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USING BLACK BEARS TO TEST IDEAL-FREE DISTRIBUTION MODELS EXPERIMENTALLY

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Models on the distribution of animals are invaluable in understanding how individuals and, ultimately, populations respond to ecological processes. Rarely, have they been applied to conservation issues at a landscape level. We capitalized on the distribution of a previously unavailable novel food resource, found at the juxtaposition of urban and wildland areas, to test the generality of ideal-free distribution (IFD) models using a mammalian carnivore, the black bear (*Ursus americanus*). The primary question we addressed was whether an increase in the prevalence of individuals in a geographical region reflects a population increase or a landscape level redistribution. Combining spatial and temporal data sets with empirically obtained information spanning 12–15 years, we contrasted demographic, life-history, and reproductive parameters between individuals at urban–wildland interface (experimental) and wildland (control) areas at the interface of the Sierra Nevada Range and Great Basin Desert in western North America. Bears were expected to respond to natural versus artificially clumped resources according to an IFD model. Evidence only partially supported this idea because individuals in urban areas had densities 3 times the historical values from the same area, sex ratios were 4.25 times more skewed toward males, bears had 30% larger body mass, home ranges were reduced by 90% for males and 70% for females, and bears entered dens significantly later than wildland conspecifics. However, females in urban-interface areas gave birth to 3 times the number of cubs, although only half as many dispersed successfully relative to wildland females. Further, urban-interface females had a higher proportion (0.57) of potential reproductive years, in which they had young, compared with wildland females (0.29). We present evidence suggesting that bears in Nevada and in the Lake Tahoe basin conform primarily to an ideal-despotic distribution model. Our findings on population reallocation, rather than demographic increase, reemphasize how knowledge about correlates of individual performance and distribution over time helps to understand the extent to which humans change ecosystems, whether their actions are intentional or not.

Key words: black bears, Great Basin, ideal-despotic distribution, ideal-free distribution, Sierra Nevada, urban interface, *Ursus americanus*

The distribution of animals in relation to their resources has been investigated empirically in laboratory and in field studies, often by reliance on competing models that describe whether individuals are ideal despotic or ideal free (Fretwell 1972; Fretwell and Lucas 1970). A primary assumption of these models is that different habitats provide varying opportunities for individuals to survive and reproduce. Where resources

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are limited, the simple assumption that competition will ensue is made (Leibold 1995). In situations conforming to the ideal-free distribution (IFD) model, animals move freely among habitats and assort themselves in proportion to resource availability; however, once a critical density is attained in preferred habitats, an individual's fitness is depressed (Fretwell 1972; Fretwell and Lucas 1970). At that point, individuals may colonize less preferred habitats where competition is less. The end result is that fitness is equal over a range of habitats, resources, or other conditions. Alternatively, the ideal-despotic distribution (IDD) model predicts that subordinate individuals are constrained in their choice of area by dominant individuals (Messier et al. 1990). In this model, fitness should vary among areas.

Carnivores, conservation, and the utility of IFD models.—Many studies have examined animal distribution relative to resource distribution on the landscape for a wide variety of taxa (Dill 1987; Harper 1982; Messier et al. 1990; Milinski 1988; Morris 1989; Parker 1978; Wahlström and Kjellander 1995). Rarely, however, have IFD models been used to address questions across broad landscapes that include anthropogenically disturbed areas. Such regions, nevertheless, present wonderful opportunities to use these perturbations as natural experiments, much as others have done when studying biogeography in altered landscapes (Simberloff 1969; Simberloff and Wilson 1969).

Because many areas of human population growth in western North America are adjacent to public lands that maintain large carnivores, it is likely that interactions that fail to facilitate carnivore conservation will increase. For instance, many regions have no ordinances, laws, or other forms of regulation prohibiting the deliberate or unintentional feeding of wildlife. The careless provisioning of food, whether deliberate or unintended, may be going on at scales substantially larger than previously thought.

In the highly altered landscapes adjacent to urban sprawl, little is known about the effects of a food resource in the form of garbage on the population demographics or on the behavior of individuals. This is particularly true for large carnivores, such as black bears (*Ursus americanus*), that can readily exploit a novel resource. The result of the availability of urban food resources is the current situation where black bears in the western United States and other parts of North America are becoming increasingly reliant on anthropogenic food sources. Many researchers have shown the overriding influence that the abundance and spatial distribution of natural food have on black bears, particularly on their movements and home-range sizes (Elowe and Dodge 1989; Garshelis and Pelton 1981; Hugie 1982; Rogers 1987a; Samson and Huot 1998; Schooley et al. 1994; Schwartz and Franzmann 1991). Similarly, it is well established that the availability of natural food resources, especially hard and soft mast, has a tremendous effect on female reproduction in black bears (Elowe and Dodge 1989; Rogers 1987a; Samson 1995). Yet, to our knowledge, no one has examined the concepts of IFD versus IDD for large carnivores at the interface of urban and wildland areas.

