Animal Conservation (2002) **5**, 317–324 © 2002 The Zoological Society of London
DOI:10.1017/S1367943002004079 Printed in the United Kingdom

Ecological and allometric determinants of home-range size for mountain lions (*Puma concolor*)

M. M. Grigione[1], P. Beier[2], R. A. Hopkins[3], D. Neal[4], W. D. Padley[5], C. M. Schonewald[6] and M. L. Johnson[7]

[1] Department of Environmental Science and Policy, University of South Florida, 4202 East Fowler Ave, SCA 238, Tampa, FL, 33620, USA
[2] School of Forestry, Northern Arizona University, Flagstaff, AZ 86011–5018, USA
[3] Live Oak Associates, Inc. 6830 Via del Oro, Suite 205, San Jose, CA 95121
[4] 6357 North Teilman Ave, Fresno, CA 93711, USA
[5] Box 41036, San Jose, CA 95160, USA
[6] Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA
[7] John Muir Institute of the Environment, University of California, Davis, One Shields Ave, Davis, CA 95616. 530–752–8837.

(Received 15 December 2001; accepted 24 July 2002)

Abstract

We examined how several ecological factors influenced home-range size for 57 mountain lions inhabiting three regions of California. Our specific objectives were to investigate: (1) the relationship between home-range size and sex, age and reproductive status; (2) how broad-scale habitat differences and prey relative abundances influenced home-range size; (3) how seasonality, within these habitats, affected home-range size; (4) whether there was a significant relationship between body mass and home-range size. Results indicate that the effects of season on home-range size influenced the study areas differently. Both intrinsic factors, such as sex and body mass, and extrinsic factors, such as deer relative abundance and study site, influenced home-range size for mountain lions in this analysis. Linear relationships, however, between body mass and home-range size were not evident for any of our study locations. Curvilinear relationships, in contrast, existed between body mass and home-range size for all study areas during particular seasons, influenced strongly by animal sex. Conservation strategies designed to protect mountain lions and their habitats should reflect the above balance between intrinsic and extrinsic factors which influence home-range size.

INTRODUCTION

Mountain lions (*Puma concolor*) are distributed throughout much of California, including the Sierra Nevada mountains, Coastal Ranges, eastern Sierran deserts and suburban areas. Despite our extensive knowledge about mountain lion ecology and natural history (Hornocker, 1969; Seidensticker *et al.*, 1973; Shaw, 1980; Hemker, Lidnzey & Ackerman, 1984; Logan & Irwin, 1985; Van Dyke *et al.*, 1986; Sweanor, 1990; Ross & Jalkotzy, 1992; Spredbury *et al.*, 1996), we know little about how ecological factors influence home-range size for mountain lions and whether they can be used to predict home-range size. In this regard, there have been no attempts to explain broad-scale patterns of mountain lion ecology by comparisons made across ecosystems.

Therefore, in this study, we attempted to identify the ecological factors that influence home-range size of 57 mountain lions across three distinct habitats in California. Identifying three variables across ecosystems will elucidate the extent to which home-range patterns are driven by ecosystem-level influences (e.g. prey abundance, climate, location) and/or by animal-specific factors (e.g. sex, body mass, age, reproductive status) that are independent of ecosystem.

We also assessed the usefulness of allometry in predicting home-range size of mountain lions. Allometric equations demonstrate whether a linear relationship exists between body mass and variables such as home-range size, and can be used to predict certain features of an organisms' life history and ecology that cannot be easily measured (Kozlowski & Weiner, 1997). This is particularly appealing for species, such as mountain lions, whose ecological requirements are difficult to measure.

By using radio-telemetry data, we assessed the relationship between body mass and home-range size within and among distinct ecological regions. Our specific objectives were to investigate: (1) the relationship between home-range size and sex, age and reproductive status; (2) how broad-scale habitat differences and relative prey abundances influenced home-range size;

All correspondence to: M. M. Grigione. Tel: 813–974–7459; Fax: 813–974–2184; E-mail: mgrigion@chumal.cas.usf.edu.

(3) how seasonality within these habitats influenced home-range size; (4) whether there was a significant relationship between body mass and home-range size.

The identification of ecosystem-level (extrinsic) and animal-specific (intrinsic) variables that influence home-range size of mountain lions will provide biologists and wildlife managers with a powerful tool to predict where and the extent to which areas can be utilized by mountain lions. To our knowledge, this approach in which we attempt to explain broad-scale patterns of mountain lion ecology by comparisons made across ecosystems has not previously been attempted.

