



Research paper

Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations

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Abstract. We developed a conceptual model of spatial organization in vertebrates based upon changes in home range overlap with habitat quality. We tested the model using estimates of annual home ranges of adult females and densities for 30 populations of brown bears (*Ursus arctos*) in North America. We used seasonality as a surrogate of habitat quality, measured as the coefficient of variation among monthly actual evapotranspiration values for areas in which study populations were located. We calculated home range overlap for each population as the product of the average home range size for adult females and the estimated population density of adult females. Home range size varied positively with seasonality; however, home range overlap varied with seasonality in a nonlinear manner. Areas of low and high seasonality supported brown bears with considerable home range overlap, but areas of moderate seasonality supported brown bears with low home range overlap. These results are consistent with behavioural theory predicting a nonlinear relationship between food availability and territoriality.

Key words: brown bear, home range, home range overlap, seasonality, space-use, spatial organization, territoriality, *Ursus arctos*

Introduction

There are two main questions in the study of how animals organize themselves in space. The first question relates to how much space an individual requires to survive and reproduce. Here we are interested in the 'home range' of an animal, the normal area that an animal uses over some specified period of time to carry out the activities of securing food, mating, and caring for young (Burt, 1943). The second question asks how much space an individual shares with competitors while carrying out the day-to-day tasks that ensure its survival and ability to reproduce. Active defence (e.g., through fighting, song, or scent) of home ranges or portions of home ranges to the exclusion of conspecifics has generally been termed territoriality (Begon *et al.*, 1990). The degree of territoriality exhibited by individuals may be measured as the degree to which home ranges

overlap (e.g., Nemptsov, 1997). The average size of home ranges and the extent to which home ranges overlap may show considerable variation among populations within a species.

Because survival and reproduction are often food-limited, the abundance and predictability of food resources in time and space are likely important factors influencing spatial organization. Food is often cited as an important limiting factor determining the size of an individual's home range (review in McLoughlin and Ferguson, 2000). This is true for both the general abundance and spatio-temporal predictability of food resources. For example, in rufous hummingbirds (*Selasphorus rufus*, Gass *et al.*, 1976; Kodric-Brown and Brown, 1978; Gass, 1979) and golden-winged sunbirds (*Nectarinia reichenowi*, Gill and Wolf, 1975), although the size of feeding territories show great variation in size and flower composition, the amount of nectar that each territory contains remains constant. For populations within the same species, home range size generally shares an inverse relationship with food abundance. This is true for several species, including voles, *Microtus townsendii*, (Taitt, 1981); bandicoots, *Isoodon obesulus* (Broughton and Dickman, 1991); roe deer, *Capreolus capreolus* (Tufto *et al.*, 1996); black bears, *Ursus americanus* (Powell *et al.*, 1997); brown bears, *U. arctos* (McLoughlin *et al.*, 1999; McLoughlin and Ferguson, 2000); lizards, *Sceloporus jarrovi* (Simon, 1975); and birds (Hixon, 1980). In addition, home range size is negatively related to predictability of food availability in red squirrels, *Sciurus vulgaris* (Wauters and Dhondt, 1992), and palm civets, *Paradoxurus hermaphroditus* (Joshi *et al.*, 1995).

The amount of intraspecific variation in home range overlap may be associated with the abundance and predictability of food. Numerous theoretical and empirical cost-benefit analyses (*sensu* Brown, 1964) suggest that food abundance and/or predictability are important factors influencing territoriality (e.g., Gill and Wolf, 1975; Carpenter and MacMillen, 1976, 1980; Gass *et al.*, 1976; Ewald and Carpenter, 1978; Kodric-Brown and Brown, 1978; Gass, 1979; Frost and Frost, 1980; Carpenter, 1987; Armstrong, 1991; Maher and Lott, 2000). A cost-benefit model developed by Carpenter and MacMillen (1976) predicts that territoriality will occur at intermediate levels of regional food abundance, with no territoriality occurring outside upper and lower thresholds of food abundance. A similar model was recently proposed by Maher and Lott (2000). The upper threshold occurs when regional food resources are at high enough levels that animals do not benefit from improved access to food by excluding intruders. A number of studies of nectarivorous birds provide corroborating evidence for this hypothesis (e.g., iiwi, *Vestiaria coccinea*, Carpenter and MacMillen, 1976; Carpenter, 1978; golden-winged sunbirds, Gill and Wolf, 1979; olive sunbirds, *N. olivacea*, Frost and Frost, 1980; and rufous hummingbirds, Carpenter, 1987), reporting abandonment of territoriality with increased regional abundance of nectar (but see Armstrong,

1992). The lower threshold occurs when regional abundance is so low that the energetic costs of defending an area of sufficient size outweigh the benefits. Evidence for this hypothesis comes from data on a number of territorial species, including iwii (Carpenter and MacMillen, 1976); Anna hummingbirds (*Calypte anna*, Ewald and Carpenter, 1978); rufous hummingbirds (Kodric-Brown and Brown, 1978); red squirrels (Wauters and Dhondt, 1992); and pronghorn (*Antilocapra americana*, Maher, 1994).

