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2 Vincenzo Penteriani

3 Spanish Council of Scientific Research (CSIC) – Pyrenean Institute of Ecology

4 penteriani@ipe.csic.es

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6 **Running Head:** Habitat use of females with cubs

7 **Female brown bears use areas with infanticide risk in a spatially confined**
8 **population**

9 Vincenzo Penteriani^{1,2†*}, Alejandra Zarzo-Arias^{2†}, María del Mar Delgado², Fredrick

10 Dalerum^{2,3,4}, Eliezer Gurarie⁵, Paloma Peón Torre⁶, Teresa Sánchez Corominas⁶, Víctor M.

11 Vázquez^{6,7}, Pablo Vázquez García⁸, Andrés Ordiz⁹

12 ¹ *Pyrenean Institute of Ecology (IPE), CSIC, Avda. Montañana 1005, 50059 Zaragoza,*
13 *Spain*

14 ² *Research Unit of Biodiversity (UMIB, UO-CSIC-PA), Oviedo University - Campus Mieres,*
15 *Mieres, Spain*

16 ³ *Department of Zoology, Stockholm University, Stockholm, Sweden*

17 ⁴ *Mammal Research Institute (MRI), Department of Zoology and Entomology, University*
18 *of Pretoria, Hatfield, South Africa*

19 ⁵ *Department of Biology, University of Maryland, College Park, MD, United States of*
20 *America*

21 ⁶ *Consejería de Desarrollo Rural y Recursos Naturales, Principado de Asturias, Oviedo,*
22 *Spain;*

23 ⁷ *Real Instituto de Estudios Asturianos (RIDEA), Oviedo, Spain*

24 ⁸ *Instituto Cavanilles de Biodiversidad y Biología Evolutiva, Universidad de Valencia,*
25 *Spain*

26 ⁹ *Faculty of Environmental Sciences and Natural Resource Management, Norwegian*
27 *University of Life Sciences, Ås, Norway*

28 *email: penteriani@ipe.csic.es

29 [†]These authors contributed equally to this work

Abstract: Areas used by female brown bears (*Ursus arctos*) with cubs-of-the-year (hereafter, FCOY) during the first months after den exit are crucial for offspring survival, primarily because of the risk of infanticide by male bears. Therefore, FCOY may allow them to avoid areas frequented by adult males during the mating season. The main aim of this study was to identify landscape features (i.e., structure, composition, and human footprint) that may differentiate the habitat use of FCOY in the small bear population of the Cantabrian Mountains (northwestern Spain) from: (a) areas frequented by females with yearlings, because older cubs are at less risk of infanticide than cubs of the year and, (b) bear mating areas, i.e., the riskiest areas for FCOY, because of the presence of adult males. During the first months after den emergence (April-June), FCOY settled in the roughest areas of the Cantabrian Mountains at most spatial scales. This settlement pattern might represent a behavioral adaptation of FCOY to reduce the risk of encounters with males during the mating season. However, FCOY also settled in similar landscapes to those used by adult bears during the mating season, which may increase the likelihood of risky encounters. Indeed, we observed a spatial overlap between observed locations of FCOY and mating areas, which may help explain the high frequency of infanticide observed in the Cantabrian Mountains. We hypothesize that the need for both shelter and food in early spring may ‘trap’ FCOY in otherwise favorable areas that overlap with mating areas. This may occur predominately in small and confined bear populations, such as the one in the Cantabrian Mountains, where a restricted range and limited habitat availability might prevent FCOY from avoiding risky areas successfully.

Key words females with cubs; human-modified landscapes; infanticide; mating areas; *Ursus arctos*

Ursus (): – ()

Life-history theory predicts that animals display optimal levels of parental investment, with energy expenditure for offspring traded off with the effects on the probability of survival and future reproduction of the parents (Roff 1992). In addition to the expenditure of nutrients associated with female brown bears (*Ursus arctos*) raising cubs for at least 1.5 years (males provide no parental care and thus offspring depend completely on their mothers; Dahle and Swenson, 2003; Palombit, 2015), the mothers

