PATTERNS OF BLACK BEAR ABUNDANCE

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ABSTRACT: The factors influencing patterns of black bear (*Ursus americanus*) abundance must be understood to conserve the species, but understanding these factors depends on study design. I synthesized reported estimates of black bear density to (1) test if 28 corresponding study attributes could explain the variation in density, and (2) identify biases and information shortfalls impeding research effectiveness. Most of the variation in 29 estimates of density was explained by the size of study area, or alternatively, by the number of bears captured/km^2. Density decreased with increasing size of study area, it increased with the number of captured bears/km^2, and it decreased with longer duration of study. The regression models predicted 20 to 52 bears in a 1-km^2 area, indicating that study area boundaries have been consistently delineated around bear aggregations. Study design can be improved to more effectively explain the variation in black bear density and relate it to other useful information. Important improvements could include: (1) extending the sampling area across larger geographic areas using sign counts; (2) choosing study sites randomly or systematically across black bear ranges; (3) extending population studies over longer time periods; and, (4) consistently measuring and reporting population and site attributes for future synthesis.

Key Words: black bears, conservation, density, sampling, study design, *Ursus americanus*.

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Estimating population density has been a prime goal in ecology, because it is a way of expressing numerical abundance relative to a defined space (Peters 1991). By comparing population densities through time or among locations, investigators can begin to understand the factors that influence patterns of abundance. Density of the American black bear has been estimated more often than most species of mammalian Carnivora (Smallwood and Schonewald 1996), perhaps due to its economic value as a harvested species, its ubiquity, or its convenience for capture and handling. Black bear management and conservation should benefit from the 113 years of cumulative field work devoted to estimating black bear density.

However, animal density consistently declines with increasing study area (Smallwood 1995, Blackburn and Gaston 1996, Smallwood and Schonewald 1996, Smallwood and Morrison in press). As the size of a study area is increased, a growing proportion of the area is devoid of the species because animal populations are typically clustered (Taylor and Taylor 1977, 1979; den Boer 1981; Hanski 1994), and investigators usually study their subject populations where density is known a *priori* to be high. Animal density is too complicated for making comparisons among studies and regions without considerable qualification as to spatial scale of observation, type of density (e.g., ecological vs. crude, where ecological density is based on only the habitat area within the study boundary and crude density is based on all of the area), and other factors such as edge conditions (Yahner 1988) and land productivity (Tilman 1983). Therefore, its usefulness to theory and conservation depends on understanding how study and interpretive design attributes affect density estimates. The purpose of this paper was to synthesize density estimates among studied black bear populations, as well as to synthesize all the study and interpretive design attributes that could be quantified from the research reports and that might possibly influence the density estimates.

METHODS

The methods of this study were consistent with the approach used for *Puma concolor* by Smallwood (1997). I summarized data from 20 black bear studies (29 estimates of abundance in 25 published reports) on 28 variables (Table 1) that described what was studied; why the study occurred; where, how, and when the study was conducted; and how it was reported. These variables were defined in Smallwood and Schonewald (1998). Then, using separate stepwise linear regression analyses and univariate statistics, I tested whether the log density of black bear populations was associated with the 28 variables. The unstandardized residuals from the regressions were tested for association with the remaining variables that did not achieve the tolerance limit for entry into the models. These additional tests for association involved regression analysis for variables measured on a continuous scale and mean comparison Analyses of Variance (ANOVA) and post-hoc t-tests for categorical variables. Density estimates were used only if the methods and study areas were reported and the estimates were not extrapolated from other research efforts (i.e., the estimates had to be made from field sampling within defined geographic areas).

I also used summary statistics to describe the study attributes reported along with density estimates.

RESULTS

I found 29 abundance estimates, some of which I averaged over multiple annual estimates reported at a single site. Overall, black bear density averaged 0.49 ± 0.59/km^2, but varied 105-fold from 0.03 to 3.11/km^2. Excluding the outlying estimates made at 43,000 and 83,000 km^2 (see Fig. 1), a lot of this variation in density could be explained by the 205-fold variation in study area (R^2 = 0.76, Root MSE = 0.23, n = 29, $P < 0.0001$), where log *Density* = 1.3 - 0.77 log *km^2 Study Area* (eqn. 1). Mean study area was 405 ± 470 km^2 (range = 11 to 2,250 km^2).

