

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

3

4

5 Ben T. Coleman<sup>1,2</sup> & Russell A. Hill<sup>1,2\*</sup>

6

7 <sup>1</sup> Department of Anthropology

8 Durham University

9 Dawson Building

10 South Road

11 Durham. DH1 3LE

12 UK

13

14 <sup>2</sup> Primate & Predator Project

15 Lajuma Research Centre

16 P.O. Box 522

17 Louis Trichardt (Makhado) 0920

18 South Africa

19

20 \*Corresponding author

21 Dr Russell A. Hill

22 Department of Anthropology

23 Durham University

24 Dawson Building

25 South Road

26 Durham. DH1 3LE

27 UK

28 Email: [r.a.hill@durham.ac.uk](mailto:r.a.hill@durham.ac.uk)

29 Tel: +44 (0) 191 3341601

30 Fax: +44 (0) 191 3341615

31

32

33 Word count: 8268

34

35

36 Spatial variation in predation risk generates a “landscape of fear”, with prey animals modifying their  
37 distribution and behaviour in response to this variable predation risk. In systems comprised of  
38 multiple predators and prey species, a key challenge is distinguishing the independent effects of  
39 different predator guilds on prey responses. Here we exploit the acoustically distinct alarm calls of  
40 samango monkeys (*Cercopithecus mitis erythrarchus*) to create a predator-specific landscape of fear  
41 for eagles to assess its impact on space use within mixed regressive–spatial regressive models  
42 incorporating data on resource distribution and structural characteristics of the environment. The  
43 landscape of fear from eagles was the most significant determinant of samango range use, with no  
44 effect of resource availability. The monkeys also selected areas of their range with higher canopies  
45 and higher understory visibility, behaviour consistent with further minimising risk of predation.  
46 These results contrast with those of vervet monkeys (*Chlorocebus aethiops pygerythrus*) at the same  
47 site where the landscapes of fear from leopards and baboons were the most significant  
48 determinants of space use. Whilst highlighting that predation risk is a key driver of primate  
49 behaviour in this population, the landscapes of fear experienced by samango monkeys and vervet  
50 monkeys appear to differ despite exposure to identical predator guilds. This emphasizes the  
51 importance of distinguishing between the risk effects of different predators in understanding prey  
52 ecology, but also that closely-related prey species may respond to these predator-specific risks in  
53 different ways.

54

55

56 Key words: blue monkey; Sykes monkey; *Cercopithecus albogularis*; *Cercopithecus aethiops*; fruit  
57 availability; intergroup competition; geographic information system (GIS); Local Convex Hulls  
58 (LoCoH) analysis; spatial regression.

59

60 Predation is a major selective force driving animal evolution ([Dawkins & Krebs 1979](#)) with almost all  
61 animal species engaged in some form of predator-prey interaction ([Abrams 2000](#)). Understanding  
62 how animals manage the risk of predation is thus a central issue in behavioural ecology ([Quinn &  
63 Cresswell 2004](#)). Predation imposes two costs on prey individuals: the direct fitness costs of  
64 mortality resulting from successful predation and the indirect costs of employing behaviours to  
65 reduce mortality risks. These non-lethal effects of predators appear to impact almost every aspect  
66 of prey behaviour and ecology ([Caro 2005](#); [Lima 1998](#); [Werner & Peacor 2006](#)). Nevertheless, these  
67 risk effects are amongst the most difficult to quantify ([Creel & Christianson 2008](#); [Creel et al. 2008](#);  
68 [Hill & Dunbar 1998](#)).

69  
70 Spatial variation in risk is a key driver of non-lethal predation effects ([Cresswell & Quinn 2013](#)),  
71 primarily due to the constraints this places on foraging behaviour and the subsequent impact this  
72 has on competitive and trophic interactions ([Creel et al. 2007](#); [Minderman, Lind & Cresswell 2006](#);  
73 [Peckarsky & McIntosh 1998](#); [Willems & Hill 2009](#)). Spatial variation in perceived predation risk has  
74 often been conceptualised as a 'landscape of fear' ([Brown & Kotler 2004](#); [Brown, Laundre & Gurung  
75 1999](#); [Laundré, Hernandez & Altendorf 2001](#)), with approaches such as giving-up densities  
76 quantifying the trade-offs animals make between nutrient acquisition and the costs of predation  
77 ([Brown 1988](#)). One of the challenges though is that these methods do not strictly measure  
78 perceived predation risk ([Searle, Stokes & Gordon 2008](#)) and in multi-predator environments they do  
79 not convey information on the impact of different predators on the behavioural responses of prey  
80 species. This latter issue is critical, since when prey are subject to attack from several predators that  
81 present different types of risk, the appropriate antipredatory responses differ between predator  
82 guilds ([Cresswell & Quinn 2013](#); [Preisser, Orrock & Schmitz 2007](#); [Shultz et al. 2004](#); [Willems & Hill  
83 2009](#)). As a consequence, to understand how prey manage the risk of predation within their  
84 environment, the risk of predation from each predator guild must be quantified independently.  
85 Nevertheless, there is a significant body of evidence to suggest that animals trade-off food

86 availability and predation risk in habitat choice ([Cowlshaw 1997](#); [Fortin & Fortin 2009](#); [Willems & Hill](#)  
87 [2009](#)). The landscape of fear is thus a powerful concept in animal ecology and has been suggested  
88 to be the key landscape within an animal's environment ([Brown & Kotler 2004](#)). To test this  
89 assertion, however, methods are required that exclusively reflect perceived predation risk and  
90 distinguish between predator-specific predation risk in determining prey behaviour.

91

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

109

110 Here we apply the framework of [Willems and Hill \(2009\)](#) to a population of samango monkeys  
111 (*Cercopithecus mitis erythrarchus*) inhabiting the same multi-predator environment as in the original

112   vervet study. Initially we directly replicate the modelling approach and variable selection of [Willems](#)  
113   [and Hill \(2009\)](#) to facilitate a direct comparison of our results to the previous models on vervet  
114   monkeys. In doing so, we assess the impact that substrate preferences (arboreality vs. semi-  
115   terrestriality) have on the exposure to different predator guilds and the implications of this for  
116   predator-specific landscapes of fear and range use. Samango monkeys, as an arboreal species, may  
117   experience different predation threats to more terrestrial species such as vervet monkeys ([Lawes](#)  
118   [1991](#); [McGraw 2002](#)), so influencing the relative importance of different predators in driving ranging  
119   behaviour.

120

121   We then extend the modelling framework of [Willems and Hill \(2009\)](#) in two ways. Firstly, we replace  
122   categorical habitat types with continuous spatial measures of resource availability and structural  
123   characteristics of habitats (e.g. canopy height, habitat visibility) to investigate the key drivers of  
124   habitat choice within the landscape of fear. Samango monkeys have been observed to spend the  
125   majority of their time high in the canopy ([Thomas 1991](#)), with the ground perceived as higher risk  
126   ([Emerson, Brown & Linden 2011](#)), suggesting that areas of tall canopy will be preferred. Similarly,  
127   habitats with dense understory vegetation may provide cover for terrestrial ambush predators ([du](#)  
128   [Bothma & Le Riche 1986](#)) while areas of high visibility may increase an individual's ability to monitor  
129   threats from predators or competitors ([Cowlshaw 1994](#); [Hill & Weingrill 2007](#); [Jaffe & Isbell 2009](#)).  
130   For example, vervet monkeys have been shown to decrease vigilance in high visibility areas  
131   ([Chapman 1985](#); [Enstam & Isbell 2002](#)). Samango monkeys are thus predicted to prefer higher  
132   visibility habitats. Since canopy height and visibility will vary independently between habitat types,  
133   consideration of the spatial variation in these parameters should be more informative than broad  
134   habitat classifications. Secondly, we explore the impact of competition with neighbouring groups.  
135   Intraspecific competition and the active avoidance of neighbouring groups has long been recognized  
136   as a significant factor shaping space-use strategies and movement decisions in many species ([Gibson](#)

137 [& Koenig 2012](#); [Markham et al. 2013](#)), and yet how intraspecific competition, predation risk and  
138 resource availability interact in determining spatial range use is largely unknown.