have to take into account the risk of infanticide by adult males, because this is a major cause of death of cubs during their first months of life in some bear populations (Steyaert et al. 2012). Sexually selected infanticide is a reproductive strategy of males that can increase their fitness by killing unrelated offspring so as to bring a female into reproductive condition and, thus, increase the chance of reproducing with her (Hrdy 1979). This form of infanticide occurs in seasonal breeders during the mating season (van Schaik and Janson 2000). Because infanticide is costly for victimized females, several counterstrategies have evolved against it (reviewed by Steyaert et al., 2016). Among them, spatial avoidance of potentially infanticidal males is similar to predation avoidance (Agrell et al. 1998), i.e., individuals selectively use space to minimize risky encounters. Following the body of theory on predator-prey interactions and ecology of fear (Brown et al. 1999), spatial segregation from risky encounters can be attained in two main ways: (1) habitat-mediated avoidance (Fedriani et al. 2000, Sergio et al. 2007), i.e., females with offspring avoid habitats associated with a high risk of male encounters, such as those preferred by males during the mating season; and (2) distance-sensitive avoidance (Palomares et al. 1996, Durant 1998). That is, regardless of habitat types, females with offspring select sites as far away as possible from adult males, exploiting discontinuities in their distribution.

Infanticide is common in some brown bear populations, e.g., in Scandinavia (Bellemain et al. 2006, Steyaert et al. 2012) and Spain (Palomero et al., 2011, Fernández-Gil, 2013, and authors' unpublished data). Females with cubs-of-the-year (hereafter FCOY) may alter their habitat selection and avoid areas frequented by adult males during the mating season to reduce the risk of infanticide (Wielgus and Bunnell 1995, Mcloughlin et al. 2002, Rode et al. 2006). For example, individuals may select

landscapes that offer shelter, possibilities of escape, and/or minimize the likelihood of risky encounters, following the patterns described in predator-prey theory (Lima and Dill 1990). Thus, habitat selection of mother bears can be an important component of offspring survival (Steyaert et al. 2016). Indeed, after den emergence, FCOY tend to adopt a secretive and sedentary lifestyle, presumably to minimize the risk of infanticide (Dahle and Swenson 2003b, Martin et al. 2013, Steyaert et al. 2013).

The main aim of this study was to describe habitat use of FCOY in the areas used by FCOY during the first months after den exit in early spring, and at different spatial scales. Our multi-scale approach compares the landscape structure and composition, as well as the presence of human infrastructure, at areas used in early spring by FCOY with: (a) areas frequented by females with yearlings (hereafter FYRL); and (b) bear mating areas, defined as areas where bears were seen copulating or at least one male and one female without cubs were observed together during the primary mating period, which is April-June in the Cantabrian Mountains (Ordiz et al. 2007, Martínez Cano et al. 2016). We expected that FCOY use areas characterized by landscape components that differ from the other 'classes' of bears, mainly as a strategy to avoid infanticide, because: (1) older cubs of FYRL are at less risk of infanticide than cubs of the year (e.g., Swenson et al., 2001); and, (2) mating areas represent the riskiest areas for FCOY, because of the presence of adult males.

Methods

Study area

We recorded bear observations in Asturias, the region inhabited by most of the Cantabrian brown bear population. The Cantabrian Mountains are one of the main mountain range systems in Spain, stretching over 300 km across the northern part of the country, running east-west parallel to the Atlantic Coast. The maximum elevation is 2648 m a.s.l. and the average elevation is around 1100 m (Naves et al. 2003, Martínez Cano et al. 2016). The oceanic climate is mild and humid throughout the year (range: 900-1900 mm; Martínez Cano et al., 2016), favoring oaks (*Quercus petraea*, *Q. pyrenaica* and *Q. rotundifolia*), beech (*Fagus sylvatica*), and chestnut (*Castanea sativa*) on north-facing slopes, whereas drier, south-facing slopes are mainly dominated by oaks (*Q. petraea* and *Q. pyrenaica*) and beech. Subalpine matorral (*Juniperus communis*, *Vaccinium uliginosum*, *V. myrtillus* and *Arctostaphylos uva-ursi*) dominates mountain areas above the treeline (~1700 m) (Martínez Cano et al., 2016). In some areas, former forests have been converted into pasture and brushwood (*Genista*, *Cytisus*, *Erica* and *Calluna*) through human activities (Naves et al. 2003, 2006). The main economic activity in brown bear range is livestock farming, followed by mining, tourism, agriculture, and timber harvesting. The human population density is <15 habitants/km² (http://ec.europa.eu/eurostat/statistics-explained/index.php/Population_grids), but areas surrounding the core bear range have experienced extensive urban and agriculture development, connected by a network of transport infrastructure (Mateo-Sánchez et al., 2016).