STUDY AREA

Radio-telemetry data were obtained from three regions of California (Fig. 1), including the Diablo Range (Hopkins, Kutilek & Shreve, 1986; Hopkins, 1989), the Santa Ana Mountains (Padley, 1990; Beier & Barrett, 1993; Beier, 1995), and the central Sierra Nevada mountains (Neal, 1990; Loft, 1992). The data were collected from 1983 to 1993. In the Santa Ana Mountains, Padley (1990) began data collection from 1986 to 1989 and Beier & Barrett (1993) continued to monitor the population in 1988–93. The three populations occupied two distinct habitats: low-elevation, chaparral–oak woodlands in the Coastal Range ecosystems of the Diablo Range and the Santa Ana Mountains, and high-elevation mixed-conifer ecosystems in the central Sierra Nevada (Tables 1 and 2). Seasonality in the Coastal Range mountains is less pronounced that in the Sierra Nevada and snowfall is uncommon in the Coastal Range mountains. The primary prey for mountain lions in both habitats, mule deer (*Odocoileus hemionus*), are not migratory in the Coastal Ranges, but are in the Sierra Nevada.

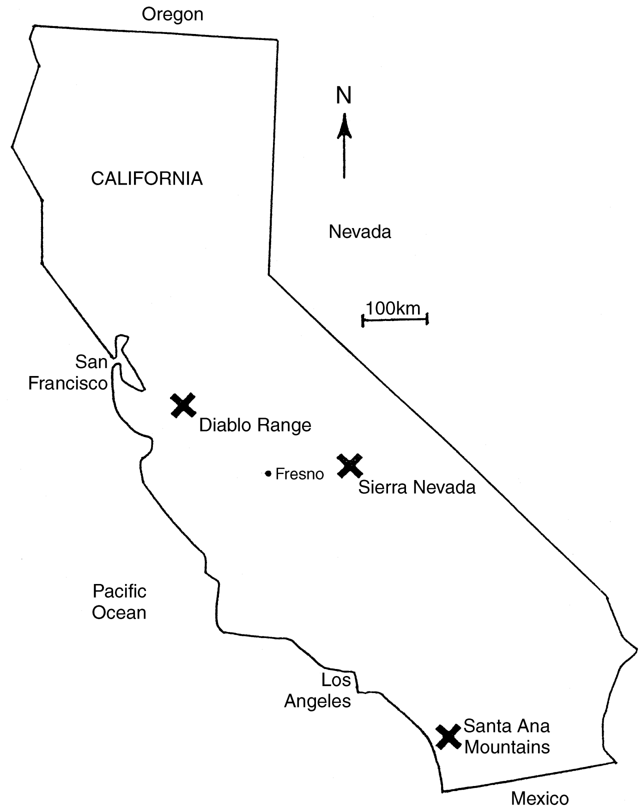

Fig. 1. Map of three study areas in California

Diablo Range

The Diablo Range is located 20 km east of San Jose, California (Fig. 1). The study area (1850 km^2) included portions of Santa Clara, Merced, Stanislaus, San Joaquin and Alameda Counties. Radio-telemetry data were

Table 1. Study area summary

Habitat characteristics	Diablo Range	Santa Ana Mountains	Sierra Nevada
Habitat type	Oak woodland, chaparral	Chaparral, oak woodland, riparian, grasslands, orchards, mixed-conifer	oak woodland, mixed conifer
Elevation	300–1000 m	sea level to 1690 m	244–4000 m
Snowfall	rare	rare	common
Road density	0.00119 m/m^2	0.00196 m/m^2	0.00073 m/m^2
Deer movements	non-migratory	non-migratory	migratory
Alternative prey	wild pig, cattle	cattle, coyotes	small mammals, cattle
Land activities	hike, hunt, grazing	hike, hunt, grazing, logging, military	hike, hunt, grazing, logging

Table 2. Mountain lion summary

Population characteristics	Diablo Range	Santa Ana Mountains	Sierra Nevada
Sample size	$N = 9$	$N = 18$	$N = 30$
(male/females)	(3/6)	(2/16)	(11/19)
Body mass (kg)			
Male: min/max/mean (± SE)	50/59/54 (± 2.6)	54/56/55 (± 1.0)	41/68/53 (± 2.4)
Female: min/max/mean (± SE)	36/38/36.3 (± 0.33)	32/47/39 (± 1.2)	18/50/32.4 (± 2.0)
Age (years)			
Male: min/max/mean (± SE)	4/8/6 (± 0.58)	6/7/6.5 (± 0.5)	1/8/3.7 (±0.52)
Female: min/max/mean (± SE)	4/9/6.4 (± 0.61)	1/13/7 (0.66)	<1/7+/2.6 (± 0.42)

obtained for 18 mountain lions from March 1984 to June 1989. Mountain lions were located on the ground and aerially using standard triangulation techniques (Mech, 1983), with no more than one location/day/lion used for all home-range analyses. All locations were recorded as Universal Transverse Mercator (UTM) points. A minimum of 30 locations per season for each animal was used to generate home-range estimates using the 95% minimum convex polygon method (MCP; Mohr, 1947); 2184 daily locations were used to compute the home ranges for four adults males, four sub-adult males, eight adult females and two female cubs (n = 18). Seasonal home-range data were available for nine mountain lions. Hence, only these animals were used for our analyses.