Carnivores not only fill important ecological niches but are also important from a human perspective because they capture public imagination and represent real threats to property, pets, livestock, and even human life. Additionally, large carnivores are important at landscape levels through trophic effects on ecosystem dynamics and processes (Berger et al. 2001). Further, effects of garbage on female reproductive success using IFD models remain unknown. However, IFD concepts have been applied to several free-ranging mammals—wild horses, *Equus caballus* (Berger 1986); muskrats, *Ondatra zibethicus* (Messier et al. 1990); and roe deer, *Capreolus capreolus* (Wahlström and Kjellander 1995).

The testing of ideal-free and ideal-des-

potic models may help to identify the relative magnitude of ecological factors that affect large carnivores, a topic that has relevance for conservation because of the potentially negative effects the careless provisioning of anthropogenic food could have on densities, behavior, and fitness. In addition, if food in the form of garbage led to a redistribution of carnivores at landscape levels by shifting populations to urban-interface areas, there would be a higher cost because mortality risks may be exacerbated due to increased exposure to anthropogenic factors such as roads. Testing resource-based models may help elucidate how novel foods affect the fitness of individuals in urban-interface areas in comparison with individuals that remain in wildland areas. For large mammalian carnivores, the issue of augmented food resources from anthropogenic factors is particularly important because these populations are usually limited by the supply of food and not by territoriality or social organization under natural conditions (Pierce et al. 2000). However, in human-altered landscapes, changes in food distribution may shift the relative importance of social organization in relation to food supply as a population regulation factor, an idea worthy of examination from a conservation perspective.

Materials and Methods

Study design, rationale, and assumptions.—We addressed the question: do black bears conform to IFD or IDD? We compared several fitness correlates between 2 spatially different groups of bears, those in urban–wildland interface (experimental) areas and those in wildland (control) areas. In doing so, we examined 6 parameters (density, body mass, home-range size, female reproductive success, sex ratio, and length of den period) critical to testing IFD models and tested fundamental predictions to distinguish between despots and ideal distributors. Van Horne (1983) cautioned that habitat quality should be defined in terms of survival and production characteristics as well as density of the species occupying the habitat. By this definition, one does not necessarily expect a positive correlation between habitat quality and density because density may be a function of conditions, both in the recent past or temporary, present conditions (e.g., small-scale variation in food resources), rather than a long-term habitat quality (Van Horne 1983). Further, Van Horne (1983) suggested that social dominance interactions can decouple the positive correlation between habitat quality and density. Therefore, we used not only measures of density per se but also measures of survival and production characteristics in our analyses of IFD and IDD models. We believe that the biological parameters we measured were reasonable surrogates as fitness correlates. For example, body mass is positively associated with litter size and cub survival in bears (Hilderbrand et al. 1999; Samson and Huot 1995).

Our predictions and rationale to distinguish IFD from IDD models are summarized as follows. First, if densities and the size of home ranges differ between the 2 different regions (urban interface versus wildland), then the idea that resource abundance varies between areas would be supported assuming that other factors are equal. Differences between the 2 different regions in reproduction and body condition parameters would support the ideal-despotic model, assuming that differences in density occur and are real. Second, if densities of black bears are different between urban and wildland areas, but reproduction and body condition parameters do not vary, an ideal-free model would be supported. Conversely, if densities are similar between areas, as are reproduction and body condition parameters, the interpretation would be that bears are conforming to an IFD. To test IFD models for bears, we examined parameters related to food availability across a gradient of habitats.

In this study, we tested the following hypotheses. If an area is limited in food resources, then biological correlates of food limitations should be detectable among individuals relative to those from non–food-restricted regions. For bears in areas with limited food, we predicted lower densities, smaller body mass, wider foraging areas and larger home ranges, lower levels of fecundity, and possibly longer denning periods. Among the resources that may change the value of habitats to bears is garbage. Garbage may be the ultimate resource for bears because it is always available regardless of environmental conditions including season, it is predictable in both

space and time (i.e., garbage cans are always set out the same day of the week), it is highly clumped (for instance, in residential areas) so that little energy is required to move from one patch (garbage can or dumpster) to the next, and it is always replenished after use. Thus, a priori, we assume that urban-interface areas would not be food resource limited. Of course, it might be possible to have little garbage and many bears, a scenario that would result in food limitation. Nevertheless, we begin with the assumption that garbage is in unlimited supply. Thus, under an IDD condition, we hypothesized that bears at an urban interface should have higher densities, larger body mass, smaller home ranges, increased levels of fecundity, and possibly shorter periods in dens. Further, we hypothesized that under despotic conditions, dominant males in urban-interface areas may limit the access of female and smaller and younger males to garbage, resulting in sex ratios skewed toward males. In contrast, if bears behave as ideal-free distributors, then the above 5 parameters should be similar across the gradient of habitat conditions present in urban-interface and wildland areas.

