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

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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 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; 2001–2016) 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 (Apr–Jun), 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: brown bear, Cantabrian Mountains, females with cubs, human-modified landscapes, infanticide, mating areas, Spain, *Ursus arctos*

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 ≥1.5 years (males provide no parental care and, thus, offspring depend completely on their mothers; Dahle and Swenson 2003a, 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

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1

fitness by killing unrelated offspring so as to bring a female into reproductive condition and, thus, increase their chance of reproducing with her (Hrdy 1979). This form of infanticide occurs in seasonal breeders during the mating season (van Schaik and Janson 2000). Infanticide is costly for victimized females, so 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 2 main ways: (1) habitat-mediated avoidance (Fedriani et al. 2000, Sergio et al. 2007)—that is, 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 male 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; 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 are 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 2,648 m above sea level and the average elevation is approximately 1,100 m above sea level (Naves et al. 2003, Martínez Cano et al. 2016). The oceanic climate is mild and humid throughout the year (range = 900–1,900 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 tree line (approx. 1,700 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/km^2 (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
We obtained the locations of FCOY, FYRL, and mating areas (Fig. 1) using 2 methods. (1) Systematic bear observations were performed by personnel of (a) the Bear Team (Patrulla Oso) of the Principado de Asturias, (b) the Asturian Foundation for the Conservation of Wildlife
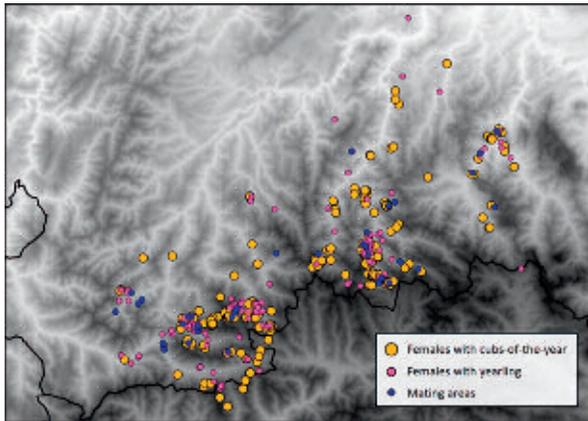
Fig. 1. Spatial distribution of localizations of brown bear (*Ursus arctos*) females with cubs (orange dots), females with yearlings (bright pink dots), and bear mating areas (blue dots) in the Cantabrian Mountains, northwestern Spain (2001–2016).

Fig. 2. The spatial distribution of the sampling effort (direct observations and camera traps) for brown bear (*Ursus arctos*) occurrence data (*n* = 8,784 locations) in the Cantabrian Mountains, northwestern Spain (2001–2016).

(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. (2) Camera-traps were placed randomly by the FAPAS and Bear Team during the past 20 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 (Fig. 2). The locations of FCOY, FYRL, and mating areas occupied approximately 1,500 km^2 (i.e., approx. 23% of the total bear range [approx. 6,520 km^2] 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. We identified the different bear families 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 us to differentiate between families observed on the same day in neighboring areas. We made all observations during daytime and from distances that varied from several
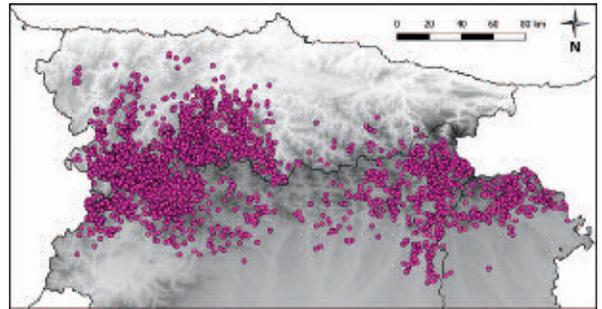
hundred meters to 1.0–1.5 km (Zarzo-Arias et al. 2018). Camera-traps allowed collection of additional information on FCOY locations, especially when they were not in open habitats.