Santa Ana Mountains

Radio-telemetry data on 18 mountain lions were collected from January 1987 to February 1993 in the Santa Ana Mountains and surrounding lands, including portions of Los Angeles, Orange, San Bernardino, Riverside and San Diego Counties (Fig. 1). The study area (2070 km^2) was bounded by three highways and the Pacific Ocean. Radio-telemetry readings from the ground occurred every 1–4 days, usually (85%) during daylight hours. Eighty-one percent of radio-locations were from ground-based triangulation. Radio-locations were obtained from the ground using standard triangulation techniques (Mech, 1983) conducted by a single observer. Because only a single observer was used, location errors were minimized by using only azimuths that differed by 60°–100° and by getting close to the animal (White & Garrott, 1990). Seventy-six percent of locations were determined from within 500 m of the focal animal, and 87% from within 1 km. The remaining 19% of locations were obtained by aerial homing from fixed-wing aircraft from flights conducted approximately once every 10 days during daylight. All locations were recorded as UTM points. Individuals were monitored for over 160 days per season. Home ranges, using the 95% MCP method, were computed for all animals, each with greater than 45 locations per season (Mohr, 1947).

Sierra Nevada mountains

This study area encompassed 2072 km^2 in eastern Fresno County, mostly within the Sierra National Forest (Fig. 1). Radio-telemetry data were collected for 30 mountain lions from August 1983 to April 1992. Data were collected daily from the ground and by aerial flights once per week. Radio-locations were obtained from the ground using standard triangulation techniques (Mech, 1983). All locations were recorded as UTM points. Seasonal home-range sizes were estimated by using the 95% MCP Method (Mohr, 1947). The animals used for the home-range analysis had a minimum of 25 locations per season and a maximum of 135 locations per season.

METHODS

All statistical analyses were performed using the *Number Cruncher Statistical System* (*NCSS*, 1996). We investigated home-range size for summer or dry season (May–October) and winter or wet season (November–April). We also analysed body mass and home-range size by sex for the Sierra Nevada and for the Coastal Range studies combined. 'Coastal Range' studies are comprised of the Diablo Range and the Santa Ana Mountains.

Seasonality and home-range size

Two-tailed paired t-tests ($\alpha = 0.05$) were performed for each data set to determine whether there was a significant effect of seasonality on mountain lion home-range size. The data were divided into two seasons for each study: winter and summer. If a pronounced seasonal effect existed, then two separate analyses were performed, one for each season.

Multivariate analysis

Stepwise multiple regressions (adjusted alpha = 0.0125) were run for all study sites during each season to explain for variation associated with home-range size. The regression model included body mass, sex (female = 1, male = 2), reproductive status (reproductive = 1, non-reproductive = 2), age (0–2) = 1, (2–4) = 2, (4+) = 3 and study site (Sierra Nevada = 1, Santa Ana Mountains = 2, Diablo Range = 3). We also incorporated deer relative-abundance estimates (low = 1; medium = 2; high = 3) into the regression based on deer density estimates from each study area (Sierra Nevada = 2 deer/2.59 km^2; Santa Ana = 6 deer/2.59 km^2; Diablo = 25 deer/2.59 km^2; for deer density estimates, see Hopkins, 1989; Neal, 1990; Beier & Barrett, 1993). Relative-abundance estimates for alternative prey were not readily available for our study areas (Table 1). Ln transformations were used to normalize the distribution of the data.

Intraspecific allometry

To test for an allometric relationship between body mass and home-range size, we calculated Ln(home-range size) and Ln(body mass) and ran 15 simple linear regressions incorporating these variables. These regressions included both winter and summer home ranges for each study (i.e. Sierra Nevada, Diablo, Santa Ana), all studies combined, and coastal studies combined (Diablo and Santa Ana). Combined winter and summer home-range data were unavailable for the Sierra Nevada study. In order to reduce the probability of committing a Type I error due to multiple linear regressions, we utilized the sequential Bonferroni's adjustment. Therefore, significant regressions for each individual test were accepted at $\alpha = 0.0033$.

If an allometry pattern was not evident and the residuals analysis indicated a non-linear trend, such as a second-degree polynomial fit, we performed non-linear regressions of body mass vs. home-range size to test whether a non-linear fit was more appropriate. Five non-linear regressions were performed (adjusted $\alpha = 0.01$) after the data were Ln transformed. These consisted of (1) winter and summer regressions for the Diablo range; (2) winter and summer for the Santa Ana Mountains during the years 1988–93; (3) winter for the Sierra Nevada. The most parsimonious non-linear model having the highest r^2 value was fit to the data.