The unstandardized residuals from this regression related significantly with none of the other 28 variables measured from reports of black bear abundance estimates ($P > 0.05$ for all regression and ANOVA tests). However, even more of the variation in density could be explained by the number of animals captured/km^2 (R^2 = 0.83, Root MSE = 0.19, n = 22, $P < 0.0001$), where log *Density* = -0.12 + 0.76 log *Captured bears/km^2* (eqn. 2). Like density, the number of bears captured/km^2 decreased with increasing study area, although this decrease was proportional (R^2 = 0.72, Root MSE = 0.29, n = 22, $P <$ 0.0001), where log *Captured bears/km^2* = 1.71 - 0.96 log *km^2 Study Area* (eqn. 3). The number of bears captured/km^2 of study area expressed both the variation in study area and the rate of change in bear abundance with changing study area (Table 2). Using this variable to predict density, the duration of study also contributed to explaining the variation in density (Adjusted R^2 = 0.86, Root MSE = 0.16, n = 22, $P < 0.0001$), where log Density = 0.10 + 0.84 log *Captured bears/km^2* - 0.04 - Years duration of study (eqn. 4).

Twelve (41%) of the abundance estimates I summarized were made for ecological hypothesis testing or for technique development, whereas 5 (17%) were made for conservation objectives and 11 (38%) for management. Most (83%) estimates were of crude density, 3 (10%) were ecological, and 2 (7%) were based on the total area method (i.e., home ranges). These estimates were made at 22 sites and described in 25 reports. They spanned North America from coast to coast, and from 28° 50' to 63° N latitude. Black bear studies ranged in elevations from 0 to 4,345 m, and averaged 1127 ± 868 m. The study site relief was rugged and mountainous for most estimates (62%), but was in mountain or glacial valleys for 3 (10%), in foothills or rolling land for 6 (21%), and on flats for 1 estimate.

Vegetation descriptions varied too greatly among the 29 reported estimates to test if vegetation influenced density. I used Kuchler's (1949) physiognomic classification to group vegetation descriptions into 19 unique combinations of vegetation categories. By using the dominant or first-described types, I reduced the comparison to 4 estimates (14%) in chaparral, 12 (41%) in deciduous forest (including sub-categories of evergreen forest, chaparral, and grassland), and 13 (45%) in evergreen forest (including sub-categories of deciduous forest, chaparral, grassland, wetland, and desert). However, these groups did not differ significantly in density (ANOVA F = 1.83, d.f. = 2, 28, P = 0.18) nor in the unstandardized residuals of log density regressed on log study area (ANOVA F = 0.97, d.f. = 2, 26, P = 0.39).

Two of the estimates (7%) were made in protected areas, 15 (52%) on multiple-use public land, 3 (10%) on single-use government land, 3 (10%) on agricultural or ranch land, and 6 (21%) on lands where the use was not described. Twenty-two of the estimated bear populations (76%) were reportedly hunted, 11 (38%) of the sites were grazed by cattle, and 18 (62%) were subjected to timber harvest. Two of the estimates (7%) were made on islands, and the rest were continental, although 3 (10%) of these were bordered by inhospitable terrain. Five of the estimates (17%) were reported to have been made at sites explicitly chosen for their known high densities of black bears.