Data collection

The locations of FCOY, FYRL, and mating areas (Figure 1) were obtained from: (1) systematic bear observations performed by personnel of (a) the Bear Team (Patrulla Oso) of the Principado de Asturias, (b) the Asturian Foundation for the Conservation of Wildlife (FAPAS, Fondo para la Protección de los Animales Salvajes); (c) the Brown Bear Foundation (FOP, Fundación Oso Pardo); and (d) the Asturian Bear Foundation (FOA, Fundación Oso de Asturias), as well as by the authors. Direct observations were performed almost daily from den exit to the end of the mating period (June), generally from sunrise to sunset; and (2) camera traps that were placed randomly by the FAPAS and Bear Team during the last twenty years, mainly in forested areas where bears are less visible (FAPAS/FIEP 2017). The presence of the above-mentioned systematic and random observations, which have previously been applied successfully to the study of this bear population (Palomero et al. 2007, Gonzalez et al. 2016), indicate that most of the area potentially favorable to bears has been covered intensively every year (Figure 2). The locations of FCOY, FYRL, and mating areas occupied ca. 1500 km², i.e., ca. 23% of the total bear range (ca. 6520 km²) in the Asturian Cantabrian Mountains.

In April-June and from 2001 to 2016, we collected 397 locations of FCOY (assigned to 84 families), 163 locations of FYRL (assigned to 48 families), and 44 locations of bears at mating areas. The different bear families were identified on the basis of : (a) color patterns of mothers, (b) number and characteristics of cubs, and by (c) distance between observations of family groups (Ordiz et al. 2007, Penteriani et al. 2018b). This information also allowed differentiating between families observed the same day in neighboring areas. We made all observations during daytime and from distances that varied from several hundred meters to 1-1.5 km (Zarzo-Arias et al. 2018).

Camera traps allowed additional information on FCOY locations, especially when they were not in open habitats.

Landscape characterization

We used a multi-scale approach of the habitat use of FCOY, considering four spatial scales, i.e., circular plots with radii of 500, 1000, 2000, and 3000 m, around each bear location. Such plots covered most of the FCOY range of movements in our study area during the first months of the year, from the abandonment of the den where they gave birth until the end of the spring-early summer (authors' unpublished data pers. obs. and Gardner et al. 2014; Ordiz et al., 2007). FCOY also have small home ranges in spring in other brown bear populations, e.g., in Scandinavia (Dahle & Swenson, 2003b; Steyaert, Swenson & Zedrosser, 2014) and in North America (Miller et al. 1997; Gardner et al. 2014; Steyaert et al. 2014), which supports our reasoning for the establishment of small spatial scales in this study.

Our multi-scale approach is also based on Johnson's (1980) conceptual framework, which assumes that animals make decisions regarding basic resources (e.g. breeding sites, cover and food) at progressively smaller scales in a hierarchical manner. The identification of the scales at which particular environmental variables influence habitat selection is crucial for understanding habitat suitability patterns as perceived by animals in complex landscapes. Indeed, what may appear important at one scale may have little relevance at another, making results scale sensitive (Ciarniello et al. 2007). In particular, habitat relationships have been shown to be highly sensitive to the scale at which predictor variables are evaluated for brown bears in the Cantabrian Mountains (Mateo-Sánchez et al. 2014).

Landscape features for FCOY, FYRL, and mating areas were characterized by three categories of variables, namely landscape structure, landscape composition, and human footprint (i.e., landscape variables associated with humans) (see Table 1 for more details). Landscape GIS layers were extracted from Cartografía Temática Ambiental of the Principado de Asturias (Hojas del Mapa de Vegetación, Litología, Roquedos y Hábitat del Oso. Escala 1:25000. © Principado de Asturias, Spain).

Statistical analyses

To explore the possibility that areas used in early spring by FCOY differed from the areas frequented by FYRL and mating areas, we modeled habitat plots using two generalized linear models for each spatial scale, assuming a logistic error structure. Within each spatial plot, one model analyzed areas of FCOY vs. FYRL and the other model, areas of FCOY vs. mating areas. Explanatory variables were represented by the landscape features and human infrastructures described in Table 1. We tested for multicollinearity and removed variables with a variance inflation factor (VIF) >10. The dataset was extremely heterogeneous, i.e., many family groups had many observations, whereas many others had only one observation (range = 1-26 observations per family group). Having many family groups with only one observation precluded us from including this variable as a random factor. This is because the intra-class variance would be underestimated, and this could bias our results. As randomly selecting one observation per family group resulted in losing less data compared to removing those family groups with only one observation, we chose the former option. This resulted in a final number of observations of 84 locations for FCOY, 48 locations of FYRL, and 44 locations of mating bears. Because of the extension of the scales (plots with radii of