139

140

## 141 **METHODS**

142

### 143 ***Study species and field site***

144 Samango monkeys are medium sized (adult females ~4.4kg, adult males ~7.6kg: [Harvey, Martin and](#)  
145 [Clutton-Brock \(1987\)](#)) arboreal, diurnal guenons. They form single-male, multi-female groups ([Henzi](#)  
146 [& Lawes 1987](#); [Rudran 1978](#)), with group sizes ranging from 4-65 ([Beeson et al. 1996](#); [Butynski 1990](#);  
147 [Houle, Chapman & Vickery 2010](#); [Lawes, Cords & Lehn 2013](#); [Smith, Link & Cords 2008](#)). Samango  
148 monkeys are primarily frugivorous but supplement their diets with leaves, insects and flowers  
149 ([Coleman 2013](#); [Lawes 1991](#); [Lawes, Henzi & Perrin 1990](#)). Like vervet monkeys, samango monkeys  
150 have acoustically distinct alarm calls for different predator guilds which can be differentiated by  
151 human observers ([Brown 1989](#); [Papworth et al. 2008](#)).

152

153 Research was conducted at the Lajuma Research Centre, located in the Soutpansberg Mountains,  
154 Limpopo Province, South Africa (23°02'23''S, 29°26'05''E). Substantial local variation in abiotic  
155 factors such as elevation and water availability results in a variety of microclimates which are able to  
156 support a substantial diversity of both flora and fauna ([Brock, Nortje & Gaigher 2003](#); [Willems 2007](#)).

157 The study area has natural fragments of tall forest (10-20m height) occurring amongst areas of  
158 natural short forest (5-10m height). Local climate is classified as temperate/mesothermal, with cool  
159 dry winters from April-September and warm to hot wet summers from October-March ([Willems](#)  
160 [2007](#)). Mean annual temperature on site averages 17.1°C, with a mean annual rainfall of 724mm  
161 ([Willems, Barton & Hill 2009](#)). On site, samango monkeys are sympatric with vervet monkeys,  
162 chacma baboon, thick-tailed galago (*Otolemur crassicaudatus*) and southern lesser bushbaby

163 (*Galago moholi*). Potential predators include leopard, crowned eagle, African black eagle (*Aquila*  
164 *verreauxii*) and African rock python. Venomous snakes, including black mamba (*Dendroaspis*  
165 *polylepis*), puff adder (*Bitis arietans*) and Mozambique spitting cobra (*Naja mossambica*), whilst not  
166 actively preying on samango monkeys, still pose potential mortality threats and may affect range  
167 use.

168

### 169 ***Behavioural data***

170 A well-habituated group of approximately 40 samango monkeys was observed over a 16 month  
171 period (September 2009-December 2010). We restrict the data presented here to that collected  
172 during the final 12 months (January-December 2010) in order to confine the analyses to a single  
173 annual cycle. Behavioural data were collected over eight full follow days per month (totalling 96  
174 days), with a successful day defined as following the group from dawn to dusk without losing  
175 audiovisual contact for more than a total of 60 minutes. Study days ranged from approximately 11.5-  
176 14 hours depending upon season. Data were collected on a palmtop (Sony Clie SL-10) with  
177 behavioural data collection software (Pendragon Forms 4.0; Pendragon Software, Libertyville,  
178 Illinois, USA) and a GPS (Garmin GPS 60CSX; Garmin, Olathe, Kansas, USA) continually recording  
179 location. Supplementary data were collected in paper notebooks.

180

181 To determine perceived predation risk, the time, location and details of alarm calls were recorded on  
182 an all-occurrence basis. There were a total of 131 alarm calls across the study (eagle=59, snake=3,  
183 other=7, unknown=62) with no confirmed leopard-specific alarm vocalisations. Since a minimum of  
184 10 observations is required for the statistical techniques used here ([Borger et al. 2006](#)), only eagle  
185 alarm calls were further investigated. Eleven of the 59 eagle alarm calls were accompanied by an  
186 eagle sighting, leaving 48 potentially “false” alarm calls; these calls still express the monkeys’  
187 perception of eagle risk, however, and are equally as informative as when a predator sighting was  
188 confirmed ([Willems & Hill 2009](#)).

189

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

194

### 195 ***Environmental data***

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

201

202 Food availability was calculated from phenological transects and random quadrat sampling; these  
203 methods are the most efficient for determining all types of density-related features ([Southwood &  
204 Henderson 2000](#)). A series of phenological transects were established, with 10 mature trees from 24  
205 potential food species then selected and tagged to ensure an even coverage of each species  
206 throughout the monkey home range as well as a range of tree sizes. All trees were monitored  
207 monthly for height, crown diameter at the widest point, number of leaves, percentage mature  
208 leaves, number of flowers, number of fruits and percentage ripeness (unripe/ripe/overripe). Where  
209 numbers of items were too large to count, estimates were made for a single branch or section and  
210 then scaled up to the size of the tree. For the purposes of this analysis, food availability estimates  
211 focussed on fruit availability due to samango monkeys' mainly frugivorous diet ([Lawes 1991](#)), with  
212 eight tree species, accounting for more than 67.1% of the total fruit intake ([Coleman 2013](#)) extracted  
213 from the phenological data set. For each species, linear regression analysis was used to derive  
214 equations that expressed annual food availability for each species as a function of tree height and/or



215 crown diameter. These equations were then used to estimate food availability for trees of known  
216 height and crown diameter from the quadrat sampling (below). Further details of the equations used  
217 are given in [Coleman \(2013\)](#).

218

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

229

230 Mean tree height per quadrat was used to determine canopy height for each of the 1268 quadrats  
231 sampled. To estimate habitat visibility, a percentage understory visibility measurement was made  
232 for 632 quadrats using a 0.8m x 0.8m checkerboard (divided into 10cm squares). An observer was  
233 located at the northwest corner of the quadrat, and a field assistant then held the checkerboard at a  
234 height of two metres and a distance of five metres in each of the four cardinal points directions. The  
235 observer recorded the proportion of the grid visible in each direction and understory visibility was  
236 calculated for each quadrat as the mean of these four measurements.

237

### 238 ***Spatial landscapes***

239 All data were imported into ArcGIS 10 (Environmental Systems Research Institute, California), with  
240 data projected into the Universal Transverse Mercator coordinate system (datum, WGS 1984; zone,

241 35 S) and the cell size of all output rasters set to 3m, consistent with GPS accuracy in the field. A  
242 series of layers were then computed to characterise the spatial distribution of the different  
243 parameters.

