Mating-related movements of male brown bears on the periphery of an expanding population

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Abstract: Use of habitat and resources of large carnivores living at the expansion front of a population can differ considerably from those living in core areas. Using GPS (global positioning system) telemetry, we studied movements of male brown bears living in the northwest edge of the Alpine–Dinaric–Pindos population in Slovenia and Italy, 2005–08. Because there was a steep gradient of female densities in the periphery of the population and females occurred only in a small portion of the area used by males, we could test how the distribution of breeding females affected the spatial distribution and movements of male brown bears. The home-range size of the males in our study was inversely related to female densities. During the mating season we observed directed movement from the periphery of the population with low female densities toward the core area with higher female densities. Our observations suggest that this strategy allows even males living at the periphery of the population, where no females were know to occur, to take part in reproduction.

Key words: brown bear, expansion front, mating, movements, population periphery, *Ursus arctos*

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Several populations of large carnivores in Europe have increased in abundance and range in recent years (Linnell et al. 2008). The demography, habitat use, dispersal, and other ecological parameters of expanding populations can be different from those of stable or declining populations (Pletscher et al. 1997, Swenson et al. 1998, Bales et al. 2005, Jerina and Adamič 2008). Habitat use and use of resources (e.g., food, mating partners) by individuals living at the expansion front of the population can differ from those in core population areas (Breitenmoser and Haller 1993, Dahle and Swenson 2003a, Zedrosser et al. 2007a).

Among brown bears (*Ursus arctos*), the ratio of males to females at the expansion front is higher than in core areas because of male-biased dispersal (Swenson et al. 1998, Kojola et al. 2003, Jerina and Adamič 2008). Therefore, males on the periphery have fewer mating opportunities and lower reproductive success (Zedrosser et al. 2007a). However, limited information is available about the mating strategies and mating-related movements of males living at the expansion front. A better understanding of movements, mating behavior, and other life-history strategies of brown bears at the periphery of expanding populations is needed to address management challenges that occur when bear populations, or those of other large carnivores, expand into areas where people are not used to coexisting with them. Understanding of mating-related movements might also be important when planning population monitoring and estimating local population abundance.

We analyzed movements of male brown bears living in the northwest edge of the Alpine–Dinaric–Pindos population. Because there was a steep gradient of female bear densities in the periphery of the population (Jerina and Adamič 2008) and females occurred only in a fraction of the area used by males, this area presented an opportunity to test how the distribution of females may affect movements of males during the breeding season. There should be strong selection against non-reproducing males, so we expected that male bears would adjust their space use to assure at least limited reproductive success. Thus, we predicted that the spatial distribution of males would change during the mating period and that these changes would be greater in the periphery compared to the core area of the population. We thus expected that males from areas without females or lower female densities will move

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to areas with higher female densities during the mating period. This information could offer valuable insights into the movements and mating behavior of male brown bears and other non-territorial, solitary carnivores living at population expansion fronts.

Study area

Brown bears in Slovenia belong to the Alps–Dinaric–Pindos population (Zedrosser et al. 2001). They live mainly in the Dinaric Mountains, which cover most of the southern portion of Slovenia. A few individuals occur outside the Dinaric range, mainly in the Alps in northwest portion of the country. There is a steep gradient in bear densities, particularly for females, with rapidly decreasing population density toward the north and west (Jerina and Adamič 2008), although suitable habitat for brown bears extends from the Dinaric Mountains in a northwest direction into the Julian Alps (Jerina et al. 2003) and further into Italy (Boitani et al. 1999) and Austria (Wiegand et al. 2004). In contrast, the bear population continues south across the border with Croatia, with densities similar to the population core area in Slovenia.