500—3000 m) of our multi-scale approach and the reported small displacements (few hundreds of meters) of FCOY after den exit, we are confident that our results are not an artefact of our random subset. Indeed, most of the bear family locations were inside these plots, and using different plot sizes around diverse random subsets of locations would have essentially described the same areas. Following Crawley (2007), model simplification was performed by backward selection of variables from the full model, and models were compared using likelihood ratio tests until a minimal adequate model was obtained. All statistical analyses were performed using R 3.3.1 statistical software (R Development Core Team 2013), and corrplot (Wei and Simko 2016) and lme4 (Bates and Maechler 2009) packages. Statistical significance was set at $\alpha < 0.05$.

Results

Our multi-scale approach showed that FCOY used cliffs more than FYRL, a pattern that was evident at 2000- and 3000-m scales (Table 2 and Supplementary Material SM1). FYRL used more riparian forests, which are located along streams at the bottom of the valleys, and were closer to human settlements than FCOY (Table 2 and Supplementary Material SM1).

We did not find differences among locations used by FCOY and mating bears at the 1000-, 2000- and 3000-m scales (Table 2). These findings suggest that the habitat use of FCOY did not generally differ from the habitat use of adult bears during the mating period.

Discussion

Maternal care strategies in brown bears include reducing movements (i.e., small home ranges) during the mating season, displaying more diurnal behavior, and spatial segregation from adult bears when females are accompanied by cubs of the year. Such strategies have been observed in several populations, both in Europe and North America (Ordiz et al., 2007; Steyaert et al., 2012 and references therein). Our study documented that, during the first few months after den emergence when bear cubs are most vulnerable, FCOY settled in potentially safe areas, like cliffs, more than did FYRL, which may provide shelter from both conspecifics and from human activities. Preference for quite inaccessible areas is likely a behavioral adaptation of FCOY to both reduce infanticide risk and survive in human-modified landscapes. However, in Scandinavia, successful mothers also selected for areas in relative close proximity to human habitations, which were avoided by adult males, showing that human footprint (i.e., landscape variables associated with humans) can locally act as protective shield for FCOY (Steyaert et al. 2016).

At the largest spatial scales, FCOY settled in landscapes with similar characteristics as areas used by males during the mating season. FCOY generally move short distances in early spring, i.e., during our study period, and are more active during the day than adult bears (authors' unpublished data and Ordiz et al., 2007), which likely represent strategies to avoid encounters with other bears (authors' pers. obs. and Fernández-Gil et al., 2006). However, similar habitat use by FCOY and males during the mating season, which might result in similar habitat use, may have increased the likelihood of infanticidal encounters. In fact, between 2013 and 2016, 15 1 km x 1 km

survey blocks contained both locations of FCOY (n total = 75 squares) and mating areas (n total = 23 squares) within the study area (authors' unpublished data). Thus, 20% of FCOY locations and 65.2% of mating areas located during the last 4 years occurred within the same 1-km² areas.

These observations provide some evidence that, in some cases, the FCOY choices for shelter and food in early spring may 'trap' them in areas where they also overlap with mating bears, which is contrary to distance-sensitive avoidance (Penteriani et al. 2018a). Evolutionary traps arise when individuals make maladaptive choices based on apparently reliable environmental cues, which ensnare individuals in situations or places that reduce their lifetime fitness or survival (Schlaepfer et al. 2002). The type of evolutionary trap we propose is different, because classical evolutionary traps are habitat types of lower fitness return that are preferred to other habitat types with higher fitness return, whereas we propose here that an individual may be constrained to use habitat types that are not optimal, which does not necessarily mean that it prefers non-optimal habitat. This scenario might be more prone to occur in small and confined populations, such as the Cantabrian bear population, where limited habitat availability and a distribution range surrounded by a variety of human activities and higher human densities might prevent FCOY from successfully avoiding areas also used by other bears (Gonzalez et al. 2016, Martínez Cano et al. 2016). Indeed: (a) most of the suitable habitat in western Asturias Province is already occupied (77 % of identified potential areas of bear expansion; Zarzo-Arias et al., submitted); and (b) the core bear range shows extensive urban and agriculture development, with a road density for the study area of ca. 47 km/100 km² (<http://www.seap.minhap.gob.es/index.html>); see also (Penteriani et al. 2017).