244

#### 245 *Utilisation Distribution*

246 Local Convex Hulls (LoCoH) analysis ([Getz et al. 2007](#); [Getz & Wilmers 2004](#)) was used to determine  
247 utilisation distribution. This method was chosen over kernel density estimation due to its superior  
248 convergence properties and ability to cope better with hard boundaries such as cliffs and rivers and  
249 clumped data points ([Getz et al. 2007](#); [Hemson et al. 2005](#); [Ryan, Knechtel & Getz 2006](#); [Silverman  
250 1986](#); [Steury et al. 2010](#)). Ranging data were filtered to give a location point every ten minutes,  
251 providing 6912 points for analysis. An adaptive LoCoH utilisation distribution ([Getz & Wilmers 2004](#))  
252 was created using R (Version 2.13: [R Core DevelopmentTeam \(2011\)](#)). The adaptive LoCoH method  
253 is one of three variations of LoCoH analysis, and enables smaller convex hulls to arise in higher usage  
254 areas, allowing more detailed information in areas of clumped data ([Getz et al. 2007](#)), such as  
255 around sleeping sites or key food resources that are used repeatedly or for long periods of time. For  
256 adaptive LoCoH analysis it is suggested that the widest point between two locations is used as the  
257 value  $a$  in order to ensure the correct formation of the 100% isopleth ([Getz et al. 2007](#)); here  $a$  was  
258 set to 1329 metres with the utilisation distribution calculated in 1% isopleths (Figure 2).

259

#### 260 *Resource availability and habitat structure*

261 Initially, estimates of mean food availability, canopy height and visibility were computed from the  
262 quadrats sampled for each of the eight habitat types (Table 1) and linked to the habitat layer within  
263 GIS. To investigate the effect of the spatial variation in environmental parameters more precisely,  
264 landscapes of fruit availability, canopy height and understory visibility were then constructed.  
265 Quadrat data for each of these variables were interpolated using kriging ([Cressie 1990](#)) to generate  
266 the landscapes (Figure 1b-d). The search radii for kriging were calculated based on the number of

267 points achieving minimum root mean squared error (food resources: 45; canopy height: 45; visibility:  
268 60) ([Salih et al. 2002](#)). Finally, access to water and sleeping sites were expressed as the shortest  
269 Euclidean distances to the nearest water source and confirmed sleeping tree taken from the  
270 behavioural data (Figure 1e-f). All layers were clipped to the utilisation distribution.

271

#### 272 *Predation risk and intergroup encounter risk*

273 A fixed kernel density estimation ([Silverman 1986](#)) was employed to create a density distribution of  
274 eagle alarm vocalisations and inter-group encounters. A PLUGIN bandwidth parameterisation was  
275 used since on smaller samples it has been shown to have less variability and outperform least-  
276 squares cross validation (LSCV: ([Gitzen, Millspaugh & Kernohan 2006](#); [Lichti & Swihart 2011](#))).

277 Following [Willems and Hill \(2009\)](#), measures of the probability of an alarm response or group  
278 encounter occurring at each point per unit of time the monkeys spent there were then calculated by  
279 dividing the kernel density estimations by the utilisation distribution within ArcGIS to create the  
280 landscapes of fear for eagles and inter-group competition (Figure 1g-h).

281

#### 282 **Statistical analysis**

283 Following [Willems and Hill \(2009\)](#), a random set of 1000 points from within the home range were  
284 selected using Geospatial Modelling Environment (Version 0.5.5 Beta: [Beyer \(2011\)](#)) and parameter  
285 values were extracted. The spatial patterns within these data were assessed by inspection of  
286 correlograms and Moran's  $I$  values calculated in ArcGIS 10.0 (Figure 3). Two mixed regressive-spatial  
287 regressive (or lagged predictor) models were conducted to determine the combined effect of the  
288 predictor variables on the intensity of space whilst also accounting for spatial autocorrelation  
289 ([Willems & Hill 2009](#)). Model A incorporated habitat types (recoded into seven dummy variables)  
290 and included perceived eagle predation risk, distance from water and sleeping sites as separate  
291 predictor variables. Model B replaced habitat types with fruit availability, canopy height and  
292 understory visibility and included perceived eagle predation risk, distance from water and sleeping

293 sites and inter-group encounter risk as separate predictor variables. Models were selected based on  
294 the AIC selection method suggested by [Richards \(2008\)](#). Initially all models with an  $\Delta$ -value  $\leq 6$  were  
295 selected with a more complex model only chosen if its AIC value was less than the AIC value of all  
296 the simpler models within which it was nested. Visual inspection of the residuals from the models  
297 confirmed the data were close to normally distributed (Figure A1). Spatial analyses were conducted  
298 using the package Spatial Analysis in Macroecology 4.0 ([Rangel, Diniz-Filho & Bini 2010](#)).

299

300

## 301 **RESULTS**

302

303 Two mixed regressive-spatial regressive models were used in order to determine the extent to which  
304 the variation in intensity of space use could be ascribed to the simultaneous effects of all  
305 investigated parameter. In Model A, containing the different habitat types, the full model included a  
306 non-significant effect of distance to water (Table A1) and water availability was dropped following  
307 AIC selection. The final model indicated significant negative relationships between intensity of range  
308 use and both perceived eagle predation and distance to sleeping sites (Table 2), with the  
309 standardised regression parameters and t values identifying eagle risk as the most important  
310 variable in the model. Significant relationships were also revealed with six of the seven habitat  
311 variables; range use intensity increased in tall forest, with highly significant negative relationships for  
312 riverine forest, open and closed mountain bushveld and open and closed rocky mountain bushveld.  
313 No significant relationship existed for short forest despite this habitat containing the highest food  
314 availability within the monkey home range (Table 1). The one preferred habitat, tall forest,  
315 contained the second highest mean canopy height of the habitats available within the home range.  
316  
317 For Model B, the habitat types were replaced with separate landscapes of food availability,  
318 understory visibility and canopy height, and intergroup encounter risk was also incorporated into the

319 analysis. The full model contained non-significant effects of intergroup encounter risk and food  
320 availability (Table A2) and these were dropped following AIC selection. The best model contained  
321 four parameters (Table 3). As for Model A, range use intensity was significantly negatively related to  
322 perceived eagle predation risk and distance to sleeping sites, with the standardised regression  
323 parameters and t values indicating that the landscape of fear of eagles had the strongest effect.  
324 Canopy height and understory visibility were positively related to the utilisation distribution with the  
325 monkeys preferring areas of tall trees and high visibility.

326

327

## 328 **DISCUSSION**

329

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

344

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

357

358 The two highest areas of perceived eagle risk in our study were close to two known nesting sites of  
359 breeding pairs of eagles; in the northwest a crowned eagle nest and in the east a black eagle pair  
360 (Figure 1g). As a consequence, direct encounters in these areas may have been more frequent.  
361 Many eagles prefer to hunt from a perched position high in the canopy, especially in areas of  
362 relatively dense vegetation or high density of prey species ([Garrett, Watson & Anthony 1993](#); [Shultz](#)  
363 [2001](#); [Valdez & Osborn 2004](#)). Since samangos select areas of tall continuous forest canopy this is  
364 likely to increase their risk of encounter with eagles, particularly in comparison to vervet monkeys.  
365 As a consequence samango monkeys may be exposed to greater risk of predation from raptors in  
366 comparison to semi-terrestrial vervet monkeys, potentially accounting for the differences in  
367 response to this predator guild between the two species and the existence of a strong eagle  
368 landscape of fear in the arboreal species.

