Oecologia (1996) 108:610–616

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Environmental influences on the sexual dimorphism in body size of western bobcats

Received: 13 June 1994 / Accepted: 25 May 1996

Abstract Sexual size dimorphism might be influenced by environmental constraints on sexual selection or by intraspecific competition between males and females. We studied bobcats (*Lynx rufus*) in collections of museum specimens from western North America to examine these hypotheses. Structural body size was estimated from several measurements of the skull, ln-transformed and indexed through principal components analysis. Sexual dimorphism in body size was estimated from the difference in size index of males and females, and compared to geographic and climatic variables associated with biotic provinces (ecoregions). Of several climatic variables that were associated with bobcat body size, only seasonality of climate was associated with sexual dimorphism. Sexual size dimorphism, longitude, elevation, and seasonality were intercorrelated. As longitude decreased (moving inland from west-coastal ecoregions), sexual dimorphism decreased with the increased elevation and seasonality of continental climates of the Rocky Mountains. We suggest that increased seasonality and the need for fasting endurance by females may place constraints on the degree of sexual dimorphism in bobcats. Sexual dimorphism of body size and sexual size dimorphism of trophic structures (teeth) exhibited a strong positive association over geography, thus indirectly supporting the hypothesis that intrasexual competition for prey could account for the geographic variation in sexual size dimorphism. Thus, both environmental constraints on sexual selection of body size and intersexual competition were supported as possible explanations of the degree of sexual size dimorphism that occurs in populations of bobcats.

Key words Body size · Climate · Geography · *Lynx* · Sexual dimorphism

Introduction

Many species of mammals exhibit sexual dimorphisms in body size, with males usually significantly larger than females (Ralls 1977; but see Ralls 1976). Fisher (1958) identified two general processes that might influence such sexual dimorphisms. First, sexual selection, through female choice or competition among males for mates, might favor males of larger body size. Second, the influence of sexual selection may be opposed and balanced by mortality selection due to environmental factors. Although sexual selection may produce sexual dimorphism in body size, it might be of greater influence on the rate of evolution than on the resulting degree of sexual dimorphism (Lande 1981). Thus, the degree of sexual dimorphism in body size might depend on environmental constraints on the size of males, as Fisher (1958) suggested. Of course, non-sexual environmental selection is also expected to influence the body size of females (Arnold 1983). Environmental factors, therefore, may play a major role in determining the degree of sexual size dimorphism that occurs within mammalian populations.

Geographic patterns of body size and sexual dimorphism may yield insights into the environmental constraints that influence sexual dimorphisms. Measurements of geographic variation in body size can be made from museum specimens and compared to information about the physical environment (e.g., Rosenzweig 1968; Brown and Lee 1969; McNab 1971; Barnett 1977; Boyce 1978; Kennedy and Lindsay 1984; Nagorsen 1985; Ritke and Kennedy 1988; Owen 1989). Environmental factors that might influence sexual dimorphisms in body size include temperature, humidity, seasonality of climate, topographic relief, and competition for resources between the sexes and among species (e.g., Ralls and Harvey 1985; Dayan et al. 1989; Sikes and Kennedy 1993). For example, of abiotic environmental factors constrain the

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body size of males or females through energetic influences such as fasting endurance (Lindstedt and Boyce 1985; Millar and Hickling 1990), then geographic patterns of body size should be produced. In turn, geographic patterns of body size together with sexual selection may produce geographic patterns of sexual size dimorphism that are associated with environmental factors.

Wigginton (1992) examined geographic patterns of body size of male and female bobcats (*Lynx rufus*), and found significant variation in body size among the ecoregions of western North America. Bobcat body sizes followed Bergmann's rule, which predicts a positive association of body size with latitude and elevation. Four hypotheses were tested to explain the geographic pattern: effects of temperature (Bergmann's rule; e.g., Mayr 1956), temperature and humidity (James 1970; Aldrich and James 1991), primary productivity (Rosenzweig 1968), and seasonality of climatic variables (Boyce 1978, 1979; Lindstedt and Boyce 1985). For male and female bobcats, seasonality of climate and the modified explanation of Bergmann's rule (James 1970) based on temperature and humidity were supported as explanations for geogaphic patterns of body size. Geographic patterns of male and female body sizes were examined separately to evaluate the above hypotheses, because sex and ecoregion exhibited a significant interaction. In other words, male and female bobcats exhibited somewhat different geographic patterns of body size, in spite of the similar geographic patterns of body size and some aspects of climate. Thus, we expected that sexual dimorphism would also vary geographically among ecoregions.