Lastly, we assessed the relationship between body mass and home-range size by conducting linear regressions between home-range size (dependent variables) and the residuals of the following variables: location, sex, age, deer relative abundance – excluding body mass. The r^2 values from these linear regressions would indicate the extent to which body mass explains variation in home-range size after all other independent variables were removed.

RESULTS

The effect of season on home-range size influenced the study areas differently. Mountain lions in the Sierra Nevada ecosystem had larger home ranges in summer and smaller home ranges in winter. In general, mountain lions in the Coastal Ranges exhibited smaller home ranges in summer and larger home ranges in winter. Both intrinsic (i.e. sex and body mass) and extrinsic factors (i.e. deer relative abundance and study site) influenced home-range size. Linear relationships between body mass and home-range size were not evident in any of our study locations. Curvilinear relationships, in contrast, existed between body mass and home-range size for all of the study areas during particular seasons.

Seasonality and home-range size

Home-range size in each ecosystem changed seasonally. Animals in the Sierra Nevada mountains had significantly larger home ranges in summer, while Coastal Range animals had larger home ranges during winter. When Coastal Range studies were combined, winter home-range size was larger than summer home-range size (Table 3). Specifically, females had an average home-range size of 90 km^2 in summer and 100 km^2 in winter. Males had an average of 300 km^2 (summer) and 350 km^2 (winter). When Coastal Range studies were analyzed separately, mountain lions in the Santa Ana Mountains monitored from 1986 to 1989 were the only ones to exhibit significant home-range size changes, with winter home ranges being larger than summer ones (Table 3).

In contrast to the Coastal Range sites, animals in the Sierra Nevada mountains had significantly larger home ranges during summer and winter (Table 3). The average home-range size for females and males was 541 km^2 and 723 km^2 in summer and 349 km^2 and 469 km^2 in winter, respectively.

Multivariate analysis

Multiple regressions, including body mass, age, sex, deer relative abundance and location, were run for all studies combined, grouped by season. The winter season regression indicated that sex, body mass and location signifi-

Table 3. Two-tailed, paired *t*-tests to determine the effects of seasonality (dry/wet seasons) on mountain lion home-range size for each study and Coastal Range studies, combined ($\alpha = 0.05$)

Location	Mean home-range size (ha)	*t*-value	DF	Prob. level	*N*
	Summer/winter				Summer/winter
Santa Ana 1988–93	17,930 (± 4743): 17,509 (± 5250)	1.00	9	0.345	10/11
Santa Ana 1986–89	6555 (± 961): 9020 (± 320)	–2.95	5	0.031	7/6
Diablo Range	14,011 (± 2592): 16,644 (± 2693)	–1.33	8	0.219	9/9
Sierra Nevada	60,808 (± 6063): 39,329 (± 5478)	6.43	29	0.000	30/30
Coastal Range studies combined	13,511 (± 2178): 15,251 (± 2438)	1.82	24	0.080	26/26

Table 4. Stepwise multiple regressions for all studies (combined), Coastal Range studies and Sierra Nevada study, during wet and dry seasons (adjusted $\alpha = 0.0125$)

Study	Sample size	Season	Regression equation	Independent variable*	Prob. level	r^2
All studies	56	winter	$Y = 13 - 1.2(\text{Ln(body mass)}) \pm 1.2\ (\text{sex}) - 0.22\ (\text{location})$	Ln(body mass)	0.00	0.52
				sex	0.00	
				location	0.00	
	56	summer	$Y = 14 - 1.2(\text{Ln(body mass)}) - 0.35\ (\text{location})$	Ln(body mass)	0.00	0.71
				sex	0.00	
				deer	0.00	
Coastal Ranges	26	winter	$Y = 7.6 + 1.2\ (\text{sex}) + 0.34\ (\text{reproductive status})$	sex	0.00	0.70
				reproductive status	0.04	
	26	summer	$Y = 7.9 + 1.2\ (\text{sex})$	sex	0.00	0.48
Sierra Nevada	30	winter	$Y = 13.9 + 1.5\ (\text{sex}) - 1.6(\text{Ln (body mass)})$	sex	0.00	0.42
				Ln(body mass)	0.00	
	30	summer	$Y = 13 - 0.99(\text{Ln(body mass)}) + 0.94\ (\text{sex})$	Ln(body mass)	0.01	0.31
				sex	0.00	

*Sex (male = 1, female = 2); location (Diablo Range = 1, Santa Ana = 2, Sierra Nevada = 3); reproductive status (repro = 1, non-repro = 2).

cantly influenced home-range size. For the summer season, sex, body mass, location and deer relative abundance significantly affected home-range size (Table 4).