Ecological significance of variation in resource quality.—To examine whether garbage was limiting the number of bears in urban areas, we derived measures of activity of bears in different locations, reasoning that animals meeting their foraging needs would become inactive sooner. We followed 10 urban-interface and 10 wildland bears for a 24-h period, recording the number of hours of activity. Data were recorded once every 30 min for a total of 48 data points per individual during the 24-h period. Bears were followed from 25 July 2001 to 23 September 2001.

Study area and species.—Black bears are large carnivores that survive as omnivores primarily subsisting on vegetation. The current distribution of bears in Nevada is restricted to the Carson Range of the Sierra Nevada, Sweetwater Range, Pine Nut Range, and the Wassuk Range in extreme western Nevada (Goodrich 1990). The nearest population to the east is in the Wasatch Range in Utah, approximately 750 km away. Each of these 4 mountain ranges was the focus of our wildland trapping efforts, such that we had several sites within the wildland category. Similarly, we trapped bears in several urban-interface areas, including Carson City, Incline Village, Glenbrook, Stateline, Minden, and Gardnerville, Nevada, and South Lake Tahoe, California.

Data collection and possible response variables.—Bears were captured using culvert traps purchased from Teton Welding (Chateau, Montana), tranquilized, and weighed to the nearest kilogram. Culvert traps are cylinder shaped and are designed specifically for the capture of bears. Dates of capture were from 1 July 1997 to 1 April 2002. A proportion of captured animals were fitted with radiocollars (urban areas: n = 41; wildland areas: n = 21) containing a mortality switch (Advanced Telemetry Systems, Isanti, Minnesota). We derived population estimates (and confidence intervals [*CI*]) using a Lincoln–Petersen approach modified by Bailey (1951) and Garshelis and Visser (1997) to account for sampling with replacement.

A priori, individuals for which ≥90% of their location points were inside urban areas (defined by town and city delineation on coverage maps in ArcView 3.2 software) were defined as ''urban.'' Such sites in the western Great Basin were Carson City, Incline Village, Glenbrook, Stateline, Minden, and Gardnerville. South Lake Tahoe, California, also was considered an urban center when calculating densities because collared bears used this area. Based on our operational definition, there was never a case where it was questionable whether a bear was an urban-interface or wildland bear. Urban-interface bears almost always had 100% of their location points within urban areas, whereas wildland bears almost always had 100% of their location points outside urban areas. Urban-interface bears were truly urban bears because, for example, 6 of them denned under the decks of homes in the Lake Tahoe basin, and 29 of the 33 urban-interface bears for which we had data denned within city limits. Response variables examined for black bears when testing IFD and IDD models are listed and referenced by numbers below.

1. Density (bears/100 km^2) estimates used a weighted approach, using the percentage of locations for each bear in an area. For example, if 97% of the locations were inside a defined urban area, then that individual was counted as 0.97 of a bear in the density estimate. Cubs (<1.5 years) were omitted from density estimates due to the dependence on their mothers and because they did not form a self-sustaining part of the population. Density of wildland bears was calculated

using the same approach after subtracting the area (km^2) of urban centers from the total area.

2. Home-range analyses were based initially on the weekly location of animals, when weather permitted, from a Cessna 206 fixed-wing airplane, from 1 July 1999 to 1 April 2002, and from the ground. Most flights occurred from 0500 to 1600 h Pacific Standard Time. We assigned Universal Transverse Mercator coordinates to each location from a global positioning system unit onboard the aircraft. Then, estimates of home-range size (km^2) were calculated using the fixed-kernel estimator, a technique that produces accurate estimates and the smallest variance when tested using computer simulations and telemetry data, specifically for black bears (Powell et al. 1997; Seaman 1993; Seaman and Powell 1996; Seaman et al. 1999; Worton 1989). Annual 95% home ranges and 50% core areas are reported only for adult bears (>3 years), which had >65 locations ($\bar{X}_{\text{number of locations per individual}} \pm SD = 105 \pm 39$), collected over at least 1 full year. We intentionally omitted juveniles (<3 years) from home-range analyses to eliminate the bias in home-range size created by dispersing individuals (Alt 1978; T. Beck, in litt.; D. Garshelis et al., in litt.; Hugie 1982; Rogers 1987a, 1987b). Because of these restrictions for individuals to be included in the analyses of home ranges, the sample sizes for home-range estimates are smaller than both the total number of captured bears and the number of collared bears in each of the 2 areas (urban interface and wildland). Fixed-kernel home ranges were estimated and mapped using the Movement extension in ArcView 3.2 software (P. Hooge and B. Eichenlaub, in litt.). We chose bandwidths for fixed-kernel estimates using a default in the Movement extension in ArcView 3.2. Because we used a default bandwidth, it is likely that our estimates of home-range size are positively biased. However, because we standardized our method of choosing bandwidths for all home-range estimates, comparisons between groups in our study should not be biased.