The purpose of the present study was to examine geographic patterns of sexual size dimorphism of bobcats in western North America. Bobcats provided an excellent opportunity to study geographic patterns of sexual size dimorphism. They exhibit significant sexual size dimorphism within populations, with males about 6–9% larger than females in linear measurements of the skull and about 26–29% larger in body mass (Hall 1981; Wigginton 1992). We first examined whether sufficient geographic variation in sexual size dimorphism occurred to warrant further study. Next, we tried to identify a suitable index of sexual size dimorphism that would be statistically independent of geographic patterns of body size. Differences in sexual dimorphism among localities could be due to covarying changes in the body size of males and females (the effects of scale), or due to variation among localities in the relationship between male and female body sizes. We examined the variation in sexual size dimorphism that could be attributed to these two alternatives. Finally, we tested hypotheses of possible influence of geographic and climatic variables on the geographic pattern of sexual size dimorphism. We also conducted a preliminary test of resource competition between the sexes. These hypotheses indicate possible environmental constraints on male and female size, and thus on the patterns of bobcat sexual dimorphism among populations.

Methods

Bobcat skulls from 25 locations ("ecoregions," see below) in western North America were measured with digital callipers to the nearest 0.01 mm. Body size was estimated as the scores on the first component (PC1) in a principal components analysis (PCA) based on the covariance matrix of five ln-transformed linear measurements of the skull: greatest length of the skull, condylobasal length, palatal length, length of the mandible, and height of the mandible. Analyses were conducted on each of the five ln-transformed individual measurements that were used to estimate body size and on the PC1 scores, to ensure that similar patterns resulted. For brevity, only the analyses of combined measurements ("size" PC1 scores) are presented. Skull measurements might provide a more reliable assessment of body size than mass, because body mass may fluctuate seasonally. In any case, linear measurements of the body and skeleton (including the skull) are strongly correlated with mass in mammalian species (e.g., Iskjaer et al. 1989; Dobson 1992; Dobson and Michener 1995), and thus skull measurements should reasonably estimate overall animal size.

Only fully grown bobcats (2 years old or older; Crowe 1975; Jackson 1987; Wigginton 1992) were measured. Four age classes of older bobcats did not exhibit biologically significant variation