Even if FCOY alter their activity times to avoid male bears (Fernández-Gil et al. 2006), a phenomenon known as temporal segregation (Fedriani et al. 1999), restricted habitat availability in a human-modified landscape and the presence of males searching for reproductive opportunities (Ordiz et al. 2007) may promote encounters among bears during the mating season, which can in turn lead to infanticide events. In bear populations confined to areas with high human encroachment, FCOY habitat-mediated avoidance may only occur at small spatial scales, e.g., in the surroundings of the den after it is abandoned in early spring. Because habitat use by FCOY did not differ from habitat use by adult bears at the largest landscape scales during the mating period, further studies should elucidate the possibility that scale-dependent differences exist regarding infanticide avoidance.

The combination of the restricted range and size of the Cantabrian bear population, the documented cases of infanticide, and the potential consequences of habitat use of FCOY overlapping with adult males in mating areas may have an overall, important impact on the bear population dynamics in the Cantabrian Mountains, where suitable bear habitats seem to be limited by human encroachment (Naves et al. 2003). Therefore, future direct monitoring of space use, movements, and rhythms of activity of both FCOY and adult bears will be crucial to understand the development of this bear population and, consequently, to plan effective conservation strategies preserving the positive trends observed recently (Pérez et al. 2014, Gonzalez et al. 2016, Martínez Cano et al. 2016). For the time being, proactive conservation of rugged terrain is an important management recommendation, as it is certainly used by FCOY, especially when such places are close to human settlements and outdoor human activities (e.g.,

ski resorts, hiking, and climbing areas), which are a potential source of disturbance and may cause displacement of FCOY from these sensitive areas.

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Table 1. Structural, human, and habitat composition variables used to characterize areas used in early spring by brown bear females with cubs, females with yearlings, and mating areas for circular plots with radii of 500, 1000, 2000 and 3000 m in the Cantabrian Mountains, Spain. Variables marked with an (*) were correlated and therefore were not included in the models.

Variable	Description
<i>Structural variables</i>	
Altitude	Altitude of the plot centers (m a.s.l.), obtained from a raster layer of altitude of the Iberian Peninsula 'http://www.diva-gis.org' and calculated by QGIS <i>Point Sampling Tool</i>
Slope orientation*	Eight orientations, i.e. the four cardinal directions and the intermediate points between them (intercardinal directions), calculated by the QGIS tool <i>Aspect (Terrain Analysis)</i> the plot centers
Ruggedness	A variable calculated as the total length (m) of the linear development of level curves within the four different circular plots with the function <i>\$length</i>
<i>Human footprint</i>	
Paved road and dirt road length	Two variables calculated as the total length (m) of their linear development within the buffers with the function <i>\$length</i>
Distance (m) to the nearest paved road, dirt road, human settlement (village/town), human infrastructure (e.g. industrial areas, power plants, mines) and river	Five variables calculated with the <i>Hub Distance</i> function in MMQGIS
<i>Habitat composition variables</i>	
% of vegetation patches	We reclassified the totality of landscape layers of the Principado de Asturias into 16 broader classes: cliff, crops, conifer, fern, forest, fruit trees, grassland, human

481 infrastructures, pasture, riparian forest,
482 rocky area, shrubland, gorse, heath,
483 villages/towns and young forest. Then, we
484 used (a) the tool *Intersect* to extract the
485 information of the layers for each plot and
486 (b) the function *\$area* to calculate the area
487 occupied by each patch of habitat, which
488 was successively converted to a %

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1 **Table 2.** Linear models fitted by maximum likelihood showing landscape and human features that differentiate early (April-June) observed
2 locations of female brown bears with cubs from (A) observed locations of females with yearlings, and (B) bear mating areas in the Cantabrian
3 Mountains, Spain. All bear locations were from the same April-June period.

4		Estimate	SE	z	P
5					
6	500 m				
7	<u>Females with cubs vs. females with yearlings</u>				
8	Intercept	-0.59	0.19	-3.08	0.002
9	Distance to village/town	-0.47	0.26	-1.80	0.07
10	% riparian forest	0.68	0.22	3.14	0.002
11	Deviance = 8%				
12					

13 Females with cubs vs. mating areas

14	Intercept	0.76	0.22	-3.47	<0.001
15	% fern	0.52	0.24	-2.22	0.03
16	% riparian forest	0.58	0.26	-2.23	0.03
17	% pasture	-0.67	0.26	-2.63	0.009
18	% rocky	-0.67	0.33	-2.01	0.04