3. Female reproductive success was estimated in 2 ways. First, we enumerated the birth of cubs per female in 3 winters (1999–2000, 2000–2001, and 2001–2002). We also examined cub mortality rate by checking females in dens during the year after birth. This procedure enabled us to assess cub survival to 16 months, the average age at dispersal (Goodrich 1990). Second, we estimated the proportion of filled potential cub-bearing years. A potential cub-bearing year was defined as a year when any female greater than 4 years of age did not give birth to cubs the previous year or had lost her cubs from the previous year before the mating season (1 June in this study population; Goodrich 1990). This measure differs from the 1st because it allowed us to measure, in both urban and wildland areas, not just how effective females were at dispersing cubs, but also the proportion of females that had cubs when they potentially could.

4. Den entry and emergence dates were estimated during 3 winters (1999–2000, 2000–2001, 2001–2002) as the date midway between the 1st location at the den and the previous location and the date midway between the last location at the den and the next location, respectively. The time period between these locations never exceeded 2 weeks. Mean Julian date of entry and the number of days bears were in dens were calculated according to location during the 3 winters. Means ± 1 *SD* and Wilcoxon rank sum test (*W*) are used unless noted otherwise. Alpha was set a priori at 0.05 for all statistical comparisons. The results are based on the capture of 99 bears, of which 71 were urban-interface and 28 were wildland bears. Total population size (±95% *CI*) was 180 ± 117.

Results

Hypothesis 1.—Resource availability varies across a range of habitat types. Density of wildland bears was 3.2 bears/100 km^2; for urban-interface bears it was 120 bears/100 km^2. Ten years ago, density for the same population was 20–40 bears/100 km^2—all of which occurred in wildland regions (Goodrich 1990). Densities have increased 3-fold over baseline, historical levels. Most importantly, urban-interface bears did not exist 10 years ago (Goodrich 1990). Changes in resources have apparently been so great that the estimated density of urban-interface bears in our study region is now the 2nd highest in North America (Carney 1985; Clark and Smith 1994; Garshelis 1994; Schwartz and Franzmann 1991).

In contrast, the historical densities for our study population had previously been low to intermediate relative to those elsewhere

TABLE 1.—Body mass (kg) of adult (>3 years of age) black bears (*Ursus americanus*) in the 2 study populations in western Nevada. Urban-interface bears are those that were located >90% of the time inside urban areas. Wildland bears are bears that were located <10% of the time inside urban areas. All comparisons were made using the nonparametric Wilcoxon rank sum test (*W*).

	Urban-interface bears		Wildland bears			
Sex	*n*	$\bar{X} \pm SD$	*n*	$\bar{X} \pm SD$	*W*	*P* value
Males	35	137.96 ± 39.53	13	115.50 ± 46.09	238	0.0326
Females	6	97.90 ± 42.95	8	65.21 ± 9.05	54	0.1436
Combined	41	132.10 ± 42.00	21	96.34 ± 43.92	446	0.0010

in North America, a finding not unexpected given the relative aridity of the western Great Basin (Garshelis 1994). The fact that densities are extremely different between urban-interface and wildland areas, although not surprising, is important because it demonstrates a real difference in resource abundance between the 2 areas. Such an empirical demonstration of differences in resource abundance is requisite to move forward with model development.

Hypothesis 2.—In IFD models, sex ratios in areas of different resource availability should be balanced because dominant individuals do not limit access to areas. In contrast, in IDD models, sex ratios would be skewed toward the dominant sex. To test this idea, we examined sex ratios in urban-interface and wildland areas. Of the 41 adult urban-interface bears, only 6 (14.6%) were females. Thus, the male–female ratio of adult urban-interface bears was 6.8:1. In contrast, 8 (38%) of the 21 adult wildland bears were females. The male–female ratio of adult wildland bears was 1.6:1. The sex ratio in urban-interface areas was 4.25 times more skewed toward males in comparison with wildland areas. Of 29 adult bears captured by Goodrich (1990), 13 were females and 16 were males; thus, the male–female ratio a decade ago was 1.2:1 and was similar to the current wildland sex ratio. The slight increase in the male-biased sex ratio in wildland areas, 10 years ago to the present, is likely the result of random sampling error because the male–female ratio of wildland bears both during this study and during Goodrich's (1990) study is not significantly different from 1:1 ($\chi^2 \leq 1.19$, $d.f. = 1$, $P > 0.10$ in both cases). However, the male–female ratio in urban areas is significantly different from 1:1 ($\chi^2 = 20.51$, $d.f. = 1$, $P < 0.001$).