Most black bear estimates were based on capture-recapture methods (59%) and one-time capture and release methods (28%). Only one was based on remote

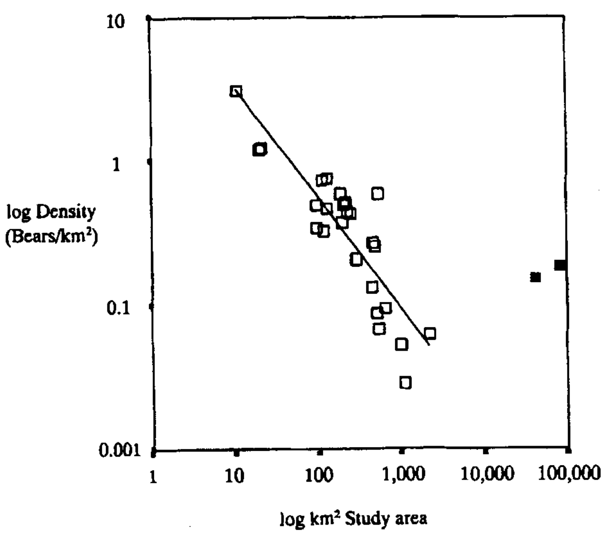

Figure 1. Density declined with increasing size of study area, except for the two largest study areas. Because outliers as extreme as the Garshelis and Visser (1997) estimates (shaded boxes) were not observed for any other species of mammalian Carnivora (Smallwood and Schonewald 1996), I excluded these 2 estimates from the regressions involving density.

methods, from synthesizing hunting records, and 3 (10%) were based on counts of bear sign. The 25 estimates based on capture methods included an average of 79 $\pm$ 51 bears captured (range = 23 to 208 bears). Of these, an average of 3 $\pm$ 2 bears (range 0 to 8) were accidentally killed due to capture, although the accident rate was reported only for 10 estimates. Serious injuries due to capture also occurred (Beck, 1991).

Twelve (41%) of the black bear abundance estimates were based on "census," and the rest were based on the Jolly-Seber, Lincoln-Peterson, Schnabel, and Age Ratio Reduction methods. These estimates were derived from an average of 4.3 $\pm$ 2.4 years (range 0.5 to 10 years). Half of the estimates represented populations sampled during the 1970s (52%), with the rest split between the 1960s, 1980s, and 1990s. Fourteen of the estimates

Table 1. Summary of study attributes related to the published density estimates synthesized in this study.

Source	Location	Kuchler's Vegetation[a]	Study area, km^2	Density (bears/km^2)	Sample method[b]	No. of captured bears
Jonkel and Cowan 1971	Big Creek Drainage, Montana	E	205	0.377	AD	158
Kemp 1972	Cold Lake, Alberta	DE	205	0.383	D	108
McIlroy 1972	Prince William Sound, Alaska	EDGGw	11	3.108	A	–
Pelton and Marcum 1975	Great Smoky Mountains National Park	DE	500	0.254	BC_r	92
Piekielek and Burton 1975	Clair-Engle Lake, N. California	EDBs	114	0.746	D	54
Kemp 1976	Cold Lake, Alberta	DEBs	207	0.494	D	–
McCaffrey et al. 1976	N. Catskills Mountains, New York	DE	1030	0.054	AD	33
McCaffrey et al. 1976	S. Catskills Mountains, New York	DE	2250	0.063	AD	–
Lindzey and Meslow 1977	Willapa NWR, Long Island, Washington	EDs	20.1	1.227	D	23
Beecham 1980	Council, Idaho	Bs	130	0.477	D	47
Beecham 1980	Lowell, Idaho	E	260	0.435	D	100
Kellyhouse 1980	Clair-Engle Lake, N. California	EBs	192	0.599	D	70
LeCount 1980	Mazatzal Mountains, C. Arizona	Bs	100	0.500	D	44
LeCount 1982	Mazatzal Mountains, C. Arizona	BsED	120	0.333	D	55
Young and Ruff 1982	Cold Lake, Alberta	D	218	0.514	D	208
Beecham 1983	Council, Idaho	EG	130	0.769	D	175
Waddell and Brown 1984	Pinaleno Mountains, Arizona	ED	466	0.275	D	91
Lindzey et al. 1986	Willapa NWR, Long Island, Washington	EO	22	1.272	CD	51
Yodzis and Kolenosky 1986	East-Central Ontario	DE	233	0.446	D	–
Miller et al. 1987	Talkeetna Range, Alaska	EDDs	531	0.090	D	24
Rogers 1987	Superior National Forest, NE Minnesota	ED	300	0.211	D	–
Hellgren and Vaughan 1989	Great Dismal Swamp NWR, Virginia	DBH	555	0.589	D	101
McCutchen 1990	Rocky Mountain Natl. Park, Colorado	EBzGD	1100	0.030	CD	23
Beck 1991	Gunnison National Forest, Colorado	DEG	450	0.136	D	129
Clark and Smith 1994	Ozark Mountains, NC Arkansas	DE	534	0.069	D	43
Clark and Smith 1994	Onochinta Mountains, WC Arkansas	ED	658	0.097	D	65
Doan-Crider and Hellgren 1996	Coahuila, Mexico	DsBzG	100	0.350	D	42
Garshelis and Visser 1997	Upper Peninsula of Michigan	DE	43000	0.156	B_t	–
Garshelis and Visser 1997	Northern Minnesota	DEGwA	83000	0.188	B_t	–