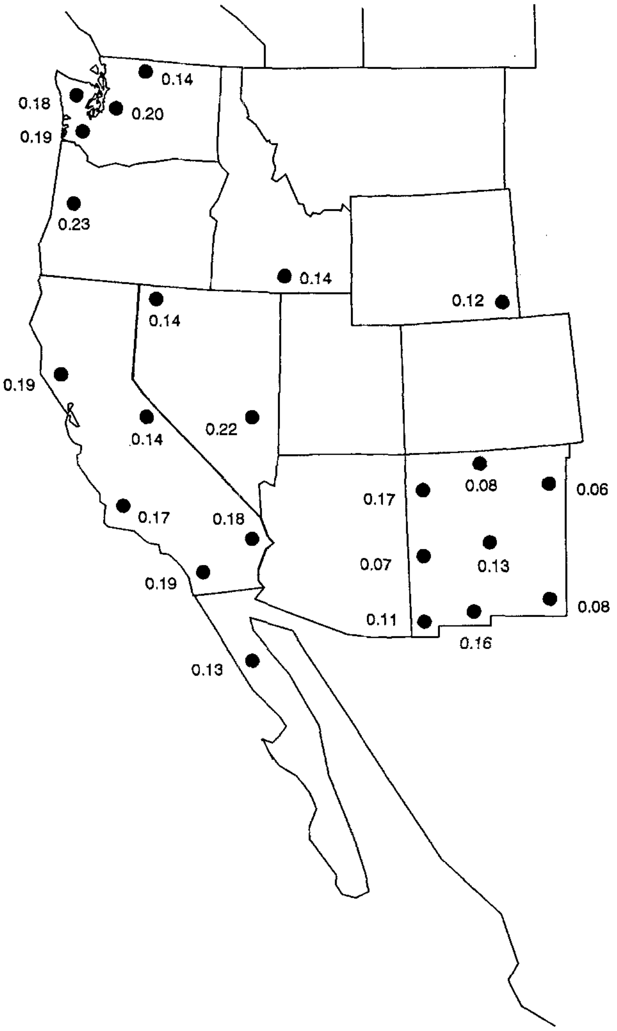

Fig. 1 Central points of ecoregions in western North America from which bobcat specimens were measured. For each ecoregion, a measure of sexual size dimorphism (mean male – mean female PC1 scores) is shown

in body size and were pooled for analyses (Wigginton 1992). Data from 501 males and 439 females were used in analyses. Further details of methods of specimen examination and aging of bobcat skulls are described by Wigginton (1992).

The size of trophic (feeding) structures of the skull was estimated as the scores on PC1 in a PCA of six measurements of the maxillary teeth and toothrow: length of the toothrow from the canine, length of the premolar and molar toothrow, length and width of the base of the canine, and length and width of the base of the carnassial. Analyses were conducted on each of the six ln-transformed individual measurements that were used to estimate the size of trophic structures and on the PC1 scores, to ensure that similar pattern resulted. For brevity, only the analyses of combined measurements ("trophic" PC1 scores) are presented.

Localities of western bobcats followed designations of ecoregions from Bailey and Cushwa (1982). Ecoregions are geographic provinces defined by climate, vegetation, and land-surface form. We used the ecoregions to define the outlines of bobcat localities. Where it was justified by large sample sizes, we divided ecoregions into convenient smaller areas to increase the number of localities. We were thus able to construct 23 localities where samples of males and females allowed estimation of sexual size dimorphism (Fig. 1).

For each ecoregion, we recorded several environmental variables. Latitude, longitudie, elevation, temperature, and morning relative humidity were taken from data compiled by the National Oceanic and Atmospheric Administration (1985a, b). Absolute humidity was estimated from temperature and relative humidity (Zimmerman and Lavine 1964). Actual evapotranspiration, an estimate of habitat productivity, was obtained from Thornthwaite Associates (1964). Latitude, longitude, elevation, and temperature for British Columbia were obtained from Hare and Thomas (1974), and for Baja California from Thornthwaite Associates (1964) and Conway and Liston (1974). Wherever possible, an average of values within a locality was used (range 1–10 values).

Monthly averages of temperature, absolute humidity, and productivity were used to calculate the coefficients of variation (CVs) of these variables. PC1 scores of a PCA of the ln-transformed CVs were used to estimate seasonality of the localities (see Wigginton 1992, for details). Analyses were conducted on each of the three ln-transformed individual CVs that were used to estimate seasonality and on the PC1 scores, to ensure that similar patterns resulted (see also Wigginton 1992). For brevity, only the analyses of combined measurements ("seasonality" PC1) scores) are presented.

Most statistical manipulations and tests were performed using the SAS Institute (1987) software programs for data analyses on microcomputer. Significance was accepted at the 0.05 level, except that when several correlations were run concurrently the 0.05-equivalent acceptance level was about 0.01 (Sokal and Rohlf 1981). PCAs were performed on covariance matrices, and linear regressions were applied. PC1 scores of skull measures should provide an adequate estimate of body size for bobcats that are highly associated with skeletal measurements and body mass (Sikes and Kennedy 1992; Wigginton 1992). A PCA of CVs of climatic variables yielded a combined estimate of seasonality (from PC1 scores) that was very highly associated with the CVs of the individual variables (temperature CV, r=0.979; humidity CV, r=0.912; productivity CV, r=0.935; all P<0.0001; Wigginton 1992). Curve fitting was done using the TableCurve software from Jandel Scientific (1992).