Hypothesis 3.—In IFD models, body mass in areas of different resource availability should be equal because dominant individuals do not limit access to areas. If food were homogenously distributed across broad areas, body mass similarities should exist between wildland and urban-interface bears, assuming that other factors are equal. Obviously, not all factors are equal, especially because density differed between wildland and urban-interface areas (see above). Mean body mass (kg) of all urban-interface adults was 37% larger than that of wildland adults ($P = 0.0010$; Table 1). This difference in body mass was not due to the inclusion of both males and females in the analysis because the relationship held true independently for each sex. Mean body mass and range for the 5 largest males and females (kg) from urban-interface and wildland sites were $\bar{X}_{\text{urban males}} = 233$ kg, range 191–284 kg; $\bar{X}_{\text{wildland males}} = 155$ kg, range 118–204 kg; $\bar{X}_{\text{urban females}} = 97$ kg, range 68–145 kg; $\bar{X}_{\text{wildland females}} = 68$ kg, range 64–73 kg. Urban-interface adult males were on average 20% larger than wildland adult males, whereas urban-interface adult females were on average 50% larger than wildland adult females (Table 1). However, small sample sizes of females resulted in weak power. Because urban-interface bears had larger body mass despite much higher densities of individuals, it is apparent that differences in

TABLE 2.—Home-range size (km^2) of adult (>3 years of age) black bears (*Ursus americanus*) in the 2 study populations in western Nevada. The 95% home ranges and 50% core areas were calculated using fixed-kernel estimators. Urban-interface bears are those that were located >90% of the time inside urban areas. Wildland bears are bears that were located <10% of the time inside urban areas. All comparisons were made using the nonparameteric Wilcoxon rank sum test (*W*).

	Urban-interface bears		Wildland bears			
Sex	*n*	$\bar{X} \pm SD$	*n*	$\bar{X} \pm SD$	*W*	*P* value
95% home range						
Males	20	52.86 ± 32.94	10	519.57 ± 527.83	251	0.0001
Females	4	55.17 ± 54.07	7	172.78 ± 198.72	20	0.2616
Combined	24	53.24 ± 35.76	17	376.78 ± 449.97	485	0.0008
50% core areas						
Males	20	7.54 ± 5.78	10	80.60 ± 91.28	247	0.0002
Females	4	6.08 ± 5.00	7	17.43 ± 21.13	21	0.3234
Combined	24	7.30 ± 5.58	17	54.46 ± 76.64	470	0.0025

resource abundance occurred across the 2 study areas in this system.

Hypothesis 4.—In IFD models, home ranges in areas of different resource availability should be equal. Resource-based models predict that use of a clumped food resource should reduce individual movements and home-range sizes (Fretwell 1972; Pyke et al. 1977), a relationship examined in some mammalian carnivores but not in bears per se (Gompper and Gittleman 1991). Mean home-range size for adult urban-interface male bears was 90% smaller relative to that for wildland males (P = 0.0001; Table 2). A similar pattern existed for females; urban-interface individuals had a mean home-range size 70% smaller than that of wildland females (Table 2). However, small sample sizes precluded the possible detection of a difference in the mean home-range sizes of females in the 2 areas despite the apparent drastic difference (Table 2). The same pattern held for the 50% core areas, with home ranges 91% and 66% smaller for urban-interface males and females, respectively (Table 2).

Hypothesis 5.—If bears are free distributors, then reproduction should be distributed equally across the landscape. Urban-interface females (n = 6) gave birth to a total of 18 cubs in 8 litters ($\bar{X}_{\text{litter size}}$ = 2.25 + 0.89). Three cubs (16.7%) dispersed successfully; hence, for offspring less than 16 months of age, the mortality rate was 83.3%. All the 15 cub deaths were anthropogenically caused: vehicles, 12; accidents, 3, e.g., capture mortality. In contrast, wildland females (n = 8) gave birth to a total of 6 cubs in 4 litters ($\bar{X}_{\text{litter size}}$ = 1.5 + 0.58; W = 18, P = 0.07), and dispersal success was 100%. Remarkably, the 6 urban-interface females gave birth to 3 times the number of cubs of the 8 wildland bears during the same time period, but the successful rate of dispersal in the former was only 50% of the latter. Further, the proportion of potential cub-bearing years in which females had cubs was 0.571 (8/14) for urban-interface bears and only 0.286 (4/14) for wildland females. These differences were not due to different ages of females in the 2 areas because the mean age of adult urban-interface ($\bar{X}$ = 8.17 + 4.49) and wildland ($\bar{X}$ = 8.50 + 4.99) females did not differ (W = 44, P = 0.4745). Thus, differences in female reproductive success are not due to age but likely a consequence of resource distribution (e.g., garbage; see below).