[a] B = evergreen broadleaf forest (Bs = shrubs >1 m tall, Bz = shrubs <1 m), D = deciduous broad-leaf forest (Ds = shrubs), E = evergreen coniferous forest, G = grasses, Gw = marsh, O = desert shrubs and cacti, H = forbs and other herbaceous plants, A = agriculture.

[b] A = hunting/trapping records, B = sign counts, B_t = marking with tetracycline, C = animal counts, C_r = radio-isotope, D = capture, resight, or recapture.

(48%) were presented as annual abundance, 2 (7%) represented spring conditions, 9 (31%) summer, and 4 (14%) autumn.

Seventy-two percent of the estimates were reported along with maps of the study site. Fifteen of these maps (71%) only showed study site boundaries, one (5%) depicted vegetation, and 5 (24%) showed bear locations (i.e., home ranges). Seven of the estimates (24%) were reported along with some quantification of the availability of vegetation categories. Four of the estimates (14%) included vegetation descriptions at the generic biome level of detail (e.g., forest, grassland), 6 (21%) were described as to type of biome (e.g., alpine steppe, conifer forest, boreal forest), and 19 (66%) included descriptions of dominant species in the vegetation complex. Five of the estimates (17%) were reported as "minimum," 2 (7%) as adults or residents only, 16 (55%) as accurate (or not reported), and 6 (21%) as unusually high density. Reports of 25 estimates (86%) were not related to past population levels, and 2 (7%) were reported as recovering from previous lows and 2 (7%) as declining. Fifteen (52%) of the estimates were compared to others, and another was both compared and extrapolated to a larger geographic area beyond the study area.

Four estimates (14%) were reported along with field estimates of body mass. Six (21%) had home range estimates, 14 (48%) had information that allowed the reader to estimate the ratio of adults to juveniles, and 20 (69%) provided gender ratios.

DISCUSSION

Black bear study areas varied greatly in spatial extent, but most were fairly small (i.e., (2,250 km^2) and most encompassed areas of high population density. The areas between black bear aggregations have not been represented by sampling. Eqns 1 and 3 both indicated that the study sites supported densities that probably do not occur throughout the geographic range of the black bear. According to the regression intercepts, a 1-km^2 area would support 20 bears/km^2 and 52 bears could be captured in that area. The highest reported density was 6 times less than that predicted by eqn. 1 on the average 1 km^2, and it was 17 times less than the number of bears predicted by eqn. 3 to be captured on this same 1 km^2. The absurd predictions of eqns. 1 and 3 were caused by bear abundance remaining relatively similar among study sites, especially sites involving capture methods, whereas the study areas ranged in size from those capable of supporting too few bears to qualify as a population to those that included more space than was occupied by the population. Eqns. 1 and 3 were mathematical artifacts of dividing near-constant bear numbers by variable study areas to calculate density. Sampling randomly from the geographic range of black bears, or sampling all the area within a region (e.g., counting all bears within a large mountain range), would yield density estimates that would probably regress on study areas with slopes approaching zero, which would be much shallower than the slopes of eqns. 1 and 3. Both alternative sampling methods would add insight to patterns of bear abundance and the environmental factors influencing those patterns.