Results

In western North America, male bobcats averaged about 6.5% larger than females in the linear skull measurements that were used to estimate body size, and about 22% of the variation in PC1 scores of skull measurements was explained by sex (Wigginton 1992). For the estimate of body size from PC1 scores, a two-way ANOVA was used to test for significance of sexual dimorphism among ecoregions, comparing the effects of sex, ecoregions, and the interaction of sex and ecoregion. The sex-ecoregion interaction term was significant (F=2.20, df=22,880, P=0.001), as were the sex and ecoregion main effects (F=367.19, df=1,880, P>0.0001; F=28.28, df=22,880, P<0.0001; respectively). The ANOVA model accounted for 58% of the variance in PC1 scores of the bobcats.

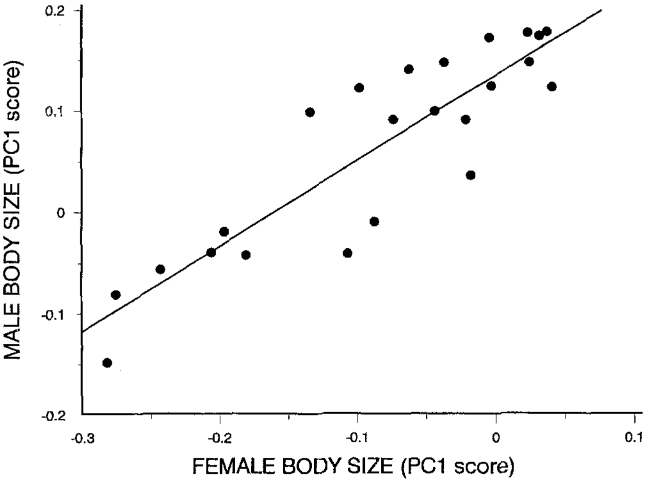

Fig. 2 For 23 ecoregions, mean male PC1 scores regressed on mean female PC1 scores. Linear regression was very close to the best fit-to-data of 3320 possible transformations of the data set. The slope of the regression line is 0.85, greater than 0, but not significantly less than 1.0

We calculated the mean "size" PC1 scores (i.e., the index of body size) for males and females in each ecoregion. Over the sample of bobcats, PC1 could account for about 93% of the variation in the five skull measurements (i.e., with sexual size dimorphism not taken into account). The mean male PC1 scores for the ecoregions were then linearly regressed on the female PC1 scores (Fig. 2). The regression was significant (F=78.54, df=1,22, P<0.0001), and mean female PC1 scores accounted for about 79% of the variance in mean male PC1 scores. The slope of the regression line was 0.85, significantly greater than 0 (t=8.86, df=1,22, P<0.0001), but not significantly different from 1.0 (t=1.63, df=1,22, P=0.11).

If the relationship of mean male and female PC1 scores were curvilinear, then a transformation of the data would be appropriate and would improve the explained variance. We made 3320 different transformations of the mean male and/or female PC1 scores for the ecoregions, and re-examined the regression of males on females (Jandel Scientific 1992). The best fit to the data was for an exponential transformation, but it resulted in only a slight (about 1%) improvement over linear regression in the variation explained by the model. Because we considered this to be a trivial amount of variation, we used the simpler linear regression model in our analyses.

We examined several possible measures of sexual dimorphism among ecoregions and their association with

Table 1 Potential measures of sexual size dimorphism of bobcats, correlations with body size (male and female PC1 scores), and deviations from a normal distribution (*W* statistic of the Shapiro-Wilk test). Means values for 23 ecoregions were examined in all tests

Estimate of sexual size dimorphism	Correlation with male PC1 scores	Correlation with female PC1 scores	Shapiro-Wilk statistic (*W*)	Significance of *W*
Males/females	–0.183	–0.142	0.59	<0.001
Males-females	0.136	–0.334	0.93	0.75
Residuals of males vs. females	0.459*	0.000	0.96	0.44
Residuals of females vs. males	0.000	0.459*	0.98	0.81