Although hypotheses concerning home range size have sometimes been tested using comparative data among populations and species (see McLoughlin and Ferguson, 2000), few studies (e.g., Maher, 1994) have used comparative data to test hypotheses concerning home range overlap (Maher and Lott, 2000). A strong test of any model of territoriality or home range overlap would be if populations of the same species, who come to occupy different environments where they are subject to different selection pressures, vary their space-use patterns in a manner similar to that predicted by 'cost-benefit' theory. In this paper, we develop a conceptual model of spatial organization based upon the synthesis of factors affecting variation in home range size and overlap. In particular, we use habitat quality as defined by regional food abundance and predictability. We then empirically test the proposed model using comparative data collected for populations of brown bears (*U. arctos*) in North America (i.e., an interpopulation analysis). Here we test predictions associated with the importance of food resources on the size of home ranges, but also aspects of territoriality models proposed by Carpenter and MacMillen (1976) and Maher and Lott (2000).

The space-use model

The model is concerned with the overlap of feeding ranges only (i.e., not breeding territories) and applies in general to food-maximizing (*sensu* Schoener, 1971), solitary-living animals. Food-maximizers are those animals whose potential reproductive success is directly related to their daily net energy gain. So defined, female mammals, especially those that must rear young by themselves, have been generally characterized as food-maximizers (Schoener, 1971). Solitary animals are those that generally do not, except when mating, cooperate with conspecifics for the purposes of rearing young, foraging, achieving matings, or defending against predators (Sandell, 1989).

We propose that for food-maximizing and solitary animals the spatial organization of individuals in response to changing habitat quality can be depicted as in Fig. 1. Here, habitat quality is defined by factors that include food abundance (e.g., primary productivity) and predictability of food in time (e.g., seasonality) and space (e.g., patchiness). Areas of high habitat quality contain

abundant foods that are predictable in time and space. Areas of low habitat quality contain low and/or unpredictable food resources. Areas of moderate habitat quality show intermediate levels of food abundance and predictability.

The model makes the following predictions. First, in areas of high habitat quality (Fig. 1A), populations are characterized by small home ranges and high home range overlap (i.e., no territoriality). Small home ranges occur where food is abundant or predictable because animals will be able to maximize energy intake over less area, with or without territorial defence (Hixon, 1980; but see Ebersole, 1980). Further, there may be no selective pressure to defend areas if limiting food resources are in regional superabundance and expelling intruders does not improve an animal's access to food (Gill and Wolf, 1975; Carpenter and MacMillen, 1976; Carpenter, 1987). Under some circumstances, increases in competitor density and thus intruder pressure – an indirect result of increased food availability – may make effective territorial defence impossible (Myers *et al.*, 1981).

Second, the model predicts a shift to larger home ranges and a decrease in home range overlap as habitat quality decreases from high to more moderate levels (Fig. 1B). Larger ranges are needed to collect more variable or less abundant food. Territorial behaviour should be adopted when habitat quality drops to more moderate levels, as it may now be economically feasible for animals to defend limited food resources (Carpenter and MacMillen, 1976).

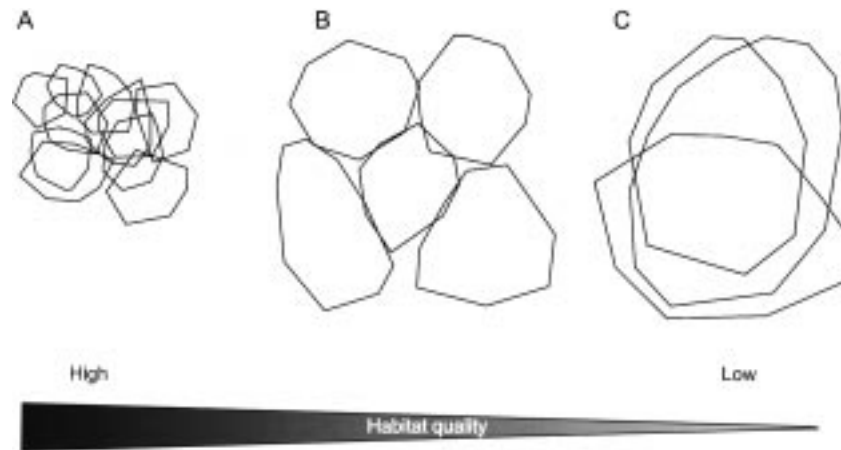


Figure 1. The spatial organization of individuals varies along a continuum according to habitat quality, which can be defined by the abundance and predictability of food resources. (A) In areas of high quality habitat, populations are characterized by high densities, small home ranges, and high home range overlap. (B) In areas of intermediate quality habitat, populations are characterized by intermediate densities, moderately sized home ranges, and low levels of home range overlap. (C) In areas of low quality habitat, populations are characterized by low densities, large home ranges, and high home range overlap.

Third, the model predicts that home ranges will continue to increase in size as habitat quality decreases from intermediate to low levels, but home range overlap will increase (Fig. 1C). In areas of lower habitat quality, animals will abandon defence of their home range as resources may be so scant or unpredictable that economically there is no benefit in defending a large territory (Carpenter and MacMillen, 1976).