369

370 We recorded no evidence of leopard-specific alarm calls by samango monkeys, despite the landscape  
371 of fear from leopards being the strongest predictor of vervet monkey space use on site ([Willems &  
372 Hill 2009](#)). [Papworth et al. \(2008\)](#) identified a leopard-specific alarm vocalisation in a population of  
373 samango monkeys in Uganda, although the male 'pyow' call has also been suggested to be a  
374 territory call ([Cords 1987](#); [Marler 1973](#)) or having the characteristics of a general alarm call ([Brown  
375 1989](#)). Further work is therefore required to determine the validity of acoustically distinct calls for  
376 different predator guilds in samango monkeys. Nevertheless, dietary data from the high-density  
377 leopard population at Lajuma (10.73 leopards per 100 km<sup>2</sup>: [Chase Grey, Kent and Hill \(in press\)](#))  
378 indicate that samangos are less frequent prey compared to vervet monkeys (vervets 12.2%;  
379 samangos 2.1%: [Chase-Grey \(2011\)](#)). This suggests that the samango monkeys are successful in  
380 avoiding predation from this species at our site. Nevertheless, further work is clearly needed to  
381 determine the extent to which fear of terrestrial predators impacts on space use in samango  
382 monkeys. Similarly, while the small number of snake alarm calls probably reflects the fact that most  
383 on-site species of snake were not true predators, additional data are needed to explore the  
384 landscape of fear from snakes further.

385

386 In combination with the results of [Willems and Hill \(2009\)](#), the current study suggests that predation  
387 risk is a key driver of ranging behaviour for both samango monkeys and vervet monkeys. It is  
388 important to note though, that the landscapes of fear experienced by the two species differ  
389 markedly in this population, despite exposure to identical predator guilds. The landscape of fear  
390 from eagles was the most significant influence on range use for samango monkeys, while fear of  
391 leopards and baboons was the key driver for the sympatric vervet monkeys ([Willems & Hill 2009](#)).  
392 Although further work is needed to assess the importance of leopards and snakes to samangos, the  
393 current findings highlight the importance of distinguishing between the risk effects of different  
394 predators in understanding prey ecology ([Cresswell & Quinn 2013](#); [Morosinotto, Thomson &](#)

395 [Korpimaki 2010](#); [Preisser et al. 2007](#)), since differences in the anti-predatory responses of species  
396 may only be apparent when risk is assessed on a predator-specific basis.

397

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

409

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



421 determine the importance of terrestrial predators in shaping the range use of these arboreal  
422 primates.

423

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

436

437 Finally, we found no effect of intergroup encounters on samango monkey space use; however, our  
438 use of annual landscapes may disguise seasonal effects (see [Markham et al. \(2013\)](#)). [Lawes and](#)  
439 [Henzi \(1995\)](#) reported that 48% of inter-group encounters in samango monkeys were food related,  
440 with territory defence and mate defence potential explanations for the remaining encounters. The  
441 relative importance of these factors is likely to vary significantly on an annual basis, leading to  
442 differing selection pressures relating to space use. In baboons, broad temporal changes in ecological  
443 resources were the major predictor of how intensively group ranges overlapped, but spacing  
444 increased significantly in weeks where social groups had high proportions of fertile females  
445 ([Markham et al. 2013](#)). Distinguishing between mating and non-mating seasons is thus a key future

446 direction, although simultaneous monitoring of the ranging behaviour of the neighbouring groups  
447 will also help to separate the independent effects of conspecific groups on range use.

448

449 Studies of the effects of predators on the behaviour and abundance of their prey have traditionally  
450 assumed that all predators have the same selective effects ([Lima 2002](#)) but the inaccuracy of this  
451 assumption is increasingly recognized ([Cresswell & Quinn 2013](#); [Preisser et al. 2007](#); [Schmitz 2008](#)).

452 The results presented here suggest that similar prey species inhabiting the same environment do not  
453 experience the same selective effects from the different predator guilds, despite being exposed to  
454 the same predator community. The challenge for future work, therefore, is to determine how  
455 predator diversity and hunting mode coupled with variation in prey responses shapes the dynamics  
456 of prey communities ([Preisser et al. 2007](#)).

457

458

#### 459 **ACKNOWLEDGEMENTS**

460

461 We thank Ian Gaigher for permission to work at the Lajuma Research Centre and for his help and  
462 support on site, and to the field assistants who contributed to data collection. Permission to  
463 conduct research in South Africa was provided by the Limpopo Province Department of Economic  
464 Development and Tourism, with the research receiving ethical approval from the Durham  
465 University's Life Sciences Ethical Review Process Committee. We thank two anonymous reviewers  
466 for their valuable comments on an earlier version of this manuscript.

467

468

#### 469 **REFERENCES**

470 **Abrams, P. A.** 2000. The evolution of predator-prey interactions: Theory and evidence. *Annual*  
471 *Review of Ecology and Systematics*, **31**, 79-105.

472 **Beeson, M., Tame, S., Keeming, E. & Lea, S. E. G.** 1996. Food habits of guenons (*Cercopithecus* spp.)  
473 in Afro-montane forest. *African Journal of Ecology*, **34**, 202-210.

474 **Beyer, H. L.** 2004. Hawth's Analysis Tools for ArcGIS (Version 9), available at  
475 [www.spatial ecology.com/htools](http://www.spatial ecology.com/htools).

476 **Beyer, H. L.** 2011. Geospatial Modelling Environment (Version 0.55 Beta), available at  
477 [www.spatial ecology.com/gme](http://www.spatial ecology.com/gme)

478 **Borger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T.**  
479 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of*  
480 *Animal Ecology*, **75**, 1393-1405.

481 **Brock, A. P., Nortje, E. & Gaigher, I.** 2003. Habitat preference of a local population of bushbuck in  
482 the Soutpansberg Mountains, South Africa. *South African Journal of Wildlife Research*, **33**, 131-135.

483 **Brown, C. H.** 1989. The active space of blue monkey and grey-cheeked mangabey vocalizations.  
484 *Animal Behaviour*, **37**, 1023-1034.

485 **Brown, J. S.** 1988. Patch use as an indicator of habitat preference, predation risk and competition.  
486 *Behavioral Ecology and Sociobiology*, **22**, 37-47.

487 **Brown, J. S. & Kotler, B. P.** 2004. Hazardous duty pay and the foraging cost of predation. *Ecology*  
488 *Letters*, **7**, 999-1014.

489 **Brown, J. S., Laundre, J. W. & Gurung, M.** 1999. The ecology of fear: Optimal foraging, game theory,  
490 and trophic interactions. *Journal of Mammalogy*, **80**, 385-399.

491 **Butynski, T. M.** 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high-density  
492 and low-density subpopulations. *Ecological Monographs*, **60**, 1-26.

493 **Caro, T. M.** 2005. *Antipredator defenses in birds and mammals*. Chicago: University of Chicago Press.

494 **Chapman, C.** 1985. The influence of habitat on behaviour in a group of St-Kitts Green Monkeys.  
495 *Journal of Zoology*, **206**, 311-320.

496 **Chase-Grey, J. N.** 2011. Leopard population dynamics, trophy hunting and conservation in the  
497 Soutpansberg Mountains, South Africa, Durham University.

498 **Chase Grey, J. N., Kent, V. T. & Hill, R. A.** in press. Evidence of a high density population of harvested  
499 leopards in a montane environment *Plos One*.

500 **Coates-Palgrave, K.** 1996. *Trees of Southern Africa (Second Revised Edition)*. Cape Town: Struik  
501 Publishers (Pty) Ltd.

502 **Coleman, B. T.** 2013. Spatial and temporal determinants of samango monkey (*Cercopithecus mitis*  
503 *erythrarchus*) resource acquisition and predation avoidance behaviour. PhD Thesis, Durham  
504 University.