* P=.0275

Table 2 Correlations of sexual size dimorphism (male PC1 score – female PC1 score), male body size (mean PC1 score), and female body size (mean PC1 score) of bobcats, and geographic and environmental variables among 23 ecoregions. Derivations of productivity and seasonality are described in the text. Sample sizes are 23 except for samples of absolute humidity and seasonality, due to a lack of data for two ecoregions

Geographic and environmental variables	Sexual size dimorphism	Male body size	Female body size
Latitude	0.424	0.522^{*2}	0.323
Longitude	0.739^{*4}	–0.042	–0.379
Elevation	–0.592^{*2}	0.214	0.483^{*1}
Mean annual temperature	0.048	–0.520^{*2}	–0.526^{*2}
Mean annual humidity	0.138	–0.647^{*3}	–0.662^{*3}
Productivity	0.230	0.178	0.067
Seasonality	–0.455^{*1}	0.560^{*2}	0.730^{*3}

^{*1} $P \leq 0.05$, ^{*2} $P \leq 0.01$, ^{*3} $P \leq 0.001$, ^{*4} $P \leq 0.0001$

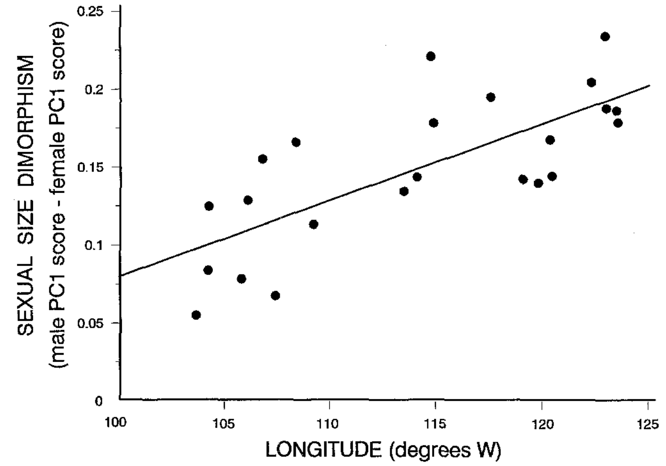

Fig. 3 Sexual size dimorphism (mean male – mean female PC1 score) regressed against longitude for 23 ecoregions. The slope of the regression line is significantly greater than 0

mean male and female body size (Table 1). The ratio of male to female PC1 scores was not significantly correlated with body size of males or females, but it was significantly non-normal. We considered using residuals from regressions of male on female PC1 scores as a sexual dimorphism index, but this measure was significantly correlated with male body size. The best index appeared to be the difference between male and female PC1 scores, because it was not significantly associated with male or female body size and it closely approximated a normal distribution. PC1 scores were derived from ln-transformed measurements, and thus the difference between males and females indicates the natural log of the ratio of male and female measurements, and ln-normal distributions of measurements (James and McCulloch 1990).

Multiple regression of latitude, longitude, and elevation on the index of sexual size dimorphism was significant, and could account for about 55% of the variation in sexual dimorphism among the 23 ecoregions (F=7.67, df=3,22, P=0.0015). The standardized partial regression coefficient of longitude on sexual size dimorphism was significant (p=0.760, df=1, t=2.36, P=0.03). This analysis examined the possible influence of longitude on sexual dimorphism with the influence of latitude and elevation held statistically invariant. The standardized partial regression coefficients for the associations of latitude and elevation, and sexual size dimorphism were not significant. By itself, longitude was highly associated with sexual size dimorphism (Table 2), and in a regression analysis could account for 55% of the variation in sexual dimorphism (Fig. 3; F=25.22, df=1,22, P<0.0001). Male bobcats did not exhibit a significant regression of body size on longitude, but the similar regression for females approached significance (Fig. 4; respectively; r^2=0.002, F=0.04, df=1,23, P=0.84; r^2=0.14, F=3.52, df=1,21, P=0.07). Female body size exhibited a slight increase as longitude decreased. Elevation and sexual size dimorphism were mildly associated, and latitude and sexual size dimorphism were not significantly associated (Table 2).