Adding 'reproductive status' to our multiple regressions enabled us to make a distinction in home-range size between females with young and those without young. However, these data were only available for Coastal Range studies. For the Coastal Ranges, during both winter and summer, animal sex significantly influenced home-range size. During winter, reproductive status influenced home-range size, but not significantly (Table 4).

A multiple regression for the Sierra Nevada animals included body mass, age and sex. Deer relative abundance could not be included within the analysis because the abundance estimate for just one study area had zero variance. For both winter and summer, animal sex and body mass significantly influenced home-range size (Table 4).

A correlation matrix was developed to detect associations between life-history variables and study areas (Table 5). In Coastal Range studies (i.e. Diablo Range and Santa Ana Mountains), we observed significant correlations between sex–body mass and deer relative abundance–location. These correlations were due to males weighing more than females and deer densities in the Diablo Range being much greater than in the Santa Ana Mountains. In the Sierra Nevada both sex–body mass and age–body mass were correlated. These correlations were due to male mountain lions weighing more than females. Also, age and body mass were correlated in the Sierra Nevada because all age classes 1–3 (i.e. from < 1 to 7 years) of mountain lions were represented, with different classes having very different body masses. For all studies combined, both sex–body mass (i.e. males weighing more than females) and age–location were correlated. Age and location were correlated because, unlike the Sierra Nevada with an even split of mountain lion ages, the Coastal Range studies had predominantly older mountain lions from classes 2 and 3 (i.e. from 4 to 13 years; Table 2).

Intraspecific allometry

Linear relationships between Ln(home-range size) and Ln(body mass) were not observed at any of our study sites (Table 6). The explanatory power was low, as only one r^2 value was below 0.50. An analysis of residuals indicated that the residuals were not normally distributed and therefore the assumption of a linear

Table 5. Pearson correlation matrix for Coastal Range, Sierra Nevada and all studies, combined*

Coastal ranges	Ln(body mass)[1]	Location[2]	Sex[3]	Status[4]	Age[5]	Deer[6]
Ln(body mass)	1	–0.03	0.82	–0.33	0.08	0.08
Location	–0.03	1	–0.15	–0.05	0.04	–0.89
Sex	0.82	–0.15	1	–0.28	0.20	0.27
Status	–0.33	–0.05	–0.28	1	0.25	0.12
Age	0.08	0.04	0.20	0.25	1	0.29
Deer	0.08	–0.89	0.27	0.12	0.29	1
*Cronbachs alpha = 0.14						
Sierra Nevada	Ln(body mass)		Sex		Age	
Ln(body mass)	1		0.71		0.65	
Sex	0.71		1		0.22	
Age	0.65		0.22		1	
*Cronbachs alpha = 0.60						
All studies	Ln(body mass)	Location	Sex		Age	Deer
Ln(body mass)	1	0.11	0.68		0.51	0.11
Location	0.11	1	–0.22		0.55	0.22
Sex	0.68	–0.22	1		0.03	–0.01
Age	0.51	0.55	0.03		1	0.48
Deer	0.11	0.022	–0.01		0.48	1
*Cronbachs alpha = 0.19						

[1] Kg
[2] Location (Diablo Range = 1, Santa Ana = 2, Sierra Nevada = 3)
[3] Sex (male = 1, female = 2)
[4] Reproductive status (repro = 1, non-repro = 2)
[5] Age (0–2 yrs = 1, 2–4 yrs = 2, 4+ yrs = 3)
[6] #/km^2

Table 6. Linear regressions of Ln(home-range size) vs. Ln(body mass) for four studies during wet and dry seasons (alpha = 0.003)

Location	Season	Regression model	Prob. level	Power (5%)	r^2
Santa Ana Mountains 1988–93	winter	$Y = -1.0 + 2.8X$	0.01	77%	0.50
	summer	$Y = 1.7 + 2.1X$	0.06	49%	0.37
Santa Ana Mountains 1986–89	winter	$Y = 9.1 - 0.1X$	0.70	6%	0.03
	summer	$Y = 10.1 - 0.39X$	0.78	6%	0.02
Diablo Range	winter	$Y = 5.6 + 1.1X$	0.17	26%	0.25
	summer	$Y = 1.6 + 2.0X$	0.08	43%	0.38
Sierra Nevada	winter	$Y = 11 - 0.10X$	0.77	6%	0.00
	summer	$Y = 11 - 8.2X$	0.79	5%	0.00

relationship between body size and home range was not met. A curvilinear relationship existed between the dependent and independent variables. Specifically, this relationship existed for both the Santa Ana Mountains (1988–93) and for the Diablo Range during both winter and summer, and for the Sierra Nevada during winter. Therefore, second-degree polynomials were fit to these data.