Testing the model

To test the proposed model of spatial organization we compared differences in the space-use patterns of adult female brown bears from 30 populations in North America (Fig. 2) with changes in habitat quality. Brown bears are well-studied in North America: extensive data exists on the space-use patterns of numerous brown bear populations inhabiting a variety of different environ-

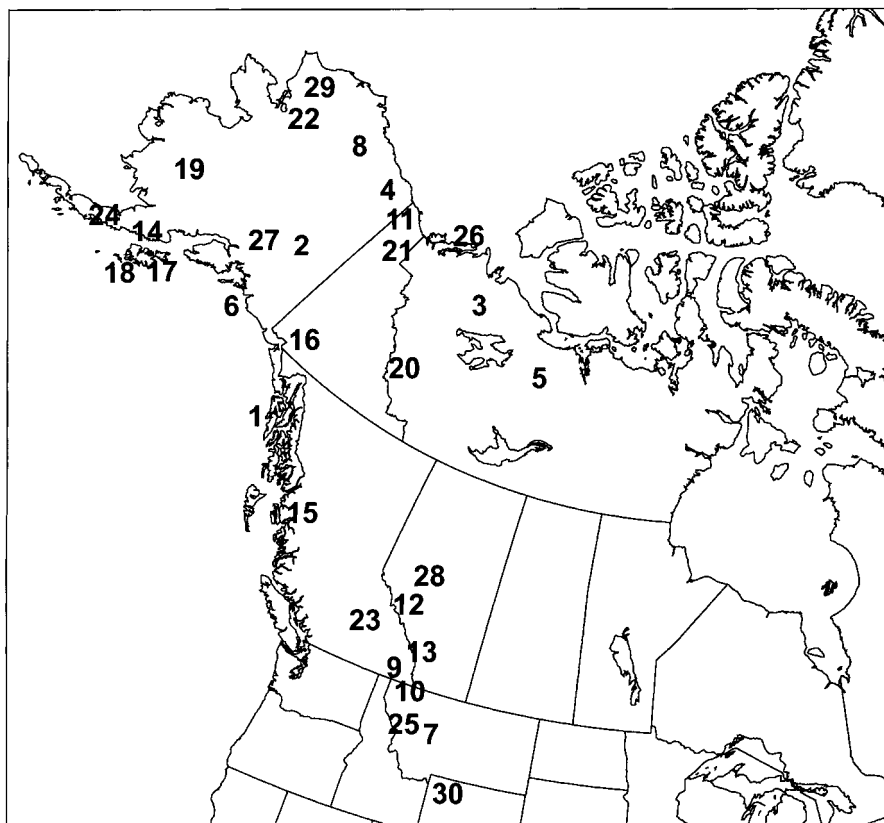


Figure 2. The location of brown bear study areas in North America (numbers as in Table 1).

ments (Table 1). Further, female brown bears are solitary and expected to be food-maximizers (Sandell, 1989). Although brown bears are generally not referred to as territorial in the strictest sense, female brown bears will vary the exclusivity of home ranges among different populations (see LeFranc *et al.*, 1987). Female brown bears have been observed to fight conspecifics and even kill the cubs of other females (McLellan, 1994). Brown bears will also mark areas of their home range through tree scratching and scent rubbing (review in LeFranc *et al.*, 1987). Here, to avoid confusion over terminology, we will not use ‘territoriality’ to describe non-random spatial organization in female brown bears; rather, we refer to ‘home range exclusivity’.

We estimated habitat quality as the seasonality of the area in which study populations were located. Seasonality, through its effects on the availability of essential resources (e.g., food, water, nutrients), is expected to exert selective pressure on life history traits (Boyce, 1979). The degree of seasonality for any given area may be defined by the relative deviation from mean annual climatic conditions (Boyce, 1978). We computed seasonality as the coefficient of variation (CV) among monthly actual evapotranspiration values (e.g., Zevuloff and Boyce, 1988; Ferguson *et al.*, 1996; Ferguson and McLoughlin, 2000). We used the Thornthwaite water balance method (FORTRAN algorithm, Willmott, 1977) of estimating actual evapotranspiration, which requires long-term temperature and precipitation records (we used 30 years), latitude, and soil water holding capacity (Willmott *et al.*, 1985). We obtained temperature and precipitation data from the nearest weather stations to brown bear study areas with climate monthly normals. For Canadian populations the data came from Environment Canada (<http://www.cmc.ec.gc.ca/climate/normals>) and for American populations the data came from state records obtained from the National Oceanic and Atmospheric Administration (orders@ncdc.noaa.gov). Soil water holding capacity estimates came from Thornthwaite and Mather (1957).

The first prediction of the model is that home range size varies positively with seasonality (i.e., home range size is at least partly determined by seasonality). To test this, we plotted the average annual range (herein after referred to as the home range) for adult females of different populations of brown bears (Fig. 2, Table 1) against measures of seasonality specific to population study areas. Home ranges were estimated using the minimum convex polygon technique (Mohr, 1947), except where otherwise indicated (Table 1). Nonlinear regression (Marquardt–Levenberg algorithm, Press *et al.*, 1986) was used to fit a curve to the data (Sigmaplot[®], Version 5.0, SPSS Inc., Chicago, Illinois). Statistical testing of the model was based on the coefficient of multiple determination (Sokal and Rohlf, 1995: 623–624).

The second prediction of the model is that home range overlap varies with seasonality in a nonlinear manner, with high overlap expected in areas of low

Table 1. The location of study areas in North America (map codes as in Fig. 2) for which densities or mean annual ranges of adult female brown bears have been calculated. Where both density and annual range estimates have been reported, *S* has been calculated. Habitat code refers to where populations were clustered by Ferguson and McLoughlin (2000): C = Pacific-coastal, I = Interior, and B = Barren-ground. A variety of methods were used to calculate density; annual ranges were primarily calculated using the minimum convex polygon technique (Mohr; 1947). Where data allowed, weighted means were used for estimates of mean annual range. Sample sizes are in parentheses