We examined the possible influence on sexual size dimorphism of four environmental variables that have been hypothesized to influence body size: temperature, humidity, productivity, and seasonality (see methods and Wigginton 1992). Multiple regression of environmental variables on sexual dimorphism was not significant, although 31% of the variation in sexual dimorphism could be accounted for by the model (F=1.69, df=4,19, P=0.20). In addition, none of the correlations between environmental variables and sexual dimorphism were significant, although the association of seasonality and sexual size dimorphism approached significance (Table

2). Longitude, elevation, and seasonality were strongly interrelated. Decreasing longitude (moving from the west coast to the Rocky Mountains) was significantly associated with increasing elevation and seasonality (r= −0.781 and −0.642, respectively; df=21, $P \leq 0.001$). In addition, elevation and seasonality were strongly associated (r=0.798, df=21, $P<0.0001$).

Finally, we conducted a PCA of six measurements of the maxillary toothrow and teeth, and used scores on PC1 as an index of the trophic structures of the skull. "Trophic" PC1 could account for 80% of the variation in the six measurements. A two-way ANOVA was used to test for significance of sexual dimorphism in trophic PC1 among ecoregions, comparing the effects of sex, ecoregions, and the interaction of sex and ecoregion. The sex-ecoregion interaction term was significant (F=1.60, df=22,698, P=0.04), as were the sex and ecoregion main effects (F=174.37, df=1,698, $P<0.0001$; F=17.58, df=22,698, $P<0.0001$; respectively). The ANOVA model accounted for 52% of the variance in trophic PC1 scores of the bobcats. We estimated geographic variation in sexual dimorphism of trophic measurements of the skull as the difference between male and female scores on trophic PC1. Sexual size dimorphism in trophic size was significantly associated with sexual dimorphism in body size (r=0.659, df=23, $P<0.001$).

Discussion

Studies of sexual size dimorphism in mammals have focused primarily on the evolutionary influence of sexual selection on body size, acting on either males or females (e.g., Ralls 1976, 1977). However, other hypotheses have been suggested (Hedrick and Temeles 1990). The alternative hypothesis that is most applicable to bobcats is the suggestion that competition between the sexes for prey could cause males and female to diverge in body size (Selander 1966, 1972; Dayan et al. 1989). We studied geographic patterns of sexual dimorphism to evaluate potential environmental constraints on sexual size dimorphism and to make a preliminary test of the idea that competition between the sexes could promote sexual dimorphism.

Our first problem was to choose a measure of sexual dimorphism. PC1 scores for males and females formed the basis for the potential measures of sexual dimorphism that were considered (Table 1). Because body size exhibits a known geographic and environmental cline that is not associated with sexual dimorphism (i.e., the association of body size with latitude and elevation; Wigginton 1992), an index of sexual dimorphism should be as independent of body size as possible. Interdependence of size and sexual dimorphism would confound patterns of differences between male and female body size with patterns of body size itself. Unfortunately, none of the possible measures of body size that we examined were completely uncorrelated with both male and female body size (Table 1). An index of sexual size dimorphism should also be normally distributed so that parametric analyses can be used. We chose the difference in mean PC1 scores between males and females as the most appropriate (i.e., least problematic) index.

Our next task was to determine whether sexual size dimorphism varied significantly among populations of bobcats in western North America. To test for sexual size dimorphism, we subjected the PC1 scores from the PCA of both males and females to a two-way ANOVA. If the difference between males and females varied among ecoregions (i.e., our localities), then the interaction term of the ANOVA should have been significant, and indeed it was. We interpret this result as indicating significant variation in sexual size dimorphism *among* ecoregions.

Differences in sexual size dimorphism among ecoregions could result from the scaling of relative differences between males and females or from independent differences in the degree of sexual size dimorphism (i.e., the residuals, or vertical distances from the points to the regression line, in Fig. 2). The ANOVA tested for absolute differences, and it was possible that relative sexual dimorphism was changing among populations that differed in average body size. If relative sexual dimorphism were scaling with body size, then a regression of male body size on female body size among ecoregions would have a slope significantly different from 1.0. The slope of this regression was about 0.85, indicating that as female body size increased, sexual size dimorphism decreased slightly. Although not significant, the decrease in sexual dimorphism with female body size undoubtedly contributed somewhat to the significant interaction term in the ANOVA.