Results of these non-linear regressions greatly improved r^2 values for three out of the five models above (Table 7). For the Santa Ana Mountains (1988–93), r^2 values changed from 0.50 to 0.78 for winter and from 0.37 to 0.82 for summer (Table 7). Similarly, in the Diablo Range, r^2 values for winter increased from 0.25 to 0.71 (Table 7). Even though r^2 values in the Sierra Nevada were not significant, an increase occurred from 0.00 to 0.14 during winter and from 0.00 to 0.16 in the summer (Table 7).

Lastly, to investigate the relationship between body mass and home-range size further, we conducted a final residual analysis where residuals of all independent variables except body mass were regressed against home-range size. Once the effects of all independent variables were removed, the contribution of body mass to home-range size was approximately $r^2 = 0.50$ for each season. Specifically, for all studies combined, linear regressions between Ln(home-range size) and the residuals from all independent variables (i.e. location, sex, age, deer relative abundance) excluding Ln(body mass) indicated r^2 values of 0.337 (summer) and 0.50 (winter).

DISCUSSION

Mountain lions in this study inhabited two very different ecological systems: the Coastal Ranges adjacent to the Pacific Ocean and the inland Sierra Nevada mountains. Home-range size for mountain lions in each of the ecosystems changed seasonally. The Sierra Nevada mountain lions had significantly larger home ranges in summer while the Coastal Range animals had larger home ranges in winter.

The most pronounced effect of seasonality on home-range size occurred in the Sierra Nevada study area during winter. Mule deer concentrated in low-elevation valleys and, consequently, mountain lions reduced their home ranges. In contrast, during summer when deer migrated to higher elevations and dispersed, mountain lions expanded their home ranges accordingly. From this pattern, it becomes clear that mountain lion home ranges are influenced by prey abundance and also by the distribution of prey through time, especially when a particular prey is a primary food source (Sandell, 1989). The seasonality in the Sierra Nevada undoubtedly influenced deer distribution. These prominent changes in deer distribution were exerting a major influence on mountain lion home-range size in this study area.

In the Coastal Ranges, climate was more moderate and seasonal differences in home-range size were not pronounced. In fact, the only significant difference in home-range size between seasons occurred in the Santa Ana Mountains during the summer of 1989, when six female mountain lions experienced a reproductive peak. During this summer, home ranges were substantially reduced for these females because they were either producing litters or behaving as if they had produced litters. Home range for these females expanded during the following season, as revealed by the home-range data for 1990.

Multiple regressions for all study sites combined enabled us to tease apart the relative influences of extrinsic factors (such as location, seasonality, deer relative abundance) and intrinsic factors (body mass, sex, age, reproductive status) on home-range size. During the summer, sex, body mass, location and deer relative abundance were statistically significant predictors of mountain lion home-range size. During the winter, sex, location and body mass were significant predictors of home-range size. Location-related differences in home-range size during both seasons were due in large part to the vast seasonal changes in home-range size that occurred in the Sierra Nevada and their subsequent effects on deer distribution. Across all study sites, deer abundance was a weak indicator of home range. However, direct tests are needed with seasonal prey abundance or density information from individual study sites to understand fully the importance of prey on mountain lion home-range size. Sex influenced home-range size in the following way: male mountain lions had larger home ranges than females for each season and in all locations.

When multiple regressions were conducted just for the Sierra Nevada, the strongest indicators of home-range size were animal sex and body mass during both winter and summer seasons. Therefore, in the Sierra Nevada, both intrinsic (sex of animal, body mass) and extrinsic (climate) factors were influencing home-range size for mountain lions.

When multiple regressions were conducted just for the

Table 7. Non-linear regressions of Ln(home-range size) vs. Ln(body mass) for three study locations during wet and dry seasons (adjusted alpha = 0.01)

Study	Season	Regression model	r^2
Santa Ana Mountains 1988–93	winter	*Y* = 191 – 99.8X + 13.6X*2	0.78
	summer	*Y* = 210 – 109X + 14.8X*2	0.82
Santa Ana Mountains 1986–89	winter	*Y* = 8.9 + 0.23X – 4.5x*2	0.03
	summer	*Y* = –52.4 + 33.8X – 4.7X*2	0.05
Diablo Range	winter	*Y* = –233 + 127X – 16.6X*2	0.71
	summer	*Y* = –12 + 9.4X – 0.95X*2	0.38
Sierra Nevada	winter	*Y* = 32.9 – 12.8X + 1.8X*2	0.14
	summer	*Y* = 31.8 – 11.9X + 17X*2	0.16

Coastal Ranges, sex was the most important indicator of home-range size. Reproductive status was a factor which non-significantly influenced home-range size during the winter. As mentioned previously, the effect of reproductive status on mountain lion home-range size is a substantial reduction in home-range size for females – as was observed in the Santa Ana Mountains in 1989. Females may enhance offspring survivorship by staying in close proximity to their offspring. Therefore, in the Coastal Ranges one intrinsic factor (animal sex) was significantly influencing mountain lion home-range size throughout the year.