505 **Cords, M.** 1987. Mixed species association of *Cercopithecus* monkeys in the Kakamega Forest, Kenya.  
506 *University of California Publications in Zoology*, **117**, 1-109.

507 **Cowlshaw, G.** 1994. Vulnerability to Predation in Baboon Populations. *Behaviour*, **131**, 293-304.

508 **Cowlshaw, G.** 1997. Trade-offs between foraging and predation risk determine habitat use in a  
509 desert baboon population. *Animal Behaviour*, **53**, 667-686.

510 **Creel, S. & Christianson, D.** 2008. Relationships between direct predation and risk effects. *Trends in*  
511 *Ecology & Evolution*, **23**, 194-201.

512 **Creel, S., Christianson, D., Liley, S. & Winnie, J. A., Jr.** 2007. Predation risk affects reproductive  
513 physiology and demography of elk. *Science*, **315**, 960-960.

514 **Creel, S., Winnie, J. A., Jr., Christianson, D. & Liley, S.** 2008. Time and space in general models of  
515 antipredator response: tests with wolves and elk. *Animal Behaviour*, **76**, 1139-1146.

516 **Cressie, N.** 1990. The origins of kriging. *Mathematical Geology*, **22**, 239-252.

517 **Cresswell, W. & Quinn, J. L.** 2013. Contrasting risks from different predators change the overall  
518 nonlethal effects of predation risk. *Behavioral Ecology*, **24**, 871-876.

519 **Dawkins, R. & Krebs, J. R.** 1979. Arms races between and within species. *Proceedings of the Royal*  
520 *Society Series B-Biological Sciences*, **205**, 489-511.

521 **du Bothma, J. & Le Riche, E. A. N.** 1986. Prey preference and hunting efficiency of the Kalahari  
522 leopard. In: *Cats of the world: biology, conservation and management*. (Ed. by S. D. Miller & D. D.  
523 Everett), pp. 389-414. Washington DC: National Wildlife Federation.

524 **Emerson, S. E., Brown, J. S. & Linden, J. D.** 2011. Identifying Sykes' monkeys', *Cercopithecus*  
525 *albobularis erythrarchus*, axes of fear through patch use. *Animal Behaviour*, **81**, 455-462.

526 **Enstam, K. & Isbell, L.** 2002. Changes in visibility affect ranging behavior and vigilance in vervet  
527 monkeys (*Cercopithecus aethiops*). *American Journal of Physical Anthropology*, 67-67.

528 **Fife-Schaw, C., Hammond, S. & Breakwell, G. M.** 2006. *Research methods in psychology (3rd*  
529 *edition)*. London: SAGE.

530 **Fortin, D. & Fortin, M.-E.** 2009. Group-size-dependent association between food profitability,  
531 predation risk and distribution of free-ranging bison. *Animal Behaviour*, **78**, 887-892.

532 **Garrett, M. G., Watson, J. W. & Anthony, R. G.** 1993. Bald eagle home range and habitat use in the  
533 Columbia River estuary. *Journal of Wildlife Management*, **57**, 19-27.

534 **Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J. & Wilmers, C. C.** 2007. LoCoH:  
535 Nonparametric kernel methods for constructing home ranges and utilization distributions. *Plos*  
536 *One*, **2**.

537 **Getz, W. M. & Wilmers, C. C.** 2004. A local nearest-neighbor convex-hull construction of home  
538 ranges and utilization distributions. *Ecography*, **27**, 489-505.

539 **Gibson, L. & Koenig, A.** 2012. Neighboring groups and habitat edges modulate range use in Phayre's  
540 leaf monkeys (*Trachypithecus phayrei crepusculus*). *Behavioral Ecology and Sociobiology*, **66**, 633-  
541 643.

542 **Gitzen, R. A., Millspaugh, J. J. & Kernohan, B. J.** 2006. Bandwidth selection for fixed-kernel analysis  
543 of animal utilization distributions. *Journal of Wildlife Management*, **70**, 1334-1344.

544 **Hart, J. A., Katembo, M. & Punga, K.** 1996. Diet, prey selection and ecological relations of leopard  
545 and golden cat in the Ituri Forest, Zaire. *African Journal of Ecology*, **34**, 364-379.

546 **Harvey, P. H., Martin, R. D. & Clutton-Brock, T. H.** 1987. Life histories in comparative perspective.  
547 In: *Primate societies* (Ed. by B. B. Smuts), pp. 181-196. Chicago: Univ. of Chicago P.

548 **Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R. & Macdonald, D.** 2005. Are kernels the  
549 mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-  
550 range analyses with least-squares cross-validation. *Journal of Animal Ecology*, **74**, 455-463.

551 **Henzi, S. P. & Lawes, M.** 1987. Breeding-season influxes and the behavior of adult male samango  
552 monkeys (*Cercopithecus mitis albobularis*). *Folia Primatologica*, **48**, 125-136.

553 **Hill, R. A. & Dunbar, R. I. M.** 1998. An evaluation of the roles of predation rate and predation risk as  
554 selective pressures on primate grouping behaviour. *Behaviour*, **135**, 411-430.

555 **Hill, R. A. & Weingrill, T.** 2007. Predation risk and habitat use in chacma baboons (*Papio hamadryas*  
556 *ursinus*). In: *Primate anti-predator strategies* (Ed. by S. Gursky & K. A. I. Nekaris), pp. 339-354. New  
557 York: Springer.

558 **Houle, A., Chapman, C. A. & Vickery, W. L.** 2010. Intra-tree vertical variation of fruit density and the  
559 nature of contest competition in frugivores. *Behavioral Ecology and Sociobiology*, **64**, 429-441.

560 **Jaffe, K. E. & Isbell, L. A.** 2009. After the fire: Benefits of reduced ground cover for vervet monkeys  
561 (*Cercopithecus aethiops*). *American Journal of Primatology*, **71**, 252-260.

562 **Laundré, J. W., Hernandez, L. & Altendorf, K. B.** 2001. Wolves, elk, and bison: reestablishing the  
563 "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology-Revue*  
564 *Canadienne De Zoologie*, **79**, 1401-1409.

565 **Lawes, M. J.** 1991. Diet of samango monkeys (*Cercopithecus mitis erythrarchus*) in the Cape Vidal  
566 Dune Forest, South-Africa. *Journal of Zoology*, **224**, 149-173.

567 **Lawes, M. J., Cords, M. & Lehn, C.** 2013. *Cercopithecus mitis* profile. In: *Primates of Africa volume II,*  
568 *The mammals of Africa* (Ed. by J. Kingdon & J. Kalina), pp. 354-362. Berkeley: University of California  
569 Press.

570 **Lawes, M. J. & Henzi, S. P.** 1995. Intergroup encounters in blue monkeys: How territorial must a  
571 territorial species be. *Animal Behaviour*, **49**, 240-243.

572 **Lawes, M. J., Henzi, S. P. & Perrin, M. R.** 1990. Diet and feeding-behavior of samango monkeys  
573 (*Cercopithecus mitis labiatus*) in Ngoye Forest, South-Africa. *Folia Primatologica*, **54**, 57-69.

574 **Lichti, N. I. & Swihart, R. K.** 2011. Estimating utilization distributions with kernel versus local convex  
575 hull methods. *Journal of Wildlife Management*, **75**, 413-422.

576 **Lima, S. L.** 1998. Nonlethal effects in the ecology of predator-prey interactions - What are the  
577 ecological effects of anti-predator decision-making? *BioScience*, **48**, 25-34.