Most of the contribution to the significant interaction term in the ANOVA should have come from the deviations of sexual dimorphism in the ecoregions away from the regression line (the residuals in Fig. 2). We found that about 79% of the variation in sexual size dimorphism among ecoregions could be accounted for by the regression, leaving 21% of the variation in the residuals. The residuals of the regression analysis represent the combined variation of measurement error, sampling error, and any geographic variation in sexual size dimorphism that was not associated with changes in female body size. It is not currently possible to further partition these sources of variation, but geographic variation was probably the primary source of contribution to the significant interaction in the ANOVA. Although this is not a direct demonstration of significant geographic variation in sexual size dimorphism, we feel that our analyses strongly suggest such variation, and it is thus reasonable to consider possible geographic and environmental associates of sexual dimorphism.

The existence of geographic variation in sexual dimorphism does not necessarily suggest a geographic cline (*sensu* Endler 1977; e.g., the cline in body size of bobcats over latitude and elevation; Wigginton 1992). If variation among local populations was due to local social conditions, like variation in the intensity of sexual selection due to random changes in sex ratio among popula-

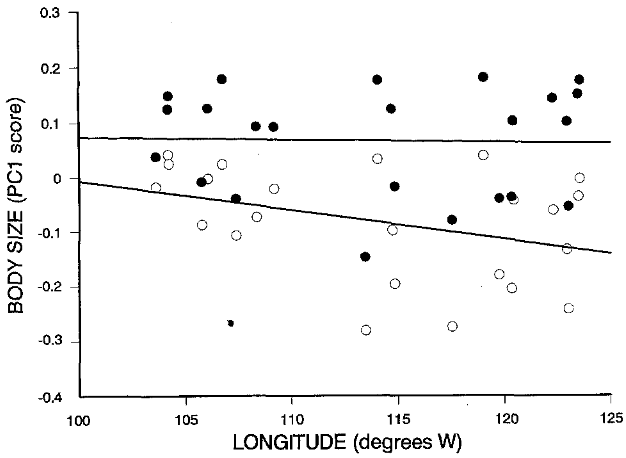

Fig. 4 Body size of male (*filled circles*) and female (*open circles*) bobcats regressed against longitude for 23 ecoregions. The *upper regression* for males is not significant, but the *lower regression* for females approaches significance

tions, then ecoregions with higher and lower degrees of sexual dimorphism might be randomly spread over western North America. Thus, we examined our index of sexual size dimorphism (mean male PC1 score minus mean female PC1 score within each ecoregion) for geographic variation. Multiple regression of latitude, longitude, and elevation with sexual size dimorphism was highly significant, but virtually all of the variation could be accounted for by regression of sexual dimorphism on longitude (Fig. 3). This geographic "cline" of decreasing sexual dimorphism towards the east was striking (Figs. 1 and 3), and highly statistically significant (Table 2). Decreasing sexual size dimorphism towards the east could be partially explained by an increase in female body size (Fig. 4).

Because males and females exhibited different geographic patterns of body size, earlier work suggested that males and females might be influenced differently by environmental factors (Sikes and Kennedy 1992; Wigginton 1992). In particular, the most significant pattern of bobcat size in western North America was for female body size to respond more strongly than male body size to seasonality of climate (also shown in Table 2). If females become larger with increased seasonality to a greater degree than males, then sexual dimorphism should decrease with increased seasonality towards the east, where higher elevations and montane continental climates occur in the interior of North America. This pattern of covariation of environmental variables and sexual size dimorphism might have produced the positive association of sexual size dimorphism with longitude, and negative associations of sexual size dimorphism with elevation and seasonality (Table 2). Such a pattern of increased female body size might be produced by constraint on the lower end of the range of body sizes through the influence of seasonality on fasting endurance (larger individuals have greater fasting endurance; Boyce 1979; Lindstedt and Boyce 1985; Millar and Hickling 1990).