Landscape characterization

We used a multi-scale approach of the habitat use of FCOY, considering 4 spatial scales (i.e., circular plots with radii of 500, 1,000, 2,000, and 3,000 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 and personal observations; Ordiz et al. 2007; Gardner et al. 2014). Females with cubs-of-the-year also have small home ranges in spring in other brown bear populations (e.g., in Scandinavia [Dahle and Swenson 2003b, Steyaert et al. 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

Table 1. Structural, human, and habitat composition variables used to characterize areas used in early spring by brown bear (*Ursus arctos*) females with cubs, females with yearlings, and mating areas for circular plots with radii of 500, 1,000, 2,000, and 3,000 m in the Cantabrian Mountains, Spain (2001–2016).

Variable[a]	Description
Structural variables	
Altitude	Altitude of the plot centers (m above sea level), obtained from a raster layer of altitude of the Iberian Peninsula (http://www.diva-gis.org) and calculated by QGIS (qgis.org/en/site/) *Point Sampling Tool*
Slope orientation[*]	Eight orientations (i.e., the 4 cardinal directions and the intermediate points between them [inter-cardinal directions]), calculated by the QGIS tool *Aspect* (*Terrain Analysis*)
Ruggedness	A variable calculated as the total length (m) of the linear development of level curves within the 4 different circular plots with the function *$length*
Human footprint	
Paved road and dirt road length	Two variables calculated as the total length (m) of their linear development within the buffers with the function *$length*
Distance (m) to the nearest paved road, dirt road, human settlement (village or town), human infrastructure (e.g., industrial areas, power plants, mines), and river	Five variables calculated with the *Hub Distance* function in MMQGIS (http://michaelminn.com/linux/mmqgis/)
Habitat composition variables	
% 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 infrastructures, pasture, riparian forest, rocky area, shrubland, gorse, heath, human settlements, and young forest. Then, we used (a) the tool *Intersect* to extract the information of the layers for each plot, and (b) the function *$area* to calculate the area occupied by each patch of habitat, which was successively converted to a percentage.

[a] Variables marked with an (*) were correlated and therefore were not included in the models.

for brown bears in the Cantabrian Mountains (Mateo-Sánchez et al. 2014).

We characterized landscape features for FCOY, FYRL, and mating areas by 3 categories of variables—landscape structure, landscape composition, and human footprint (i.e., landscape variables associated with humans; see Table 1 for more details). We extracted landscape Geographic Information System layers 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 2 generalized linear models for each spatial scale, assuming a logistic error structure. Within each spatial plot, one model analyzed areas of FCOY versus FYRL and the other model analyzed areas of FCOY versus 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 >10. The data set was extremely heterogeneous (i.e., many family groups had many observations, whereas many others had only one observation [range = 1–26 observations/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. Randomly selecting one observation per family group resulted in losing fewer data compared with removing those family groups with only one observation, so we chose the former option. This resulted in a final number of observations of 84 locations for FCOY, 48 locations for FYRL, and 44 locations for mating bears. We are confident that our results are not an artefact of our random subset because of our extension of the scales (plots with radii of 500–3,000 m) of our multi-scale approach and our reported small displacements (few hundreds of meters) of FCOY after den exit. 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), we performed model simplification by backward selection of variables from the full model, and compared models

using likelihood ratio tests until we obtained a minimal adequate model. We performed all statistical analyses using Program R 3.3.1 statistical software (R Development Core Team 2013), and corrplot (Wei and Simko 2016) and lme4 (Bates and Maechler 2009) packages.

Results

Our multi-scale approach showed that FCOY used cliffs more than FYRL did, a pattern that was evident at 2,000- and 3,000-m scales (Table 2; Supplemental Material Table S1). Females with yearlings used more riparian forests, which are located along streams at the bottom of the valleys, and were closer than FCOY to human settlements (village or town [Table 2; Supplemental Material Table S1]).

We did not find differences among locations used by FCOY and mating bears at the 1,000-, 2,000-, and 3,000-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, such as cliffs, more than did FYRL; such areas 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 relatively 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 a protective shield for FCOY (Steyaert et al. 2016).