578 **Lima, S. L.** 2002. Putting predators back into behavioral predator-prey interactions. *Trends in Ecology*  
579 *& Evolution*, **17**, 70-75.

580 **Markham, A. C., Guttal, V., Alberts, S. C. & Altmann, J.** 2013. When good neighbors don't need  
581 fences: temporal landscape partitioning among baboon social groups. *Behavioral Ecology and*  
582 *Sociobiology*, **67**, 875-884.

583 **Marler, P.** 1973. A comparison of vocalizations of red-tailed monkeys and blue monkeys,  
584 *Cercopithecus ascanius* and *C. mitis*, in Uganda. *Zeitschrift Fur Tierpsychologie-Journal of*  
585 *Comparative Ethology*, **33**, 223-247.

586 **McGraw, W. S.** 2002. Diversity of guenon positional behavior. In: *The guenons: Diversity and*  
587 *adaptation in African monkeys* (Ed. by M. A. Glenn & M. Cords). Kluwer Academic, New York, pp113-  
588 132.

589 **Minderman, J., Lind, J. & Cresswell, W.** 2006. Behaviourally mediated indirect effects: interference  
590 competition increases predation mortality in foraging redshanks. *Journal of Animal Ecology*, **75**, 713-  
591 723.

592 **Morosinotto, C., Thomson, R. L. & Korpimäki, E.** 2010. Habitat selection as an antipredator  
593 behaviour in a multi-predator landscape: all enemies are not equal. *Journal of Animal Ecology*, **79**,  
594 327-333.

595 **Mucina, L. & Rutherford, M. C.** 2006. *The Vegetation of South Africa, Lesotho and Swaziland*. South  
596 African National Biodiversity Institute, Pretoria.

597 **Papworth, S., Bose, A. S., Barker, J., Schel, A. M. & Zuberbühler, K.** 2008. Male blue monkeys alarm  
598 call in response to danger experienced by others. *Biology Letters*, **4**, 472-475.

599 **Peckarsky, B. L. & McIntosh, A. R.** 1998. Fitness and community consequences of avoiding multiple  
600 predators. *Oecologia*, **113**, 565-576.

601 **Preisser, E. L., Orrock, J. L. & Schmitz, O. J.** 2007. Predator hunting mode and habitat domain alter  
602 nonconsumptive effects in predator-prey interactions. *Ecology*, **88**, 2744-2751.

603 **Quinn, J. L. & Cresswell, W.** 2004. Predator hunting behaviour and prey vulnerability. *Journal of*  
604 *Animal Ecology*, **73**, 143-154.

605 **Rangel, T. F. L. V. B., Diniz-Filho, J. A. F. & Bini, L. M.** 2010. SAM: a comprehensive application for  
606 Spatial Analysis in Macroecology. *Ecography*, **33**.

607 **Richards, S. A.** 2008. Dealing with overdispersed count data in applied ecology. *Journal of Applied*  
608 *Ecology*, **45**, 218-227.

609 **Rudran, R.** 1978. Socioecology of the blue monkeys of the Kibale Forest, Uganda. *Smithsonian*  
610 *Contributions to Zoology*, **249**, 1-88.

611 **Ryan, S. J., Knechtel, C. U. & Getz, W. M.** 2006. Range and habitat selection of African buffalo in  
612 South Africa. *Journal of Wildlife Management*, **70**, 764-776.

613 **Salih, I. M., Petterson, H. B. L., Sivertun, A. & Lund, E.** 2002. Spatial correlation between radon in  
614 groundwater and bedrock uranium: GIS and geostatistical analyses. *Journal of Spatial Hydrology*, **2**, 1-  
615 10.

616 **Schmitz, O. J.** 2008. Effects of predator hunting mode on grassland ecosystem function. *Science*, **319**,  
617 952-954.

618 **Searle, K. R., Stokes, C. J. & Gordon, I. J.** 2008. When foraging and fear meet: using foraging  
619 hierarchies to inform assessments of landscapes of fear. *Behavioral Ecology*, **19**, 475-482.

620 **Shultz, S.** 2001. Notes on interactions between monkeys and African crowned eagles in Tai National  
621 Park, Ivory Coast. *Folia Primatologica*, **72**, 248-250.

622 **Shultz, S., Noe, R., McGraw, W. S. & Dunbar, R. I. M.** 2004. A community-level evaluation of the  
623 impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings*  
624 *of the Royal Society of London Series B-Biological Sciences*, **271**, 725-732.

625 **Silverman, B. W.** 1986. *Density Estimation for Statistics and Data Analysis*. London: Chapman and  
626 Hall.

627 **Smith, L. W., Link, A. & Cords, M.** 2008. Cheek pouch use, predation risk, and feeding competition in  
628 blue monkeys (*Cercopithecus mitis stuhlmanni*). *American Journal of Physical Anthropology*, **137**,  
629 334-341.

630 **Southwood, T. R. E. & Henderson, P. A.** 2000. *Ecological Methods*, 3rd edn. Oxford: Blackwell Science.

631 **Steury, T. D., McCarthy, J. E., Roth, T. C., Lima, S. L. & Murray, D. L.** 2010. Evaluation of Root-n  
632 Bandwidth Selectors for Kernel Density Estimation. *Journal of Wildlife Management*, **74**, 539-548.

633 **Team, R. D. C.** 2011. R: A language and environment for statistical computing. Vienna, Austria.: R  
634 Foundation for Statistical Computing.

635 **Thomas, S. C.** 1991. Population densities and patterns of habitat use among anthropoid primates of  
636 the Ituri Forest, Zaire. *Biotropica*, **23**, 68-83.

637 **Valdez, U. & Osborn, S.** 2004. Observations on the ecology of the black-and-chestnut eagle  
638 (*Oroaetus isidori*) in a montane forest of southeastern Peru. *Ornitologia Neotropical*, **15**, 31-40.

639 **Werner, E. E. & Peacor, S. D.** 2006. Lethal and nonlethal predator effects on an herbivore guild  
640 mediated by system productivity. *Ecology*, **87**, 347-361.

641 **Willems, E. P.** 2007. From space to species. PhD Thesis, University of Durham.

642 **Willems, E. P., Barton, R. A. & Hill, R. A.** 2009. Remotely sensed productivity, regional home range  
643 selection, and local range use by an omnivorous primate. *Behavioral Ecology*, **20**, 985-992.

644 **Willems, E. P. & Hill, R. A.** 2009. Predator-specific landscapes of fear and resource distribution:  
645 Effects on spatial range use. *Ecology*, **90**, 546-555.

646

647

648 **LIST OF FIGURES**

649

650 **Figure 1:** Spatial distribution of (a) habitat types with colours denoting food availability (CM - Closed  
651 Mountain; CR - Closed Rocky; OM - Open Mountain; OR - Open Rocky; RF - Riverine Forest SF - Short  
652 Forest; TF - Tall Forest; W - Wetland), (b) fruit availability, (c) canopy height, (d) understory visibility,  
653 (e) Euclidean distance to sleeping sites, (f) Euclidean distance to water sources, (g) landscape of fear  
654 from eagles, and (h) landscape of inter-group encounter risk in the samango monkey home range.

655

656 **Figure 2:** Home range and utilisation distribution of the study group (54.7ha) constructed using  
657 Adaptive LoCoH analysis. The black outline indicates the edges of the home range with dark blue  
658 indicating areas of high utilisation.

659

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

662

663 **Figure A1:** Residual distributions from the spatial regressive-mixed regressive models. Model A:  
664 skewness = 0.018; kurtosis = 0.274. Model B skewness = -0.103; kurtosis = -0.211. Any score  $\pm 1$  is  
665 considered strongly non-normally distributed ([Fife-Schaw, Hammond & Breakwell 2006](#)).