Therefore, for our study areas in California, intrinsic factors (body mass and animal sex), unique to mountain lions and independent of particular locations, appear to exert a strong influence on home-range size. Although not significant, reproductive status was also evident. Age of animal did not appear to influence home-range size. For extrinsic factors, the effects of season on home range were not significant, except in the Sierra Nevada where seasonal changes are pronounced, influencing deer distributions. We were unable to detect significant effects of deer relative abundance on home-range size; however, deer distribution appears to be a meaningful component of home-range size.

There appeared to be a uniformity among study sites with regard to the appropriateness of linear allometric models for predicting home-range size. Based on body mass alone, no statistically significant linear relationship existed between body mass and home-range size. The lack of an intraspecific allometric relationship could be due to the fact that home-range size in mountain lions reflects an 'intensive property' – a property characterizing an organism that may be size independent, rather than an 'extensive' property that is linked with body mass, such as metabolism (Heusner, 1982, 1984, 1991). Allometric relationships between body mass and home-range size have generally been derived from data collected across many species, where a positive, linear trend exists between home-range size and species body mass (McNab, 1963; Harestad & Bunnell, 1979; Damuth, 1981; Peters & Wassenberg, 1983; Peters & Raelson, 1984; Lindstedt, Miller & Buskirk, 1986).

It is unclear whether interspecific patterns reflect actual intraspecific relationships. Kozlowski & Weiner (1997) believe that functional explanations at the interspecific level imply that interspecific and intraspecific patterns are virtually identical. Empirical intraspecific allometries are rare, however – perhaps because factors other than an animal's size or bioenergetic requirements influence how much habitat it requires. Social factors, for example, may require an animal to create a larger home range than it would need from a bioenergetic standpoint. For mountain lions, if their home-range sizes are not directly associated with body mass – and hence, how much food they require – other factors are influencing this critical parameter.

For our study, the linear relationship between body mass and home-range size was weak, although for some of our study sites during particular seasons there was a curvilinear relationship between body mass and home-range size. This curvilienar relationship underscores the importance of animal sex on home-range size. Body mass clearly overlapped between the sexes in our study populations. Male mountain lions, however, despite similarities in weight to female animals, had larger home ranges than females. In addition, younger females (age < 1 year) had larger home ranges than reproductively active females whose home ranges had been established. Energetic constraints appear to be of secondary importance to animal sex when interpreting these curvilinear relationships.

The results of our residual analysis support the results of the multiple regression analyses in highlighting the weak relationship between body mass and home-range size. Clearly, results of the residual analysis were influenced by a multitude of other factors, in addition to body mass, such as densities of conspecifics, alternative prey densities and densities of roads/human development. We were unable to quantify these for this present analysis but are currently investigating the effects of road density, river density and habitat type on mountain lion home-range size (unpublished data).

Home ranges for mountain lions in this study, as revealed by this novel approach, were not simple extensions of an individual's bioenergetic requirements. The influence of climate on the Sierra Nevada study area affected both deer distribution and mountain lion home-range size. There were other biological factors influencing home-range size which varied between ecosystems (reproductive status in the Coastal Ranges and body mass in the Sierra Nevada) but these appear to be of secondary importance to animal sex. Sex of the animal exerts a strong influence on home-range size across all ecosystems in our study, during both winter and summer. Additionally, young animals and males have, in general, larger home ranges than adult females, regardless of season, body mass or study area.

Habitat conservation strategies for mountain lions should reflect the above complexity by conservatively assessing home-range requirements. Those that do not consider both intrinsic and extrinsic variables in protecting habitat for large carnivores like mountain lions may fall short of their potential by rescinding important home areas.

Acknowledgements

The authors thank the California Department of Fish and Game (including Eric Loft, Steve Torres and Vernon Bleich) and the USDA Forest Service Pacific Southwest Research Station (Fresno, CA) for their logistic assistance with this project. Dirk Van Vuren, Mike Bank, Warren Johnson and Ron Sarno provided critical review and thoughtful comments on the manuscript and Prabir Burman statistical recommendations. Alfred Heusner and Shawn Smallwood participated in many informative conversations on the usefulness of allometric equations in ecology. Jeffrey Oliver, Melissa Pitman and Jennifer Cody are thanked for data entry.

REFERENCES

Beier, P. (1995). Dispersal of juvenile cougars in fragmented habitat. *J. Wild. Mgmt.* **59:** 228–237.

Beier, P. & Barrett, R. H. (1993). *The cougar in the Santa Ana Mountain Range, California*. Final Report: Orange County Cooperative Mountain Lion Study. Department of Forestry and Resource Management, University of California, Berkeley.

Damuth, J. (1981). Population density and body size in mammals. *Nature* **290:** 699–700.