Sikes and Kennedy (1993) found a significant negative association of longitude and sexual size dimorphism in bobcats of eastern North America, the opposite of the pattern in our results. They did not examine seasonality of climatic variables, but they found the lowest degrees of sexual size dimorphism in the continental climates of the great plains and Michigan. The highest degrees of sexual dimorphism were in their localities closest to the east coast of North America. Thus, sexual size dimorphism generally might be most constrained in the center of the continent. Naturally, where differences in body size between the sexes are not greatly constrained, sexual selection might be expected to produce the greatest degrees of sexual size dimorphism in polygynous and promiscuous mammals like bobcats.

An alternative hypothesis to explain geographic variation in sexual dimorphisms is that competition between the sexes for prey items varies geographically, with competition strongest near the coastal regions of North America. Sikes and Kennedy (1993) rejected a role for intersexual competition for prey as a cause of sexual size dimorphism in bobcats in eastern North America, because they did not find significant geographic variation in sexual dimorphism of cranial trophic structures (although they found significant sexual dimorphism in trophic measurements). We conducted a similar test of the possible role of competition in producing the geographic pattern in sexual size dimorphism. Unlike Sikes and Kennedy (1993), however, we found a significant pattern geographic variation in sexual size dimorphism of trophic structures that was strongly associated with the geographic pattern of sexual size dimorphism. Thus, the competition hypothesis was indirectly supported through our failure to reject its prediction that the geographic pattern of sexual dimorphism should be similar in body size and trophic structures.

In addition to influences of intraspecific competition on sexual size dimorphism, interspecific competition could be influential in bobcats. Interspecific competition might explain why female body size increased from coastal regions eastward into the middle of the continent. Bobcats, however, probably do not overlap greatly in major diet items with other cat species within their range (bobcats are generalist predators on small mammals and birds; Hall 1981). Lynx (*Lynx canadensis*) are a major predator of snowshoe hare, but the geographic range of lynx does not overlap with most of the range of western bobcats. Mountain lions (*Puma concolor*) have extensive range overlap with bobcats in western North America, but mountain lions are much larger than bobcats and likely take larger prey items. Smaller possible competitors, such as weasels, also are very different from bobcats in body size (unpublished data, compared to measurements in Dayan et al. 1989; see also Hall 1981). Currently, variations in seasonality associated with fasting endurance appear to be a better supported explanation of the change in size of female bobcats with longitude and elevation.

Acknowledgements Several curators and their institutions allowed JDW to examine and measure bobcat specimens, and we thank them for their good help: V. Rick McDaniel, Collection of Recent Mammals, Arkansas State University; Philip Myers, Mammal Division, Museum of Zoology, University of Michigan; Robert M. Timm, Museum of Natural History, University of Kansas; Eric A. Rickart, Utah Museum of Natural History, University of Utah; Ellen B. Kritzman, Slater Museum of Natural History, University of Puget Sound; John Rozdilsky, University of Washington-Washington State Museum, University of Washington; Richard J. Cannings, Cowan Vertebrate Museum, University of British Columbia; Barbara R. Stein, Museum of Vertebrate Zoology, University of California, Berkeley; Stephen F. Bailey, California Academy of Sciences; Sarah B. George, Natural History Museum of Los Angeles County; Amadeo Rea, San Diego Natural History Museum; William L. Gannon, Museum of Southwestern Biology, University of New Mexico; Robert D. Fisher, United States National Museum of Natural History. We also thank M.S. Boyce, C. Guyer, G.R. Hepp, D.L. Schultz, and M.C. Wooten for insightful discussions and ideas. T. Mack introduced us to the TableCurve software, and performed the curve-fitting procedures. C. Guyer, G.R. Hepp, G.J. Kenagy, and M.C. Wooten read and made insightful comments and suggestions on earlier drafts of the manuscript. The Alabama Agricultural Experimental Station funded analysis and manuscript preparation (AAES and Journal No. 15-933490).

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