Map code	Study area	Reference(s)	Female annual range (km ²)	Adult female density (bears/km ²)	<i>S</i>	Annual primary productivity (g/m ²)	CV	Habitat code
1	Admiralty Island, AK	LeFranc <i>et al.</i> (1987); Schoen and Beier (1986, 1990); Schoen <i>et al.</i> (1986)	24 (12)	0.238	5.71	1159.6	86.6	C
2	Alaska Range	Reynolds and Hetchel (1983); Reynolds (1993)	132 (11)	0.007	0.92	722.1	135.3	I
3	Anderson-Horton Rivers, NWT	Clarkson and Liepins (1989, 1994)	1182 (14)	0.004	5.29	383.3	154.7	B
4	Arctic National Wildlife Refuge, AK	Reynolds and Garner (1987); Young and McCabe (1998)	–	0.005	–	555.0	155.7	–
5	Central NWT	P.D. McLoughlin and F. Messier, University of Saskatchewan, data on file	2577 (35)	0.001 ^a	2.03	526.4	182.4	B
6 ^b	Copper River, AK	Campbell (1985)	174 (4)	0.021	3.74	1058.8	105.2	C
7	East Front Montana	Aune and Kasworm (1989) in McLellan (1994); Aune <i>et al.</i> (1986); LeFranc <i>et al.</i> (1987)	413 (17)	0.002 ^a	0.65	926.5	101.9	I
8	Eastern Brooks Range	Reynolds (1976)	230 (8) ^c	0.002	0.41	555.0	155.7	B
9	Flathead (North), BC	McLellan (1981, 1984, 1989)	200 (5)	0.015	3.00	1077.5	102.7	I
10	Glacier National Park, MT	Martinka (1974)	–	0.003 ^a	–	999.6	103.8	–
11	Ivvavik National Park, YK	MacHutchon (1996)	149 (15) ^d	–	–	555.0	155.7	–

Table 1. Continued

Map code	Study area	Reference(s)	Female annual range (km ²)	Adult female density (bears/km ²)	S	Annual primary productivity (g/m ²)	CV	Habitat code
12	Jasper National Park, AB	Russell <i>et al.</i> (1979); LeFranc <i>et al.</i> (1987)	331 (5) ^d	0.002 ^a	0.66	1018.9	107.0	I
13	Kananaskis, AB	Carr (1989); Wielgus and Bunnell (1994)	179 (5)	0.003	0.61	1030.4	104.3	I
14	Katmai National Park (coast), AK	Sellers <i>et al.</i> (1993)	–	0.175	–	1159.6	85.4	–
15	Khutzeymateen Valley, BC	MacHutchon <i>et al.</i> (1993)	52 (13) ^d	–	–	1224.4	71.9	–
16	Kluane National Park, YK	Pearson (1975); Robert McCann, University of British Columbia, data on file	122 (54)	0.011 ^a	0.53	688.7	129.2	I
17	Kodiak Island (Terror Lake), AK	Smith <i>et al.</i> (1984) in LeFranc <i>et al.</i> (1987); Barnes <i>et al.</i> (1988); Smith and Van Daele (1990)	28 (14)	0.072	2.00	1092.4	97.3	C
18 ^b	Kodiak Island (Uyak Bay), AK	Troyer and Hensel (1964) in LeFranc <i>et al.</i> (1987); Barnes <i>et al.</i> (1988); Barnes (1990)	71 (33)	0.040	2.84	1092.4	97.3	C
19	Kuskokwim Mountains, AK	Van Daele <i>et al.</i> (1999)	398 (29)	0.011 ^a	4.33	817.2	129.0	I
20	Mackenzie Mountains, NWT	Miller <i>et al.</i> (1982)	265 (6)	0.003	0.92	838.2	139.8	I
21	Northern Yukon	Nagy <i>et al.</i> (1983a); LeFranc <i>et al.</i> (1987)	210 (8) ^e	0.007	1.57	555.0	155.7	B
22	NW Alaska	Ballard <i>et al.</i> (1993)	993 (33)	0.005	5.28	547.9	151.4	B
23 ^b	Revelstoke, BC	Woods <i>et al.</i> (1997)	73 (11)	0.011	0.77	1156.0	100.4	I

Table 1. Continued

Map code	Study area	Reference(s)	Female annual range (km ²)	Adult female density (bears/km ²)	S	Annual primary productivity (g/m ²)	CV	Habitat code
24	SW Alaska Peninsula (Black Lake)	Glenn (1975); Glenn and Miller (1980); LeFranc <i>et al.</i> (1987); Miller and Sellers (1992)	293 (30)	0.040	11.68	829.8	110.7	C
25 ^b	Swan Mountains, MT	Mace and Waller (1997, 1998)	125 (29) ^f	0.005 ^a	0.63	1123.6	102.5	I
26	Tuktoyaktuk, NWT	Nagy <i>et al.</i> (1983b); LeFranc <i>et al.</i> (1987)	670 ^e	0.001	0.75	334.7	156.1	B
27	Upper Susitna River, AK	Miller and Ballard (1980) in LeFranc <i>et al.</i> (1987); Miller and Ballard (1982); Ballard <i>et al.</i> (1982)	408 (13)	0.005	1.88	765.8	134.9	I
28	West Central Alberta	Nagy <i>et al.</i> (1988)	364 ^e	0.001	0.46	1018.9	107.0	I
29	Western Brooks Range, AK	Reynolds (1980); Reynolds and Hetchel (1984); LeFranc <i>et al.</i> (1987)	225 (35)	0.006	1.43	547.9	151.4	B
30	Yellowstone (1975–1989), WY	Blanchard and Knight (1980, 1991); Knight <i>et al.</i> (1985, 1986)	281 (48)	0.006	1.60	877.7	107.1	I

^a Minimum density estimate from marked or identifiable bears in study area.