The present distribution of brown bear is mainly a function of habitat characteristics, human infrastructure, and past management. The corridor of suitable habitat from the Dinaric range toward the Alpine region is interrupted by a 4-lane, fenced highway from Ljubljana to Postojna (toward Trieste in Italy; Fig. 1), which provides limited opportunities for wildlife crossings. Although individual bears have been recorded crossing the road, this highway and the railway next to it may present a formidable barrier for bears and other large carnivores and a direct mortality threat due to vehicle collisions (Kaczensky et al. 2003, Krofel et al. 2006, Skrbinšek et al. 2008). Within the Dinaric range a Core Bear Protective Area of 3,500 km^2 was established in 1966 (Simonič 1994). Inside this area bear hunting has been strictly regulated (with moderate hunting quotas, year-round protection of females with cubs, and designated hunting season), whereas bears dispersing outside this area were not protected until the beginning of the 1990s and therefore experienced higher harvests (Kryštufek and Griffiths 2003). In 1992, brown bears were also protected outside the Core Bear Protective Area, which, together with moderate harvest in the core area, led to expansion toward the Alpine region in the late 1990s (Jerina and Adamič 2008). However, high bear damage and decreased human tolerance in the Alpine region in subsequent years led to increased harvest inside and outside the Core Bear Protective Area, which apparently halted further northwest expansion (Kryštufek and Griffiths 2003, Jerina and Adamič 2008).

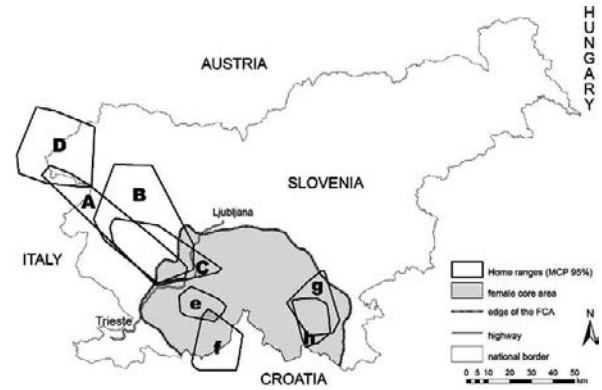

Fig. 1. Home ranges of male brown bears in the northern Dinaric Mountains and Julian Alps, 2005–2008. Four male bears (A–D) in the peripheral area (in northwest Slovenia and Italy), where there was low bear density, had significantly larger home ranges than 4 males (e–h) living in the female core area (FCA; grey area). During the mating period, 3 of 4 males from periphery moved into the female core area.

The number of brown bears in Slovenia at the end of the 2007 was estimated to be 394–475 animals, with 19–23 occurring northwest of the Ljubljana–Postojna–Trieste highway (Skrbinšek et al. 2008). According to analysis of >300 genetic samples and harvest records, all brown bears in the Alpine region were males, whereas all females west of the Ljubljana–Postojna highway were restricted to the Dinaric range adjacent to the highway (Guiatti et al. 2008, Jerina and Adamič 2008, Skrbinšek et al. 2008).

Methods

We captured bears in spring using free-range techniques and Aldrich leghold snares at feeding sites visited by bears throughout the Alpine and Dinaric range (see capture protocols in Filacorda et al. 2008). All adult animals were fitted with 3-D GPS-GSM (global positioning system, global system for mobile communication) collars (Vectronic Aero-

Table 1. Distances from the female core area (FCA) for GPS-collared male brown bears from northern Dinaric Mountains and Julian Alps, Slovenia and Italy, 2005–2008.

Bear	Age (years)	Radio-tracking period	Home range (km^2)	Relative female density (dead females/ year/ 100 km)	Difference in median distance to the edge of the FCA[a]	
					(km)	P[b]
A	5	Mar–Oct 07	1,010	0.06	15.00	<0.001
B	14	Apr 07–Jan 08	1,620	0.05	23.78	<0.001
C	13	Apr 07–Mar 08	850	0.23	13.63	<0.001
D	10	Apr–Sep 07	1,020	0.00	−4.51	0.511
e	13	Mar–Dec 05	230	1.30	−2.85	0.272
f	5	Mar 05–Apr 06	470	0.49	3.78	0.001
g	8	Apr–Dec 05	440	0.77	6.76	<0.001
h	6	Apr–Nov 06	280	0.85	0.18	0.940

[a]Difference between mating season (May–mid Jun) and non-mating season distance to female core area (FCA).
[b]Mann-Whitney *U*-test

space GmbH, Berlin, Germany) programmed to attempt a GPS fix every hour, 24-hours per day, for one year. In 2007, we collared 4 male bears (ages 5 to 14 years) in the peripheral area (Table 1). Two were captured in Slovenia and 2 in Italy. In the core area, we monitored 4 males (ages 5 to 13 years) during 2005–06. Not all bears were monitored throughout the entire year, due to collar failure or death of the bear. However, all males included in this study were monitored before, during, and after the mating season (Table 1).