666

667 **TABLE 1** Mean fruit volume per 25m<sup>2</sup>, canopy height and understory visibility in the eight habitat  
668 types in the samango monkey home range.

<b>Habitat</b>	<b>Mean Fruit Volume (cm<sup>3</sup>)</b>	<b>Mean Canopy Height (m)</b>	<b>Mean Visibility (%)</b>
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

669

670



671 **TABLE 2** Parameter estimates and key statistics of Model A, expressing utilisation distribution as a  
 672 function of perceived eagle predation risk, habitat type and distance to sleeping sites.

673

Predictor	$\beta$	B	SE B	SE $\gamma$	t	P
<i>Landscape of fear</i>						
Eagle	-0.329	-0.338	0.028	0.192	-11.583	<0.001
<i>Habitat types</i>						
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	-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
<i>Environmental factors</i>						
Sleeping sites	-0.353	-0.154	0.063	0.006	-5.582	<0.001

674

675 Habitat types are presented in descending order of fruit availability. Model statistics:  $N=1000$ ;

676  $R^2=0.312$ ;  $\rho=0.992\pm 0.172$ ;  $\gamma = 0.992$ ;  $AIC_c=8046.844$ . Terms:  $\rho$ , spatial autoregressive parameter;  $\gamma$ ,

677 spatial cross-regressive parameter;  $\beta$ , unstandardised regression parameter; B, standardised

678 regression parameter.

679

680 **TABLE 3** Parameter estimates and key statistics of Model B, expressing utilisation distribution as a  
 681 function of predator perceived eagle predation risk, understory visibility, height of trees and sleeping  
 682 site location.

683

Predictor	$\beta$	B	SE B	SE $\gamma$	t	p
<i>Landscapes of fear</i>						
Eagle	-0.271	-.278	0.029	0.192	-9.322	<0.001
<i>Environmental factors</i>						
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

684

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

686

687 **Table A1:** Parameter estimates and key statistics of full Model A, a mixed regressive-spatial  
 688 regressive model expressing utilisation distribution as a function of perceived eagle predation risk,  
 689 habitat type and distance to sleeping sites and water.

690

Predictor	<i>B</i>	$\beta$	SE $\beta$	SE $\gamma$	<i>t</i>	P
<i>Landscape of fear</i>						
Eagle	-0.329	-0.338	0.028	0.192	-11.568	<0.001
<i>Habitat types</i>						
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	-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
<i>Environmental factors</i>						
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

691

692 Habitat types are presented in descending order of fruit availability. Model statistics:  $N=1000$ ;  
 693  $R^2=0.312$ ;  $\rho=0.992\pm 0.172$ ;  $\gamma = 0.992$ ;  $AIC_c=8051.019$ . Terms:  $\rho$ , spatial autoregressive parameter,  $\gamma$ ,  
 694 spatial cross-regressive parameter; *B*, unstandardised regression parameter;  $\beta$ , standardised  
 695 regression parameter.

696

697 **Table A2:** Parameter estimates and key statistics of the full Model B, a mixed regressive-spatial  
 698 regressive model expressing utilisation distribution as a function of perceived eagle predation risk,  
 699 inter-group encounter risk and other environmental factors.

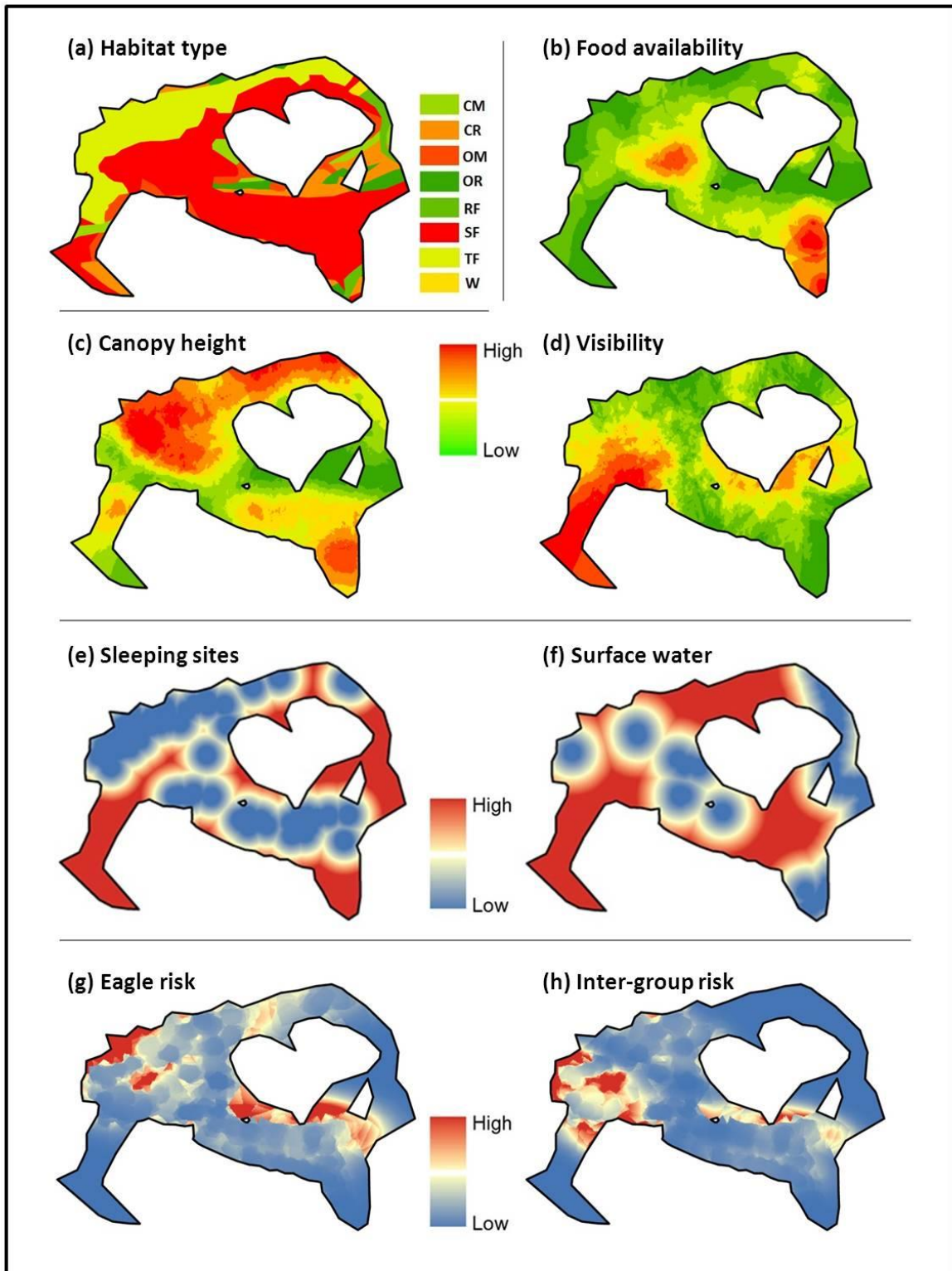
700

Predictor	<i>B</i>	$\beta$	SE $\beta$	SE $\gamma$	<i>t</i>	P
<i>Landscapes of fear</i>						
Eagle	-0.272	-0.279	0.033	0.192	-8.309	<0.001
Inter-group	-0.018	-0.023	0.028	0.447	-0.656	0.512
<i>Environmental factors</i>						
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