19 Deviance = 14%

20

21 **1000m**

22 Females with cubs vs. females with yearlings

23	Intercept	-0.63	0.20	-3.20	0.001

24

25

Ruggedness	-0.49	0.22	-2.30	0.021

26

Distance to dirt road	0.60	0.20	3.04	0.002

27

% riparian forest	0.45	0.21	2.18	0.03

28 Deviance = 11%

29

30 Females with cubs vs. mating areas

31

No significant differences

32 2000 m

33 Females with cubs vs. females with yearlings

34

Intercept	-0.65	0.20	-3.24	0.001

35

36

% cliffs	-0.47	0.27	-1.75	0.08

37

Dirt road length	0.39	0.21	1.84	0.07

38

Distance to village/town	-0.58	0.24	-2.43	0.015

39

% riparian forest	0.65	0.23	2.82	0.005

40

41 Deviance = 11%

42

43 Females with cubs vs. mating areas

44

No significant differences

45

46 3000 m

47 Females with cubs vs. females with yearlings

48	Intercept	-0.68	0.21	-3.29	0.001

49	Distance human settlement	-0.47	0.22	-2.14	0.03

50	% cliffs	-0.44	0.26	-1.71	0.09

51	% grassland	-0.56	0.30	-1.87	0.06

52	% riparian forest	0.51	0.23	2.23	0.03

53

54 Deviance = 11%

55

56 Females with cubs vs. mating areas

Figure 1. Spatial distribution of localizations of brown bear females with cubs (orange dots), females with yearlings (bright pink dots) and bear mating areas (blue dots) in the Cantabrian Mountains, NW Spain.

Figure 2. The spatial distribution of the sampling effort (direct observations and camera traps) for brown bear occurrence data ($n = 8,784$ locations) in the Cantabrian Mountains.

Supplementary Material SM1. Values (mean $\pm$ SD, min, max) of the significant parameters (see Table 2) that characterized the comparisons between areas used in early spring by female brown bears with cubs and (1) females with yearlings, and (2) bear mating areas in the Cantabrian Mountains, Spain.

Spatial Level	Significant variables	Mean	SD	min - max	Mean	SD	min - max
500 m	% riparian forests Distance to villages (m)	Females with cubs of the year			Females with yearlings		
		0.8	1.7	0 - 10.6	2.1	2.9	0 - 11.6
		375.8	116.9	133.2 - 494.2	34.7	69.3	25.7 - 430.6
500 m	% fern % riparian forests % pasture % rocky	Females with cubs of the year			Mating areas		
		0.5	1.8	0 - 10.0	1.5	3.8	0 - 13.1
		0.8	1.7	0 - 10.6	2.1	3.8	0 - 14.6
		13.6	17.5	0 - 68.2	10.0	17.0	0 - 44.3
		3.3	5.8	0 - 24.6	1.1	5.4	0 - 11.7
1000 m	Ruggedness (total length in m of the linear development of level curves) Distance to dirt roads (m) % riparian forests	Females with cubs of the year			Females with yearlings		
		17.9	2.6	11.9 - 28.8	17.1	2.9	8.8 - 10.7
		130.7	264.3	1.3 - 908.9	312.2	339.3	0.4 - 942.4
		1.0	1.4	0 - 6.4	1.7	1.5	0 - 7.5
1000 m	NONE	Females with cubs of the year			Mating areas		
		-			-		
2000 m	% cliffs Dirt road length Distance to village/town % riparian forest	Females with cubs of the year			Females with yearlings		
		4.2	5.2	0 - 32.8	3.2	3.5	0 - 12
		1.9	2.6	0 - 10.5	2.6	2.6	0 - 8
		688.5	644.1	0-1992.4	499.8	640.4	0-1578.1
		0.9	0.8	0 - 4	1.3	0.8	0 - 5.3
2000 m	NONE	Females with cubs of the year			Mating areas		
		-			-		
3000 m	% cliffs % riparian forests % grasslands Distance human settlements	Females with cubs of the year			Females with yearlings		
		3.9	4.7	0 - 24.5	2.8	3.3	0 - 16.9
		0.9	0.5	0 - 3	1.2	0.5	0 - 3.5
		1.0	1.3	0 - 5.2	0.5	0.6	0 - 2.3
		598.7	1003.9	0 - 2877.5	301.6	1000.3	0 - 2506.1
3000 m	NONE	Females with cubs of the year			Mating areas		
		-			-		