We analyzed GPS telemetry data using the animal movement extension (Hooge and Eichenlaub 1997) to Arcview GIS (Environmental Systems Research Institute Inc., Redlands, California, USA) and Biotas 1.03.1 (Ecological Software Solutions LLC, Sacramento, California, USA). We estimated the home range area of each male bear using the 95% minimum convex polygon (MCP) method. We used this method because it enables better visualization and comparison of results with previous studies, although it may have lower ability to detect biologically meaningful patterns when variation in home range sizes is small (Nilsen et al. 2008). During our study, brown bears in Slovenia experienced high mortality (mainly because of hunting and vehicle collisions), so we used a dataset of 219 dead females recorded between 2004 and 2008 to delineate a female core area (FCA). Similar to Swenson et al. (1998), we defined the FCA as the 95% fixed-kernel of all recorded female mortality locations. There was a decreasing gradient of female densities toward the periphery of the bear population (Jerina and Adamič 2008), so we considered distance from the boundary of the FCA as a good indicator of female density for this study. We refer to the area outside the FCA (the Alpine region and the most northwest portion of the Dinaric Mountains) as the peripheral area and to male bears with all or most of their home ranges in this area as peripheral males.

We calculated the relative female density within home ranges of radiocollared males based on average annual female mortalities/100 km^2 of home range area. For all GPS locations of male bears, we determined the distance to the closest edge of the FCA. Because high female densities continued far into Croatia, we did not take the southern Slovenian national border as the edge of FCA, but rather used the northern FCA boundary for calculation, even if GPS locations were closer to the national border (Fig. 1). For males inside the FCA we also calculated distances to the nearest FCA boundary to determine if they moved further into the core area. To separate these movements from those of the peripheral males toward the FCA, we used negative values for bears inside the FCA.

We defined the mating season to be from early May–mid June, when most copulations take place in Slovenia (Krže 1988, Jonozovič 2003; unpublished data). For each bear, we tested for differences in median distances of GPS locations from the FCA between mating and non-mating periods (Mann-Whitney *U*-test; Statistica 6.0, StatSoft, Inc., Tulsa, Oklahoma, USA). We used the same test to evaluate differences in home-range size between peripheral males and males living within the FCA. We used Spearman rank correlations (Statistica 6.0) to examine the relationship between male home-range size and relative female density and the relationship between the median distance to the FCA boundary and the difference in that distance between the mating and non-mating seasons.

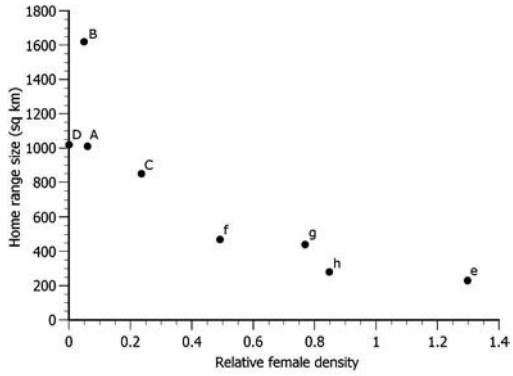

Fig. 2. Male brown bear home-range size plotted against relative female density (annual number of female mortalities/100 km^2 of each male home range), northern Dinaric Mountains and Julian Alps, Slovenia and Italy, 2005–08. Spearman $r = -0.976$, $n = 8$; $P < 0.001$. Male bears A–D were from the periphery of the population; bears e–h lived inside the female core area (FCA).