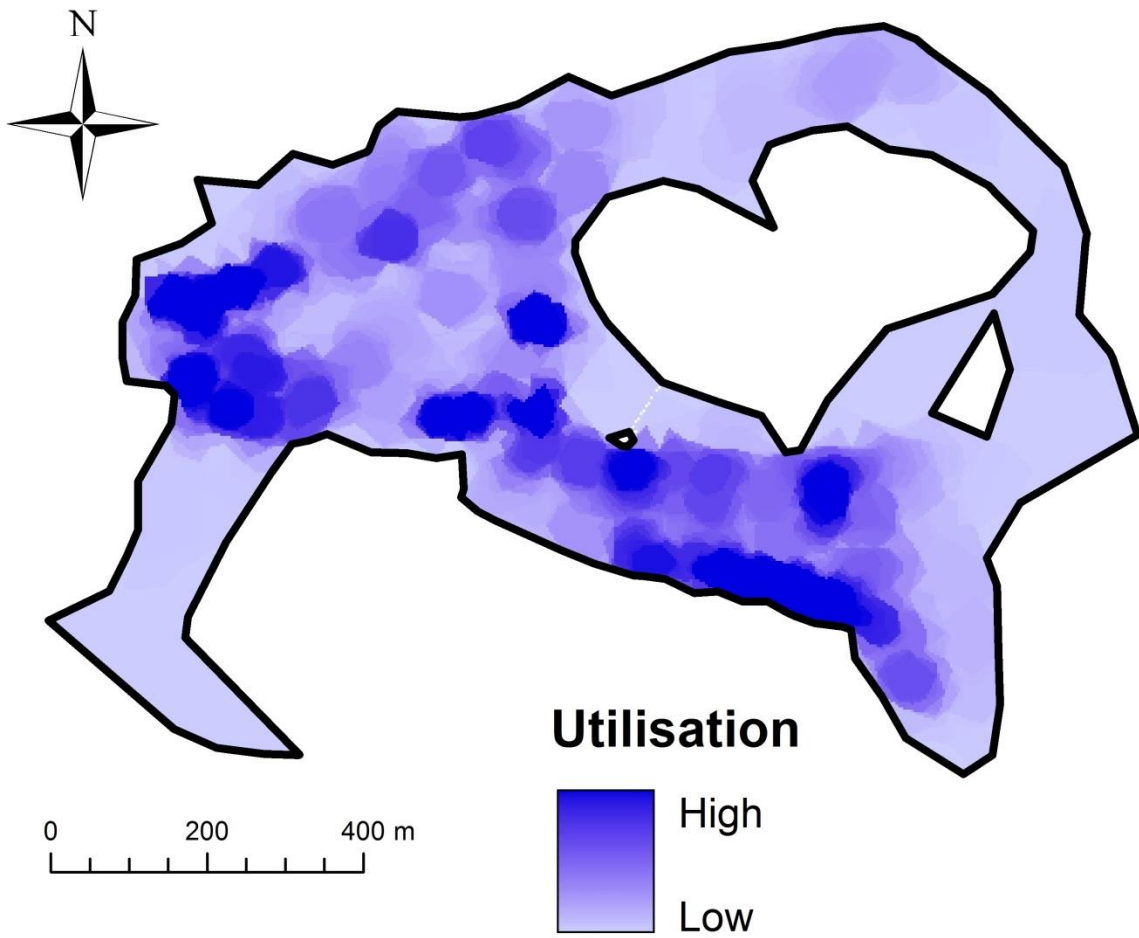
701

702 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.

703

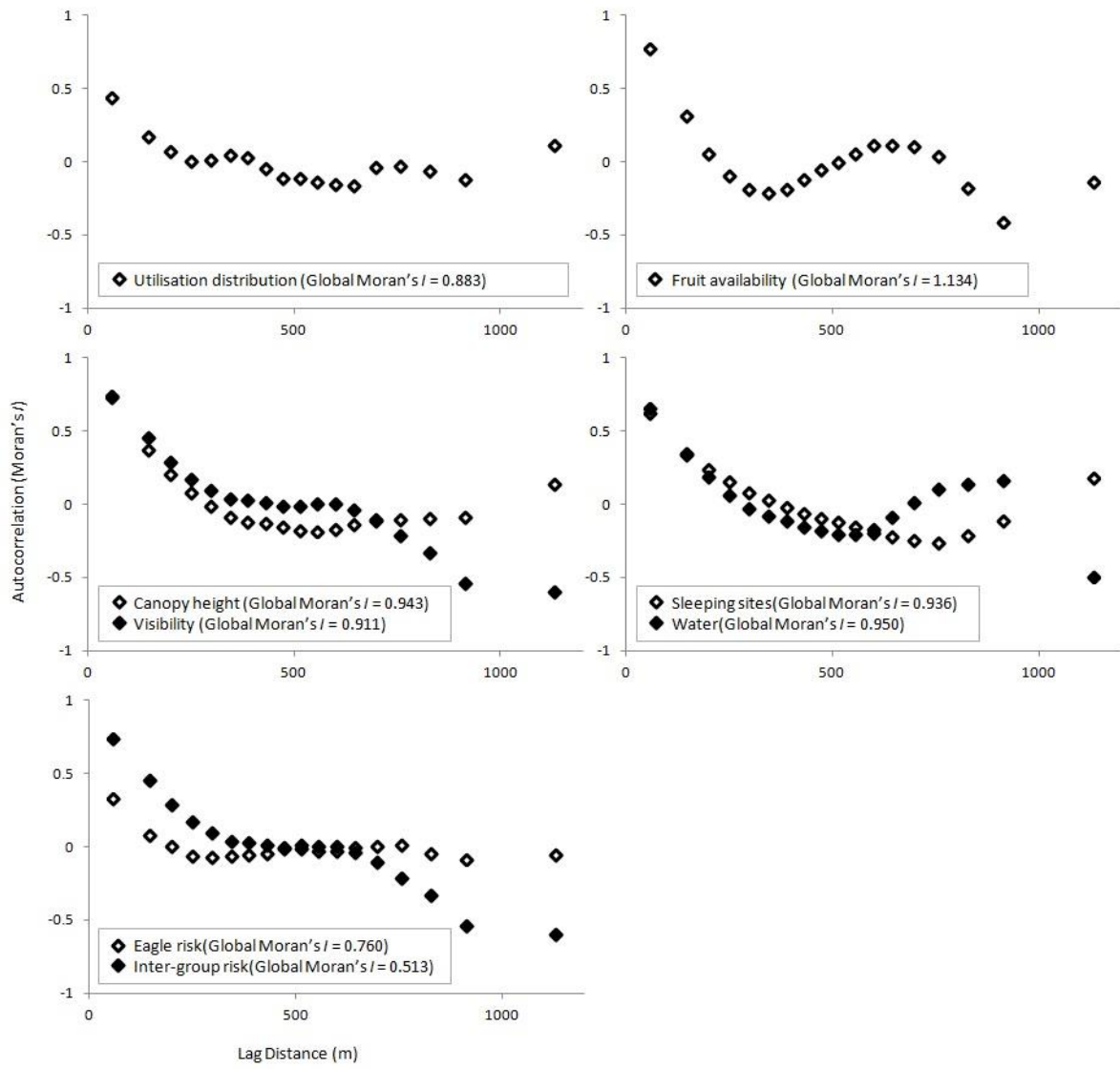


707 **FIGURE 2**



708

709



711

712