At the largest spatial scales, FCOY settled in landscapes with characteristics similar to areas used by males during the mating season. Females with cubs-of-the-year generally move short distances in early spring (i.e., during our study period) and are more active during the day than are adult bears (authors, unpublished data; Ordiz et al. 2007), which likely represents strategies to avoid encounters with other bears (authors, personal observations; Fernández-Gil et al. 2006). However, similar habitat use by FCOY and males during the mating season may have increased the likelihood of infanticidal encounters. In fact, between 2013 and 2016, 15 1-km × 1-km survey blocks contained both locations of FCOY (total $n = 75$ squares) and mating areas (total $n = 23$ squares) within the study area (authors, unpublished data). Thus, 20% of FCOY locations and 65.2% of mating areas located during the past 4 years occurred within the same 1-km^2 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 nevertheless preferred to other habitat types with greater 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 individual 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. 2019); and (b) the core bear range shows extensive urban and agriculture development, with a road density for the study area of approximately 47 km/100 km^2 (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 levels of human encroachment, FCOY habitat-

Table 2. Linear models fitted by maximum likelihood showing landscape and human features that differentiate early (Apr–Jun) observed locations of female brown bears (*Ursus arctos*) with cubs from (a) observed locations of females with yearlings, and (b) bear mating areas in the Cantabrian Mountains, Spain. All bear locations were from the same April–June period (2001–2016).

Model		Estimate	SE	z	P
500 m					
Females with cubs vs. females with yearlings					
	Intercept	−0.59	0.19	−3.08	0.002
	Distance to human settlements	−0.47	0.26	−1.80	0.07
	% riparian forest	0.68	0.22	3.14	0.002
Deviance = 8%					
Females with cubs vs. mating areas					
	Intercept	0.76	0.22	−3.47	<0.001
	% fern	0.52	0.24	−2.22	0.03
	% riparian forest	0.58	0.26	−2.23	0.03
	% pasture	−0.67	0.26	−2.63	0.009
	% rocky	−0.67	0.33	−2.01	0.04
Deviance = 14%					
1,000 m					
Females with cubs vs. females with yearlings					
	Intercept	−0.63	0.20	−3.20	0.001
	Ruggedness	−0.49	0.22	−2.30	0.021
	Distance to dirt road	0.60	0.20	3.04	0.002
	% riparian forest	0.45	0.21	2.18	0.03
Deviance = 11%					
Females with cubs vs. mating areas					
	No significant differences				
2,000 m					
Females with cubs vs. females with yearlings					
	Intercept	−0.65	0.20	−3.24	0.001
	% cliffs	−0.47	0.27	−1.75	0.08
	Dirt road length	0.39	0.21	1.84	0.07
	Distance to human settlements	−0.58	0.24	−2.43	0.015
	% riparian forest	0.65	0.23	2.82	0.005
Deviance = 11%					
Females with cubs vs. mating areas					
	No significant differences				
3,000 m					
Females with cubs vs. females with yearlings					
	Intercept	−0.68	0.21	−3.29	0.001
	Distance human settlements	−0.47	0.22	−2.14	0.03
	% cliffs	−0.44	0.26	−1.71	0.09
	% grassland	−0.56	0.30	−1.87	0.06
	% riparian forest	0.51	0.23	2.23	0.03
Deviance = 11%					
Females with cubs vs. mating areas					
	No significant differences				

mediated avoidance may only occur at small spatial scales (e.g., in the surroundings of the den after it is abandoned in early spring). Habitat use by FCOY did not differ from habitat use by adult bears at the largest landscape scales during the mating period; therefore, 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 important overall 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 because 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.

Acknowledgments

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Table S1. Values (mean ± SD, min., max.) of the significant parameters (see Table 2) that characterized the comparisons between areas used in early spring by female brown bears (*Ursus arctos*) with cubs and (1) females with yearlings, and (2) bear mating areas in the Cantabrian Mountains, Spain (2001–2016).