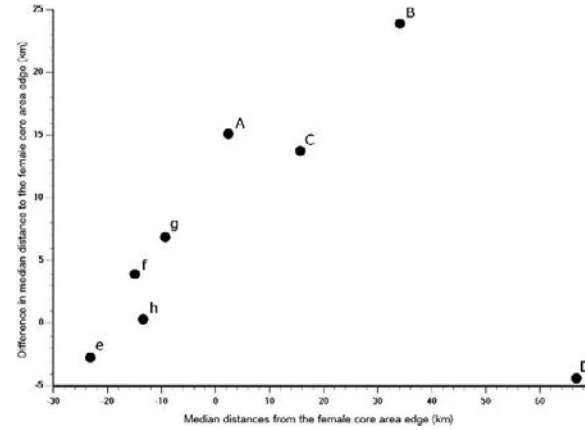

Fig. 3. Median distance of male brown bears to the female core area (FCA) plotted against the difference in this distance from mating and non-mating seasons, northern Dinaric Mountains and Julian Alps, Slovenia and Italy, 2005–08. Spearman $r = 0.929$, $n = 7$; $P = 0.003$ (outlier male D was excluded). Bears A–D were from the periphery of the population; e–h lived inside the FCA. Peripheral males A–C moved toward the FCA during the mating season, whereas male D remained in the periphery and was presumably not involved in reproduction. Negative median distances indicate that the bear was inside the FCA.

Results

Home ranges of male brown bears inside the FCA varied from 231 to 474 km^2 ($\bar{x}$ = 358 km^2, n = 4). Home ranges of peripheral males were larger (Mann-Whitney U = 0.00; n = 8; P = 0.021), varying from 851 to 1,624 km^2 ($\bar{x}$ = 1,126 km^2, n = 4; Fig. 1). There was negative correlation between home-range size and relative female density (Spearman r = −0.976, n = 8; $P < 0.001$; Fig. 2). During the mating season, we noted a shift in spatial distribution for 3 out of 4 peripheral males, which exhibited directional movements toward the FCA (Fig. 3). The median distances from the FCA boundary were 13.6 to 23.8 km closer during the mating season than during the non-mating season (Table 1). These movements represented 47–59% of their home-range diameter. For all 3 peripheral bears, the median distance to the FCA boundary was lowest in May. One male remained in the Alpine region during the mating season and was apparently not involved in mating. Among the males in the FCA, we observed a change in the median distance to the FCA boundary for 2 out of 4 males (Table 1), who moved further into the FCA. Excluding male D, which we considered an outlier (Fig. 3), we observed a correlation between relative female density and change in distance to the FCA boundary between the mating and non-mating season. The greatest change occurred among males living in areas with fewer females (Spearman r = 0.929, n = 7; P = 0.003; Fig. 3).

Field observations (B. Semenič and V. Šemrov, Slovenian Hunting Association, Nova Gorica and Hotedršica, Slovenia, personal communication, 2007) suggested that at least 1 female was present on the Hrušica Plateau close to the FCA boundary during the mating season (Fig. 4). This female bear was a regular visitor to a local feeding site in previous years, when she was accompanied by cubs and was easily recognized by her specific external characteristics. Three of the collared males visited this area during the 2007 mating season: bear A visited once during 24–27 May, bear B twice during 12–27 May, and bear C twice during 9 May–2 June. At least 2 of these males were observed together with the female in the field (B. Semenič, personal communication, 2007). Based on the GPS locations, we also noted movement changes among these 3 males. During the mating period, locations sometimes became concentrated for a few days, indicating limited movements (Fig. 4). However, unlike foraging movements, these bears did not return to the same locations but kept moving slowly. There were

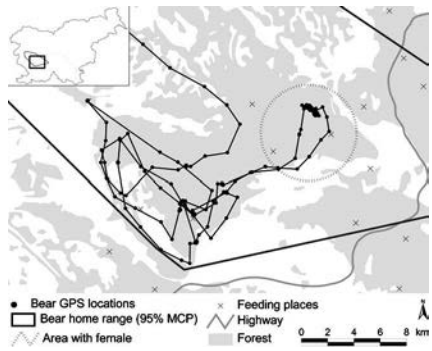

Fig. 4. Movements of male brown bear C in the northern Dinaric Mountains in Slovenia during the mating period, 19 May–4 Jun 2007. Distances between consecutive locations shortened when this bear moved to the Hrušica Plateau (marked with circle), where at least 1 female was located (25–26 May 2009).

no feeding sites at these clusters of locations and we did not observe such movement patterns outside of the mating period or for bear D, who remained in the Alpine region.