If urban-interface areas have increased the availability of resources during the last 10–15 years, then differences in reproductive output between urban-interface and wildland bears should also have occurred. When Goodrich (1990) and Goodrich and

TABLE 3.—Julian date of entry into dens for all urban-interface and all wildland black bears (*Ursus americanus*) and number of days in dens for bears in the 2 study areas in western Nevada. Julian dates greater than day 365 correspond to the equivalent Julian date the subsequent year. Urban-interface bears are those that were located >90% of the time inside urban areas. Wildland bears are those that were located <10% of the time inside urban areas. All comparisons were made using the nonparametric Wilcoxon rank sum test (*W*).

	Urban-interface bears		Wildland bears			
Sex	*n*	$\bar{X} \pm SD$	*n*	$\bar{X} \pm SD$	*W*	*P* value
Julian date of entry into den						
Males	29	367.55 ± 13.85	17	337.06 ± 16.28	196	0.0001
Females	4	356.75 ± 16.26	9	340.44 ± 19.75	36.5	0.1194
Combined	33	366.24 ± 14.34	26	338.23 ± 17.24	454.5	0.0001
Number of days in den						
Males	19	76.74 ± 19.62	9	109.00 ± 21.85	193.5	0.0024
Females	3	74.33 ± 27.39	6	132.00 ± 27.51	7	0.0444
Combined	22	76.41 ± 20.05	15	118.60 ± 25.91	418.5	0.0001

Berger (1994) studied bears in the identical region more than a decade ago, females in the Carson Range had a mean litter size of 1.55 (n = 11 litters), and females in the Sweetwater Range had a mean litter size of 1.75 (n = 4 litters). Urban-interface bears in this study (that did not exist during the previous studies) had a mean litter size higher than those reported a decade ago, whereas wildland bears had a mean litter size slightly lower than those reported by Goodrich (1990). Further, the mean litter size recorded for urban-interface bears was higher than the mean for western populations ($\bar{X}_{\text{litter size, western populations}} = 1.71$; $n = 148$) of black bears and equivalent to the mean reported for all of North America ($\bar{X}_{\text{litter size, North America}} = 2.25$; $n = 516$—Bunnell and Tait 1981).

Hypothesis 6.—If bears are ideal-free distributors, then resources should be limited for individuals across the landscape at similar times of the year. Thus, we assumed that den chronology should be similar in urban and wildland areas in IFD models. Mean Julian date of entry into hibernacula for 33 urban-interface bears was 1 January, a date later than that for 26 wildland bears (4 December [day 338]; $P < 0.0001$; Table 3). Additionally, urban-interface bears (n = 22) were in dens on average for 42 days less than wildland bears (n = 15, P = 0.0001; Table 3), a pattern that held for males and females ($P < 0.05$; Table 3). Urban-interface bears were in dens for fewer days as a result of a later entry-into-den date. These findings are suggestive of differences in food availability between areas.

Inferences on ecological significance of variation in resource quality.—The mean number of hours for which urban-interface bears were active ($\bar{X}_{\text{hours}} = 8.50 + 2.64$) was only about 65% that of wildland bears ($\bar{X}_{\text{hours}} = 13.3 + 2.67$; Wilcoxon paired sample test; $T = 145$, $P = 0.0037$). The urban-interface bears were significantly less active in late summer–early fall, a period when black bears are at their maximum caloric intake over the annual cycle, which suggests that urban-interface bears were meeting their caloric intake requirements quicker each day in contrast to wildland bears. Further, urban-interface bears became satiated and quit foraging, although garbage still was available inside the dumpsters they had been foraging in. These data coupled with body mass, bear density, and length of denning data suggest that garbage is likely not a limiting resource in urban-interface areas in this system.

DISCUSSION

Evaluating IFD and IDD model predictions.—Overall, our results based on 6 pa-

rameters (density, sex ratio, body mass, home-range size, female reproductive success, and den chronology) show significant patterns of differentiation between wildland and urban-interface bears. The primary differences are that urban-interface areas had densities of bears 3 times the historical densities, bears were 30% larger, had home ranges reduced by 70–90%, had sex ratios 4.25 times more skewed toward males, and entered dens significantly later, and females had significantly more cubs and potential cub-bearing years filled than did wildland conspecifics. These parameters, when used to evaluate IFD and IDD model predictions, support the notion that bears, at least in the western Great Basin desert and in the Lake Tahoe basin, conform to what would appear to be an ideal despotic distribution.

