visibility habitats are also high in fruit biomass such that interactions between these habitat effects may mask any direct influence of resource availability on ranging (Coleman, 2013). In using annual fruit availability in our spatial models we may not have detected the more subtle seasonal effects resulting from samangos exploiting areas of short-term high fruit availability (Willems et al., 2009). Samango monkeys also possess cheek pouches that are thought to play an important role in minimizing exposure to predators (Smith et al., 2008). Samangos may thus minimize time in areas of high food availability but high predation risk by filling their cheek pouches and then moving to areas of low food availability but increased safety from predators to consume the food. Further research examining cheek pouch use within the landscape of fear is required to confirm this prediction.

Finally, we found no effect of intergroup encounters on samango monkey space use; however, our use of annual landscapes may disguise seasonal effects (see Markham et al., 2013). Lawes and Henzi (1995) reported that 48% of intergroup encounters in samango monkeys were food related, with territory defence and mate defence potential explanations for the remaining encounters. The relative importance of these factors is likely to vary significantly on an annual basis, leading to differing selection pressures relating to space use. In baboons, broad temporal changes in ecological resources were the major predictor of how intensively group ranges overlapped, but spacing increased significantly in weeks in which social groups had high proportions of fertile females (Markham et al., 2013). Distinguishing between mating and nonmating seasons is thus a key future direction, although simultaneous monitoring of the ranging behaviour of the neighbouring groups will also help to separate the independent effects of conspecific groups on range use.

Studies of the effects of predators on the behaviour and abundance of their prey have traditionally assumed that all predators have the same selective effects (Lima, 2002) but the inaccuracy of this assumption is increasingly recognized (Cresswell & Quinn, 2013; Preisser et al., 2007; Schmitz, 2008). The results presented here suggest that similar prey species inhabiting the same environment do not experience the same selective effects from the different predator guilds, despite being exposed to the same predator community. The challenge for future work, therefore, is to determine how predator diversity and hunting mode coupled with variation in prey responses shapes the dynamics of prey communities (Preisser et al., 2007).

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APPENDIX

Table A1

Parameter estimates and key statistics of full Model A, a mixed regressive–spatial regressive model expressing utilization distribution as a function of perceived eagle predation risk, habitat type and distance to sleeping sites and water

Predictor	*B*	β	SE β	SE γ	*t*	*P*
Landscape of fear						
Eagle	−0.329	−0.338	0.028	0.192	−11.568	<0.001
Habitat types						
Short forest	0.018	0.018	0.039	0.171	0.478	0.633
Open mountain	−0.092	−0.121	0.022	0.518	−4.129	<0.001
Closed rocky	−0.233	−0.289	0.024	0.408	−9.780	<0.001
Tall forest	0.091	0.083	0.046	0.118	1.998	0.046
Closed mountain	−0.095	−0.138	0.019	0.758	−4.978	<0.001
Riverine forest	−0.162	−0.211	0.022	0.495	−7.357	<0.001
Open rocky	−0.132	−0.190	0.020	0.736	−6.499	<0.001
Environmental factors						
Sleeping sites	−0.354	−0.155	0.066	0.006	−5.399	<0.001
Water	0.003	0.001	0.066	0.006	0.05	0.960

Habitat types are presented in descending order of fruit availability. Model statistics: $N = 1000$; $R^2 = 0.312$; $\rho = 0.992 \pm 0.172$; $\gamma = 0.992$; $AIC_c = 8051.019$. Terms: ρ, spatial autoregressive parameter, γ, spatial cross-regressive parameter; *B*, unstandardized regression parameter; β, standardized regression parameter.

Table A2

Parameter estimates and key statistics of the full Model B, a mixed regressive–spatial regressive model expressing utilization distribution as a function of perceived eagle predation risk, intergroup encounter risk and other environmental factors

Predictor	*B*	β	SE β	SE γ	*t*	*P*
Landscapes of fear						
Eagle	−0.272	−0.279	0.033	0.192	−8.309	<0.001
Intergroup	−0.018	−0.023	0.028	0.447	−0.656	0.512
Environmental factors						
Fruit availability	−0.086	−0.054	0.050	0.027	−1.711	0.087
Understory visibility	0.200	0.126	0.052	0.027	3.813	<0.001
Height of trees	0.434	0.302	0.047	0.041	9.304	<0.001
Sleeping sites	−0.266	−0.116	0.074	0.006	−3.606	<0.001
Water	−0.208	−0.089	0.077	0.006	−2.698	0.007

Model statistics: $N = 1000$; $R^2 = 0.176$; $\rho = 0.992 \pm 0.172$; $\gamma = 0.992$; $AIC_c = 8218.341$. Terms as for Table A1.

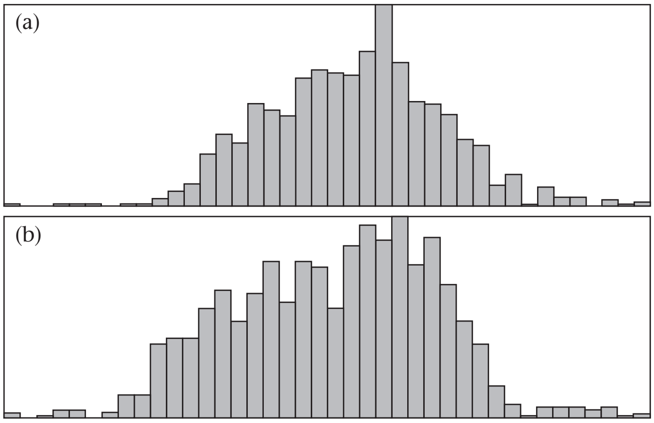

Figure A1. Residual distributions from the spatial regressive–mixed regressive models. (a) Model A: skewness = 0.018; kurtosis = 0.274. (b) Model B: skewness = −0.103; kurtosis = −0.211. Any score ±1 is considered strongly non-normally distributed (Fife-Schaw, Hammond, & Breakwell, 2006).