^b Study area not presented in Ferguson and McLoughlin (2000); the same habitat code was assigned as that of the nearest study area for which Ferguson and McLoughlin conducted their analysis.

^c Estimate contains some multianual home ranges. Calculated using the modified exclusive boundary technique.

^d Weighted mean calculated from data presented.

^e Weighted means from Nagy and Haroldson (1990), data presented as midpoint between mean for females with and females without cubs. Females without cubs only for NY.

^f Calculated using the adaptive kernel method.

seasonality, no overlap (exclusivity) expected in areas of moderate seasonality, and high overlap expected in areas of high seasonality. To quantify the extent of home range overlap for females of each brown bear population we used the index of home range overlap, S , developed by Damuth (1981). We computed S as the product of the average home range size for adult females and the population density of adult females. The index represents the average number of adult females of a given population that are expected to be found in an area equal to the average home range of one adult female. Values of less than one imply spaces between the home ranges of adjacent individuals and values greater than one indicate that there is some degree of home range overlap (Damuth, 1981). S is an average and need not represent any actual configuration or distribution of individuals at any point in the environment (Damuth, 1981).

For the analysis, estimates of adult female density (bears/km²) for brown bear populations in North America were obtained from literature accounts (Fig. 2, Table 1). For several study populations we obtained adult female density from estimates of overall population density by correcting for the documented proportion of adult females in the population. Density estimates were plotted against estimates of seasonality, and nonlinear regression (as above) was used to fit a curve to the plot. To demonstrate the effects of habitat quality on home range overlap we multiplied the curve fitted to the plot of home range size *versus* seasonality and the curve fitted to the plot of adult female density *versus* seasonality (i.e., to give a plot of S *versus* seasonality).

Because seasonality and density were clearly correlated, we used partial correlation to determine whether the relationship between home range size and seasonality was genuine, rather than resulting from the fact that both home range size and seasonality are associated with density. This was necessary to separate the effects of intruder pressure/competition (density) and resource quality (seasonality) on determining home range size; our model predicts that seasonality has a nonspurious positive relationship with home range size. We tested for relationships with home range size (ln-transformed) and seasonality, but also testing with a second-order term (seasonality²) to allow for nonlinearity, while simultaneously controlling for density (ln-transformed) (SPSS Inc., 1999).

To obtain secondary confirmation of how home range overlap varies with habitat quality, populations were assigned different categories of habitat quality based on the results of a cluster analysis that grouped brown bear populations into three regions in North America (Ferguson and McLoughlin, 2000) (Fig. 2, Table 1). These regions included: (1) Pacific-coastal populations characterized by high population density and large females that live in areas of high primary productivity and low seasonality (i.e., high quality habitat), (2) interior populations characterized by moderate density and intermediate-sized

females that live in areas of moderate primary productivity and high seasonality (i.e., medium quality habitat), and (3) barren-ground (Arctic) populations characterized by low density and small bears that live in areas of low productivity and extreme seasonality (i.e., low quality habitat). According to the space-use model, we predicted home range overlap in the Pacific-coastal region, less overlap or exclusivity of home ranges in the interior region, and home range overlap in the barren-ground region. We used an analysis of covariance (ANCOVA) model to determine whether the extent of home range overlap differed between the three regions, with seasonality as a covariate. Here, home range overlap (S) was calculated directly using the method of Damuth (1981) for populations for which both average adult female home range size and adult female density were available. The model was weighted by the sample sizes used to obtain estimates of home range size when values of S were calculated (i.e., we used a weighted least-squares regression; SPSS Inc. 1999). Where no sample size was given (two cases), a sample size of one was used. Estimates of S and seasonality were \log_{10} -transformed prior to analysis to meet assumptions of normality and homogeneity of variances. Thus, log-values of S above zero implied overlap of home ranges; those below zero implied exclusivity of home ranges. Tukey's honestly significant difference (HSD) test was used to compare differences between marginal means (Zar, 1984; SPSS Inc., 1999).

Results

Information from 30 populations of brown bears in North America was available to analyse patterns of female space-use with changing habitat quality (Fig. 2, Table 1). Density estimates likely varied according to the technique used to estimate density (various mark-recapture and direct count methods were used).

Mean home ranges of adult females increased exponentially with seasonality ($r = 0.89$, $F_{2,24} = 45.2$, $p < 0.0001$; Fig. 3), but adult female density decayed exponentially with seasonality ($r = 0.80$, $F_{2,25} = 21.5$, $p < 0.0001$; Fig. 4). For simplicity, the same equation was used to fit curves to both plots as line fits were similar regardless of the type of exponential equation (number of parameters) used. Results of the partial correlation analysis indicated that \ln (home range size) was significantly correlated with seasonality ($r = 0.52$, $p = 0.009$) and seasonality² ($r = 0.52$, $p = 0.009$), while controlling for \ln (density). This supports the first prediction of the model. Home range size is positively related to seasonality (resource quality), although in a nonlinear manner (exponential), and not due to the fact that both home range size and seasonality are associated with density.