After the mating period, distance from the FCA increased for males A, B, and C. Two returned to the Alpine region and 1 remained in the intermediate area between the Alps and the Dinaric Mountains. Only bear C crossed the highway and went further into the FCA. In the beginning of the mating season, bear B moved close to the highway and the FCA. He moved along the highway fence for >20 km in both directions, without crossing, finally stopping on the Hrušica Plateau where the previously mentioned female was located.

Discussion

Home ranges of male brown bears at the periphery of the population were >3 times larger than home ranges for males within the FCA. This finding supports the observations from the expanding population in Scandinavia, which Dahle and Swenson (2003*a*) attributed to fewer intraspecific interactions and less competition for space in the periphery, rather than food availability. We suggest the same may be true for brown bears in the Dinaric–Alpine subpopulation, although we cannot dismiss the possible influence of availability and distribution of foods between the FCA and the peripheral, Alpine region.

We suggest that the 3 male bears that moved from the population edge closer to the FCA did so to mate. Indeed, 2 of the collared males for which we documented movement to the FCA were observed together with a female on the Hrušica Plateau (B. Semenič, personal communication, 2007) during the mating period. Several studies have shown that female brown bears often mate with several males during the same mating season (Dahle and Swenson 2003b, Bellemain et al. 2006). Because the 3 males moved to the same area one after another, it is possible that all of them mated with this female, although other females may have also been present in the area at that time.

Female brown bears occasionally exhibit long-distance dispersal in expanding populations (Swenson et al. 1998, Jerina and Adamič 2008), but despite intensive genetic sampling we found no evidence of females in the Julian Alps, which was the extreme periphery of the population, during our study (Guiatti et al. 2008, Skrbinšek et al. 2008). During the mating period, 3 of the 4 peripheral males directed their movements toward the FCA and came to a region where at least one female was present. Similar changes in male movement during the mating season toward an area where females were located was observed in an experiment with bank voles (*Myodes glareolus*), where females were artificially restricted to a small outdoor enclosure (Ylönen and Mappes 1995). To our knowledge this has never been documented in brown bears, although Dahle and Swenson (2003a) noted an increase in home ranges among brown bears in Scandinavia during the mating period. Similar increases in male home ranges during the breeding period have been recorded for other carnivores (e.g., Lindzey and Meslow 1977, Erlinge and Sandell 1986). Sandell (1989) predicted that, in general, male spatial organization in solitary carnivores is influenced by the distribution of food resources outside the mating season and distribution of estrous females during the mating period.

Our observations suggest that male brown bears living at the periphery of a population where apparently no females are present may attempt to mate by moving closer the core area of a population. However, the success rate of those males is probably lower than males in the core area, where the density of females is higher, as was shown for Scandinavian brown bears (Zedrosser et al. 2007a). In extreme instances, an individual disperses so far that its home

range may not overlap with any female home ranges, which may have been the case for one of the males in our study. However, we only monitored that bear over 1 mating season and we cannot exclude the possibility that he was involved in reproduction in other years. The home range of that male was comparable in size to other males in the peripheral area, and we assume that movements toward the core area during the mating period are not the main reason for larger home ranges of males in the peripheral area. Although dispersal can bring direct benefits, such as avoidance of inbreeding and reduced intraspecific competition for food, females, and other resources (Shields 1987, Dahle and Swenson 2003c, Støen et al. 2006, Zedrosser et al. 2007b), there is probably a trade-off between the benefits of dispersal and reduced reproduction success.

Our observations were based on a small number of bears. Further research is needed to test hypotheses of directed movements of males bears in peripheral areas toward areas with higher female densities during mating season and any trade-offs associated with possible lower reproductive success.

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