Population increase or redistribution under ideal-free models?—Models on the distribution of animals have proved invaluable for identifying features, demographic, ecological, and social, that constrain patterns across a landscape. Rarely, however, has such knowledge been used by wildlife practitioners or state or federal agencies to address conservation issues at a landscape level. For instance, increased sightings of mammalian carnivores and scavengers such as skunks, coyotes (*Canis latrans*), raccoons (*Procyon lotor*), or bears in or near many urban settings (G. Sanderson, in litt.) could be the result of either local population increases or a redistribution across a landscape, although, of course, these need not be exclusive alternatives. In our study areas, however, the increased prevalence of bears has been viewed as an overall increase in population size by the California Department of Fish and Game, Nevada Division of Wildlife, and by the public, without recognition of the possibility that wildland areas have been partially or mostly depopulated (California Department of Fish and Game, in litt.).

Whether bear populations have increased in our study region has not been especially clear, but the evidence suggests that this is not the case. Although the number of interactions involving bears and humans has increased >1,000% from 1990 to 2000, our estimated population size of 180 ± 117 bears differs little from the estimate of 150–290 individuals in the same population a decade ago, when extrapolating from Goodrich's (1990) density estimates (20–41 bears/100 km^2) to the total area of available habitat. The relatively close estimates of population size further support the notion that the increase in complaints and anthropogenic causes of bear mortality during the last decade are due to bear redistribution across the landscape and not to an increase in the number of bears. In addition, we captured fewer wildland bears (n = 28) in 5 years than did Goodrich (n = 29) in 3 years, despite the fact that we had a greater trapping effort (600 total trap nights versus 301), we worked in 2 additional mountain ranges that Goodrich did not study, and we captured 3 times the total number of bears compared with Goodrich (1990). All these data further support the notion of a redistribution of bears across the landscape, irrespective of the large variance associated with both current and historical population estimates.

We assume that differences in resources exist between urban and wildland areas because urban food resources are drawing bears from the wildland areas and concentrating them at highly exaggerated densities, and thus we can proceed in testing IFD models. Higher densities of black bears in urban areas were accompanied by a 90% reduction in mean home-range size for males and a 70% reduction in mean home-range size for females. We believe that resources in the form of garbage in urban areas have led to a radical shift of bears across the landscape.

Garbage is a high-caloric, highly valuable, and often unlimited resource for bears, as borne out by several studies that demonstrate that fitness is associated with this artificially provided resource (Badyaev 1998; Blanchard and Knight 1991; Eber-

hardt and Knight 1996). Additionally, male urban-interface bears in our study areas have increased in mean body size by 20% and females by 50% relative to wildland bears. Moreover, 1 out of every 4 adult male black bears in urban areas exceeded 182 kg (400 pounds). It is apparent that garbage is a good resource for black bears in terms of increasing and maintaining body mass. Remarkably, 4 different urban-interface males gained mass during the winter, 1 November to 1 March, whereas hibernating bears did just the opposite—lost mass (Harlow et al. 2001; Tinker et al. 1998). In our study, these bears gained mass despite snowpack levels >102 cm (40 inches) at Lake Tahoe (elevation 1,895 m; 6,220 feet) during 2 winters. This demonstrates that urban food resources in the form of garbage are both important and reliable, despite environmental conditions, and are conducive to weight gain when natural food resources are not available.

Evidence suggesting that large male bears are despots.—Male black bears have the ability to preclude females from preferred habitats (dump areas—Bunnell and Tait 1981; oak stands—Garshelis and Pelton 1981; blueberry patches—Jonkel and Cowan 1971; Rogers 1976, 1987a). In doing so, sex-specific reproductive strategies, as mediated through mass gain, may regulate the distribution of the local population. Bunnell and Tait (1981) stated that dominance hierarchies at concentrated food sources, such as berry patches, salmon streams, and dumps, demonstrate not only the lability of social organization in bears but also the importance of social organization in allocating food resources. It appears in our study system that large males were limiting the access of both female and younger and smaller males to urban food resources, at least based on measures of distribution and home range.

Our findings suggest that males are concentrated in high densities in urban areas. It is possible that there was a trap bias toward males in urban areas and a trap bias toward females in wildland areas. This is highly unlikely, however, because this would require a complete reversal in the trap bias from urban-interface to wildland areas. We observed a male trap bias in both urban-interface and wildland areas, which is consistent with observations of other researchers working on black bears (Hamilton 1978; Hellgren and Vaughan 1989; Smith 1985). Although the trap bias was consistently toward males in both areas, we trapped 2.6 times the proportion of females in wildland areas relative to urban-interface areas. Thus, the observed difference of males being in urban areas and females being in wildland areas was most likely a true segregation of the sexes and not a product of sampling technique and bias.