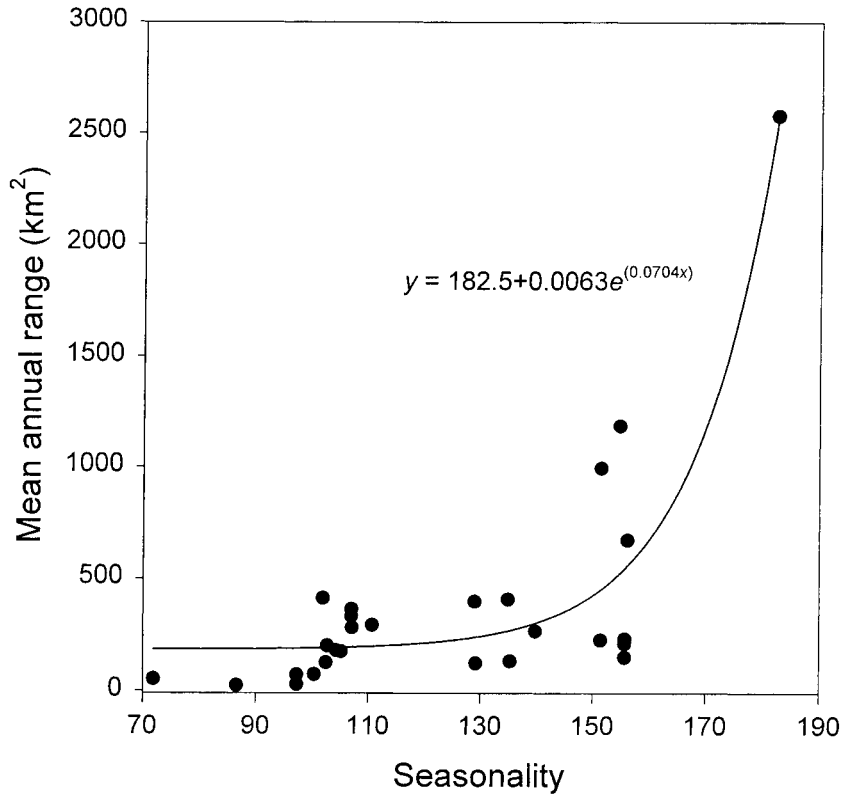


Figure 3. Mean home range (km²) of adult females for selected populations of brown bears in North America *versus* seasonality. The equation for the line is $y = y^{\circ} + a e^{bx}$, where y° is the y -intercept, a and b are constants, and e is the base of natural logarithms. Standard errors for estimated parameters are 66.89, 0.015, and 0.013 for y° , a , and b , respectively.

Home range overlap (S) related nonlinearly with seasonality (Fig. 5). Home range overlap of female brown bears was high for areas of relatively low seasonality, however, at moderate levels of seasonality (i.e., CV values of 115–140) home ranges were near exclusive (S approached 1). Above CV values of 140 home range overlap returned to higher levels. The nonlinear (U-shaped) function obtained from multiplying the curves for home range size and density (*versus* seasonality) was robust to changes in the number of parameters in the exponential equations used for curve-fitting.

Home range overlap varied among Pacific-coastal (high quality habitat), interior (intermediate quality habitat), and barren-ground (low quality habitat) populations of brown bears (ANOVA, $F_{2,22} = 7.64$, $p = 0.003$) in a manner consistent with the predictions of the space-use model (Fig. 6). Within regions, variation in home range overlap was not well-explained by changes in sea-

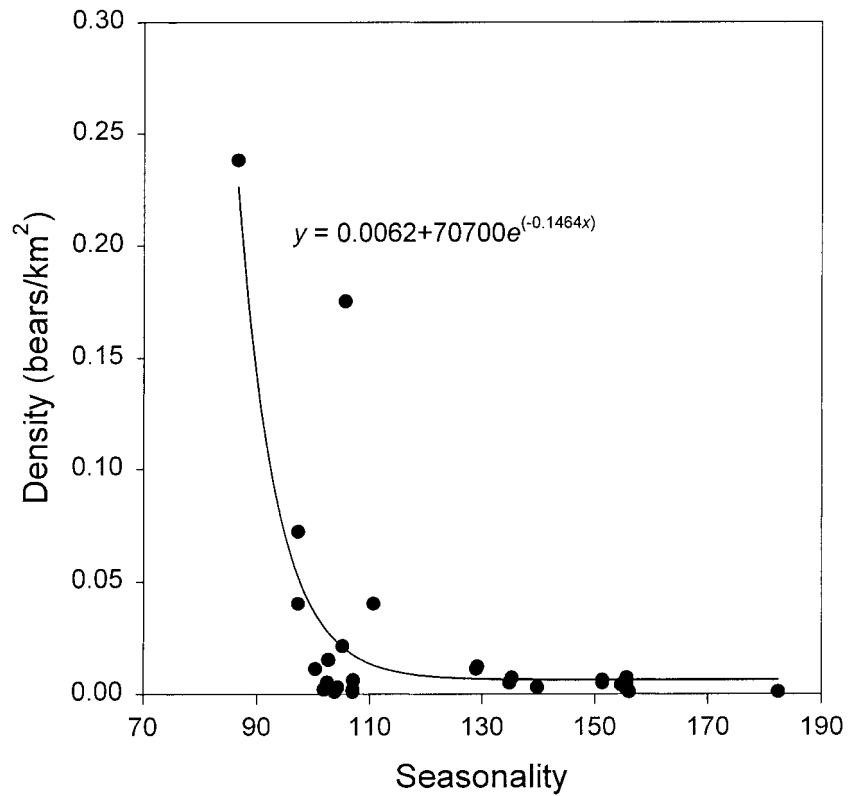


Figure 4. Density (bears/km²) of adult females for selected populations of brown bears in North America versus seasonality. The equation for the line is $y = y^{\circ} + a e^{-bx}$, where y° is the y -intercept, a and b are constants, and e is the base of natural logarithms. Standard errors for estimated parameters are 0.0092, 175500, and 0.0364 for y° , a , and b , respectively.