Synthesis also revealed a decline in black bear density estimates with longer duration of study (eqn. 4), consistent with spatial shifting of high-density clusters from study sites or long-term cycling in abundance. For example, Taylor and Taylor (1977, 1979) synthesized population study results from among various taxonomic groups exhibiting spatial shifting of clusters. Population cycles among species of Carnivora have been documented (Keith 1963, Peterson et al. 1984) and suspected (Smallwood 1997). Pelton and van Manen (1996) also found population trend interpretations for black bear to change depending on which 5 or 10-year intervals were examined among their 28 years of population study. I agree with Pelton and van Manen (1996) and Cyr (1997) that too few population studies have been conducted for more than 5 years (also see Smallwood and Schonewald 1998).

Because most black bear density estimates were derived from use of capture methods, density could be related to the number of animals captured per unit study area. As expected, these variables were highly correlated (eqn. 2). However, the change in density was less than proportional to the change in bears captured/km^2. The model in eqn. 4 predicted 52 captured bears in a study area of 1 km^2, a prediction much higher than what is likely. Indeed, the ratio of the bears captured to the estimated abundance tended to decline with increasing spatial extent of study area. That is, the proportion of bears captured within a study area declines faster with increasing study area size than does density. Further research will be needed to determine if accuracy in density estimation is improved with greater catch effort in smaller areas.

Black bear population estimates also differed from those of most other mammalian carnivore species in purpose and method. All black bear estimates were published in outlets focused on wildlife management, and most were reported to have been made as contributions to solving management-related problems. This management focus might have been more prominent for black bears because North Americans generally regard black bears as ubiquitous across their expansive geographic range, and therefore in no threat of decline. Perhaps this view of black bear status contributed to captures becoming the sampling method of choice, even though black bears and their sign are conspicuous and conducive to non-intrusive sampling methods such as remote photography (Mace et al. 1994, Karanth 1995) and sign counts (Smallwood and Fitzhugh 1993, 1995). Because capture methods risk accidental injury and death to the study animals, they are used sparingly among threatened and endangered species of Carnivora. Therefore, the investigators' perceived level of threat to the species appears to influence counting methods, which may influence inter-specific comparisons of density.

Despite the perception that black bears are common across North America, black bear populations have been decimated in the past due to over-harvest and human encroachment (Lindzey et al. 1976, Manville 1980, Smith et al. 1990). They are vulnerable to anthropogenic intrusions. Therefore, the existing collection of estimates could be enhanced in value by adding more estimates from protected areas and by more frequently relating the new estimates to what is known of the population from the past.

Methods for understanding the factors that influence patterns of black bear abundance should include longer-term population studies outside and inside areas of bear aggregations, either by using much larger study areas or by randomly or systematically selecting study sites from within the species' range. Sign counts can facilitate this need by extending sampling beyond the spatial extent of study area in which capture methods are pragmatic. Random or large-area sampling should also be used to determine the frequency and magnitude of spatial shifting of populations. Environmental conditions outside the traditional study areas can influence patterns of bear abundance at least as much as conditions inside the study area boundaries. Black bear density estimates also would be more useful in the future by measuring and reporting population parameters such as body mass, home range sizes, and sex and age ratios. Finally, vegetation and other site attributes need to be reported in a consistent manner that is comparable and can potentially be translated to ecological expressions such as primary productivity and species diversity.

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Table 2. Multiple regression models of black bear density using log km^2 Study Area and log Captured bears/km^2 on the study area. Log km^2 Study Area entered first left 19% of the sum of squares to be explained by log captured bears/km^2, and entered seconded added only by 1.2% of the sum of the squares.

Source	Adjusted R^2	Sum of Squares	Degrees of Freedom	Mean Squares	F-ratio	P
Model 1						
Study area	0.665	2.776	1	2.776	42.688	<0.0001
Captures/km^2	0.824	3.427	2	1.714	50.108	<0.001
Model 2						
Captures/km^2	0.822	3.385	1	3.385	97.835	<0.001
Study area	0.824	3.427	2	1.714	50.108	<0.001
Either Model						
Error		0.650	19	0.034		
Total		4.077	21			

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