Harestad, A. S. & Bunnell, F. (1979). Home range and body weight – a reevaluation. *Ecology* **60:** 389–402.

Hemker, T. P., Lindzey, F. G. & Ackerman, B. B. (1984). Population characteristics and movement patterns of cougars in southern Utah. *J. Wildl. Mgmt.* **48:** 1275–1284.

Heusner, A. A. (1982). Energy metabolism and body size. Is the .75 mass exponent of Kleiber's Equation a statistical artifact? *Respir. Physiol.* **48:** 1–12.

Heusner, A. A. (1984). Biological similitude: statistical and functional relationships in comparative physiology. *Am. Physiol. Soc.* **15:** 839–846.

Heusner, A. A. (1991). Size and power in mammals. *J. Exper. Biol.* **160:** 25–54.

Hopkins, R. A. (1989). *Ecology of the puma in the Diablo Range, California*. PhD dissertation, University of California, Berkeley.

Hopkins, R. A., Kutilek, M. J. & Shreve, G. L. (1986). Density and home range characteristics of mountain lions in the Diablo Range of California. In *Cats of the world: biology, conservation and management*: 223–235. Miller, S. D. & Everett, D. D. (Eds). Kingsville, TX: Caesare Kleberg Wildlife Research Institute.

Hornocker, M. G. (1969). Winter territoriality in mountain lions. *J. Wildl. Mgmt.* **33:** 457–464.

Kozlowski, J. & Weiner, J. (1997). Interspecific allometries are by-products of body size optimization. *Am. Nat.* **149:** 352–380.

Lindstedt, S. L., Miller, B. J. & Buskirk, S. W. (1986). Home range, time, and body size in mammals. *Ecology* **67:** 413–418.

Loft, E. (1992). *Summary of the North Kings mountain lion home range analysis.* Sacramento: California Department of Fish and Game.

Logan, K. A. & Irwin, L. L. (1985). Mountain lion habitats in the Big Horn Mountains, Wyoming. *Wildl. Soc. Bull.* **13:** 257–262.

McNab, B. K. (1963). Bioenergetics and the determination of home range size. *Am. Nat.* **894:** 133–140.

Mech, L. D. (1983). *Handbook of animal radio-tracking.* Minneapolis: University of Minnesota Press.

Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* **37:** 223–249.

Neal, D. L. (1990). The effect of predation on deer in the central Sierra Nevada. In *Predator management in north coastal California: proceedings of a workshop:* 53–61. Giusti, G. A., Timm, R. M. & Schmidt, R. H. (Eds). Hopland, CA: University of California, Hopland Field Station.

Number Cruncher Statistical System (NCSS) 6.0.21. (1996). Statistical system for windows. Kaysville, UT.

Padley, W. D. (1990). *Home ranges and social interactions of mountain lions (Felis concolor) in the Santa Ana Mountains, California.* MSc thesis, California State Polytechnic University, Pomona.

Peters, R. H. & Raelson, J. V. (1984). Relations between individual size and mammalian population density. *Am. Nat.* **124:** 498–517.

Peters, R. H. & Wassenberg, K. (1983). The effect of body size on animal abundance. *Oecologia* **60:** 89–96.

Ross, I. P. & Jalkotzy, M. G. (1992). Characteristics of a hunted population of cougars in southwestern Alberta. *J. Wildl. Mgmt.* **56:** 417–426.

Sandell, M. (1989). The mating tactics and spacing patterns of solitary carnivores. In *Carnivore behavior, ecology, and evolution:* 164–182. Gittleman, J. L. (Ed.). NY: Comstock Publishing Associates, Cornell University Press.

Seidensticker, J. C., Hornocker, M. G., Wiles, W. V. & Messick, J. P. (1973). Mountain lion social organization in the Idaho Primitive Area. *Wildl. Monogr.* **35:**1–60.

Shaw, H. G. (1980). *Ecology of the mountain lion in Arizona.* A final report: Research Branch, Arizona Game and Fish Department. Federal Aid in Wildlife Restoration, project W-78-R. Phoenix, AZ.

Spreadbury, B. R., Musil, K., Musil, J., Kaisner, C. & Kovak, J. (1996). Cougar population characteristics in southeastern British Columbia. *J. Wildl. Mgmt.* **60:**962–969.

Sweanor, L. L. (1990). *Mountain lion social organization in a desert environment.* MSc thesis, University of Idaho, Moscow.

Van Dyke, F. G., Brocke, R. H., Shaw, H. G., Ackerman, B. B., Hemker, T. P. & Lindzey, F. G. (1986). Reactions of mountain lions to logging and human activity. *J. Wildl. Mgmt.* **50:** 95–102.

White, G. C. & Garrott, R. A. (1990). *Analysis of wildlife radio-tracking data.* San Diego, California: Academic Press.