sonality (ANCOVA, $F_{1,21} = 0.49$, $p > 0.45$), so the covariate was removed from the analysis of variance model. Female brown bears in populations from Pacific-coastal (mean $\log_{10}(S) = 0.67$, SE = 0.15, $n = 5$) and barren-ground habitats (mean $\log_{10}(S) = 0.36$, SE = 0.12, $n = 7$) demonstrated overlap in their home ranges (Fig. 6). Marginal mean estimates of overlap between the two regions did not significantly differ (Tukey's HSD test, $p = 0.25$). In contrast, home range overlap of female brown bears of interior populations closely approached zero (mean $\log_{10}(S) = 0.026$, SE = 0.092, $n = 13$), indicating exclusivity among home ranges (Fig. 6). Marginal means of home range overlap for interior populations were significantly lower than both Pacific-coastal (Tukey's HSD test, $p = 0.003$) and barren-ground populations (Tukey's HSD test, $p = 0.09$).

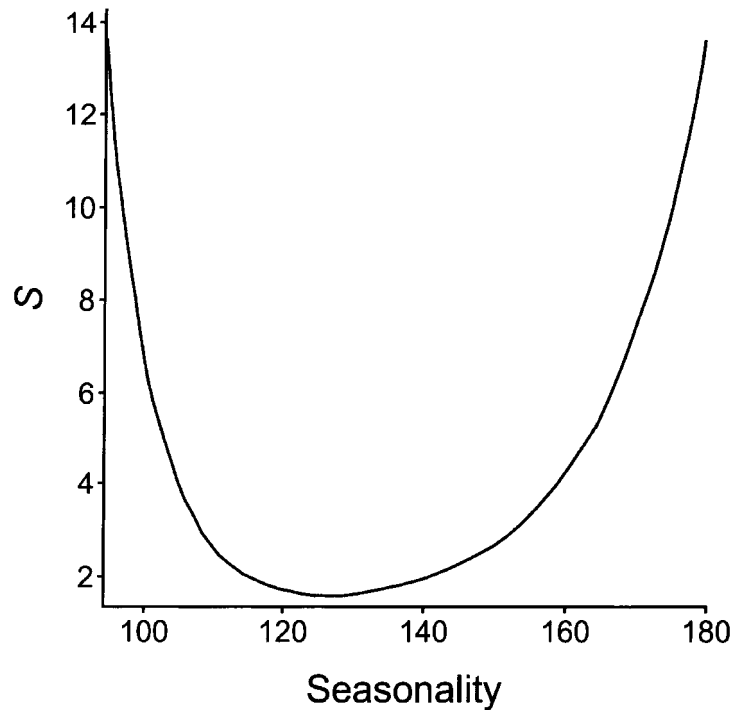


Figure 5. Index of home range overlap (S) for selected populations of female brown bears in North America versus seasonality.

Discussion

Average home range size of female brown bears was shown to vary positively with seasonality. Further, the results suggest that home range overlap in female brown bears varies with habitat quality in a nonlinear manner, with minimum overlap occurring at intermediate levels of seasonality. These results support the main predictions of our space-use model, that among populations of solitary, food-maximizing individuals: (1) average home range size will show an inverse relationship with habitat quality (note that higher seasonality equates to lower habitat quality), and (2) areas of high and low habitat quality will support individuals with relatively high home range overlap, but areas of moderate habitat quality will support individuals with relatively low home range overlap. This latter observation provides quantitative support for the territoriality models proposed by Carpenter and MacMillen (1976) and Maher and Lott (2000).

The idea that home range size is inversely related to habitat quality, where habitat quality is determined by the abundance and predictability of food, is