There are 2 reasons why females avoid taking advantage of a food resource such as garbage. First, males may be socially regulating access. Females may be avoiding urban areas that have extremely high densities of males, which are also significantly larger (>20%) than wildland males. Second, sex ratios that skewed toward males in urban areas may just be the product of a random process created by male-biased dispersal patterns or a result of females avoiding urban areas for reasons other than males.

Under the assumption of IFD, individuals, irrespective of sex, should use urban-interface areas until density imposes a cost in response parameters (body condition, size, reproduction). Instead, we observed substantial between-site differences in female and male body mass as well as in female reproduction. Bears, at least in this system, are not distributed freely but instead behave in a despotic manner. Bears are obviously not distributed in proportion to food resources in the system, and it is still likely that despite extreme densities of bears in urban-interface areas, they have yet to reach maximum possible densities given the superabundant resource of garbage. This is evident by the fact that fitness-associated parameters of urban-interface fe-

males have not been reduced to levels equal to those of wildland females.

Another possible way in which males act as despots is through intraspecific killing. Because intraspecific killing does occur in black bears (Davis and Harstad 1996; Garshelis 1994; Lecount 1982; Lindzey and Meslow 1977; Rogers 1977; Tietje et al. 1996), and because of the fact that there was such a high density of large males in urban areas, it may be that females were avoiding urban areas to protect themselves and their cubs. Female black bears with cubs have been documented to avoid adult males (Powell et al. 1997). Adult males do tend to kill subadults in denser populations (Jonkel and Cowan 1971; Rogers 1987a). Garshelis (1994) suggested, however, that intraspecific killing in black bears is so uncommon that it rarely, if ever, contributes to density-dependent population regulation, at least in the range of densities generally reported in the literature. It is possible that at extremely high densities of males, such as what we observed in urban areas, just the possibility of intraspecific killing may lead to females and smaller and younger bears avoiding these areas, an idea that warrants further investigation.

Explanations alternative to that of bears as despots.—It is possible that female bears avoided urban areas not because of males but because of fear of people, vehicles, or losing offspring to anthropogenic factors (or all). Data on some mammals where females may not be handicapped by being smaller than males, such as black rhinos (*Diceros bicornis*), show that as a form of parental investment, females may avoid areas that males frequent (Berger and Cunningham 1995). Nevertheless, active avoidance by females seems unlikely because in at least 2 cases, females in urban areas lost their entire litter due to vehicle collisions, and yet the females continued to use urban areas. Alternatively, our females from wildland areas may be genetically predisposed to avoid conditions such as those found in urban areas, but our data preclude the evaluation of this issue relative to individual variation. Additionally, it is possible that lower reproductive rates of females in wildland areas may be the result of a lack of males to impregnate females in these areas and not a result of resource distribution. Data demonstrating that male black bears move over larger areas during the breeding season, however, likely dismiss this idea (Hirsch et al. 1999; this study).

Finally, females may not avoid urban areas at all; instead, male-biased sex ratios in urban-interface areas are the product of a random process. Black bears exhibit male-biased dispersal, and thus dispersing males move around the landscape much more than females (Alt 1978; T. Beck, in litt.; D. Garshelis et al., in litt.; Hugie 1982; Rogers 1987a, 1987b); thus, males may just encounter urban food resources more frequently. Consistent with this idea is that 3 of our collared, dispersal-age males moved repeatedly between the Carson Range of the Sierra Nevada and the Pine Nut Range, separated by a distance of over 32 km (20 miles), before establishing permanent home ranges much smaller in size. One bear moved from Fallon, Nevada, to South Lake Tahoe, California, a straight-line distance of over 112 km (70 miles). In contrast, 3 dispersal-age females born in Little Valley (7 km^2), Nevada, eventually established home ranges in the same valley. Thus, based on random probability, it has been proposed that males are more likely to encounter urban food resources on the landscape, and our findings of high male densities may simply reflect that 10–15 years have been an inadequate period for females to discover clumped resources at an urban interface.

Conclusions

Ultimately, we are not arguing that reproductive success is not directly tied to food availability in black bears, but we are suggesting that in this system, males apparently were limiting access of females to urban food resources. Dominant male bears likely were limiting access to food resourc-

es, thus densities and fitness varied across a gradient of habitat conditions for both males and females. We conclude, therefore, that bears in Nevada and the Lake Tahoe basin must be distributed primarily in an ideal-despotic manner. Further, the data presented here suggest that increased incidence of carnivore and human interactions do not necessarily reflect an increase in the population of the carnivore as is assumed in many areas but may merely represent a human-induced redistribution of the population at a landscape level.

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