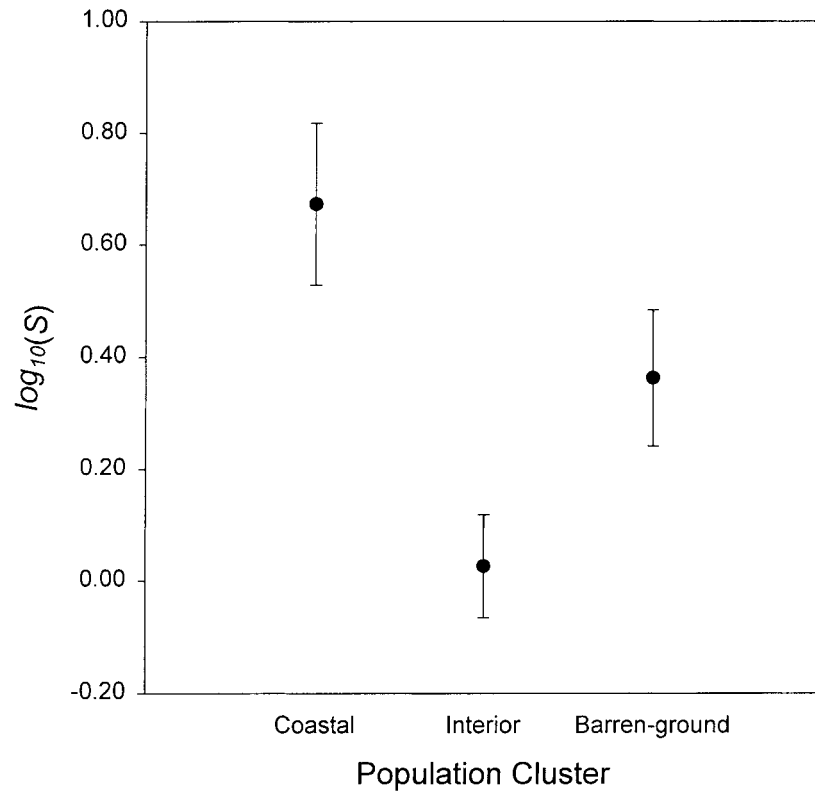


Figure 6. Marginal mean indices of home range overlap $\log_{10}(S)$ for populations of female brown bears clustered into Pacific-coastal (high-quality habitat), interior (intermediate-quality habitat), and barren-ground (low-quality habitat) populations (Ferguson and McLoughlin, 2000). Error bars indicate ± 1 SE.

not new (see McLoughlin and Ferguson, 2000). Increases in food abundance or decreases in variation in food availability may directly affect the size of home ranges by allowing individuals to obtain sufficient energy to meet life requisites over smaller areas. Increases in food abundance or predictability may also indirectly affect range size through effects on population density. Increases in population density, when food availability is high, may result in decreases in home range size through crowding or intruder pressure (Wolff, 1993).

Increases in intruder pressure may explain high home range overlap in female brown bears when food abundance and/or predictability are high (i.e., areas of low seasonality, Pacific-coastal North America). Local concentrations of high quality, predictable food resources may undermine territorial behaviours through competitor interference (Myers *et al.*, 1981). However, high regional food availability may also lead to abandonment of home range exclusivity if food becomes so abundant that defense of food resources yields

no net benefit to defending a home range (Carpenter and MacMillen, 1976; Carpenter, 1987).

The economics of food defense is also a likely explanation for why female brown bears in highly seasonal environments (i.e., barren-ground populations) also exhibit high home range overlap. When food resources are so scarce or unpredictable that defense of those food resources yields no net benefit to the home range owner, we may expect the abandonment of territorial behaviour (Carpenter and MacMillen, 1976) and thus increases in home range overlap. Similar reasoning was invoked by Maher (1994) to explain variation in spatial organization among populations of pronghorn, where males in areas of low primary productivity occupied undefended home ranges although males in other areas maintained territories. Because of high costs associated with defending home ranges in areas of high or low food availability, only at intermediate levels of food availability may defense of a home range be economically feasible. This would account for the relative exclusivity of home ranges of female brown bears at only moderate levels of resource quality (i.e., areas of moderate seasonality, interior North America). The results of this study support the qualitative predictions of the territoriality models proposed by Carpenter and MacMillen (1976) and Maher and Lott (2000).

Although we argue that home range overlap in brown bears is related to habitat quality as defined by the availability of food resources, there are alternative hypotheses to what determines exclusivity of home ranges. For example, Wolff (1997) and Wolff and Peterson (1998) suggested that female territoriality should occur in those species which have altricial young. They hypothesized that territoriality serves as a counter-strategy to infanticide from conspecific females rather than results from the distribution and abundance of food resources. Female brown bears will kill the cubs of other females (McLellan, 1994); however, the majority of published cases where female-perpetrated infanticide has been observed has been in areas where we would expect very high home range overlap (i.e., a lack of territoriality). Long-term focal studies of congregating brown bears at the McNeil River Falls in southwest Alaska, where home range overlap is likely among the highest in North America, provide three of only five published cases of female-perpetrated infanticide (McLellan, 1994). Data on infanticide in brown bears is extremely difficult to obtain due to the generally solitary lifestyle and secretiveness of bears. Higher rates of female-perpetrated infanticide may occur in areas of low home range overlap relative to areas where home ranges overlap extensively, but data necessary to test this is presently unavailable. Still, the infanticide hypothesis is not exclusive to our food availability hypothesis as the risk of infanticide may be linked to habitat quality.

It is also possible that observed patterns of home range overlap result from patterns of genetic relatedness, rather than the relative availability of food. The

hypothesis here is that high genetic relatedness undermines territorial behaviour to favour the indirect fitness of an individual through the sharing of resources with related kin. Indeed, for several areas where home range overlap is high among brown bears, such as on Kodiak Island, Alaska, genetic relatedness is also relatively high (Paetkau *et al.*, 1998). Nevertheless, we found that the correlation between home range overlap and the total expected probability of identity [$p(\text{ID})$] from 10 brown bear populations in North America (Paetkau *et al.*, 1998) was equivocal. Also, if genetic relatedness influences the exclusivity of home ranges we might expect high natal philopatry where there is high home range overlap. Schenk *et al.*, (1999), however, concluded that extensive home range overlap among female black bears in Ontario was not a consequence of natal philopatric tendencies (i.e., no relationship was found between spatial proximity of female bears and average genetic relatedness). That genetic relatedness determines the extent of home range overlap, rather than the distribution and abundance of food or habitat quality, does not appear to be supported by available evidence.

The space-use model presented here provides an example of how the environment may select for animal behaviour. Patterns of life history and behaviour may vary over space and time with environmental change. The ability to adapt life history and behavioural patterns to changes in the environment enables species to occupy wide distribution ranges and heterogeneous environments. For solitary, food-maximizing animals, our space-use model provides synthesis between models of space-use behaviour (i.e., home range size and overlap) and demonstrates how space-use may vary with changes in the environment.

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