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**DYNAMICS OF A BLACK BEAR POPULATION WITHIN A DESERT
METAPOPOPULATION**

Running head: Black Bear Population Dynamics

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Abstract:

Understanding metapopulation dynamics in large carnivores with naturally fragmented populations is difficult because of the large temporal and spatial context of such dynamics. We coupled a long-term database of visitor sighting records with an intensive 3-year telemetry study to describe population dynamics of recolonization by black bears (*Ursus americanus*) of Big Bend National Park in Texas during 1988-2002. This population, which occurs within a metapopulation in western Texas and northern Mexico, increased from a single pair of known breeding-age animals in 1988 to 29 bears (including 6 females of breeding age) in March 2000 ($\lambda = 1.25/\text{yr}$). A migration and dispersal event in August-December 2000 reduced the population to 2 adult females and as few as 5-7 individuals. One-way movement distances from the study area during this event averaged 76 km for females ($n = 7$) and 92 km for males ($n = 4$), and 3 animals conducted migrations of at least 154, 178, and 214 km, respectively. Our observations exemplify the importance of stochastic events on demographics of small populations and highlight the potential scale of bear movement among montane islands of southwestern North America. They also provide insight into the use of dispersal data in parameterizing metapopulation models for large carnivores.

Keywords: Big Bend National Park, Black bear, Metapopulation, Migration, Population dynamics, Recolonization, *Ursus americanus*

I. Introduction

Islands of montane forest and woodland in the desert Southwest and the Great Basin of North America exist among a matrix of deserts, grasslands, and shrublands, and have served as sites of classic case studies of island biogeography in continental systems (Brown, 1971, 1978; Lomolino et al., 1989; Lawlor, 1998). The work conducted in these areas has focused, like much of island

biogeography, on groups of species such as mammalian assemblages. However, with the paradigm shift in ecology toward metapopulation biology, these montane islands (also known as sky islands, a term attributed to Weldon Heald by Warshall [1994]) provide useful opportunities to study dynamics in large carnivores that have the mobility to move through the intervening matrix. For example, the montane islands of the Chihuahuan desert have provided a case study of metapopulation dynamics on mountain lions (*Puma concolor*) in southern New Mexico (Sweanor et al., 2000).

A metapopulation can be defined as a “set of local populations within some larger area, where typically migration from one local population to at least some other patches is possible” (Hanski and Simberloff, 1997:11). The mainland-island metapopulation model, which involves the presence of suitable habitat patches located within dispersal distance from a large habitat patch that supports a permanent population of the species (Hanski and Simberloff, 1997), fits black bear dynamics in the Chihuahuan desert region. Prime habitat for black bears (*Ursus americanus*) in southwestern North America is restricted to chaparral and woodlands in mountainous areas ranging from 900 to 3000 m in elevation (Pelton 2003). In the Chihuahuan desert, the only forested woodlands capable of supporting viable populations of black bear occur at elevations > 1,500 m. Several mountain ranges between southern New Mexico and the Mexican states of Chihuahua and Coahuila meet this criterion (Onorato and Hellgren, 2001; Fig. 1). The largest of these ranges, the Sierra del Carmen and the Serranias del Burro (Fig. 1), exceed 1,000 km² and have large populations of black bears (Doan-Crider and Hellgren, 1996; Doan-Crider, 2003). Other smaller ranges, such as the Chisos Mountains (Fig. 1), represent islands of bear habitat. The lowland desert matrix between these mountain ranges does not support resident populations of black bears. However, mitochondrial and nuclear genetic data support the existence of a mainland-island

metapopulation of black bears in the western Texas-northern Mexico border area by indicating that populations are linked by male movements and structured by female philopatry (Onorato, 2003; Onorato et al., 2004).

Modeling metapopulation dynamics of animal species can be done with incidence-function approaches (Hanski and Simberloff, 1997) or with patch-specific demographic models, in which dispersal links habitat patches (Beissinger and Westphal, 1998). The latter models are hampered by a lack of empirical data on variance in vital rates of component populations and knowledge of dispersal processes (Beissinger and Westphal, 1998). Our objective was to describe dynamics of an island population of black bears in a metapopulation found in the Chihuahuan desert of western Texas and northern Mexico using data from field study and park visitor observations. The population, which occurred in Big Bend National Park, was extirpated in the mid-1940's and recolonized from Mexico in the late 1980s (Onorato and Hellgren, 2001). We detail colonization, growth, and rapid decline in this population during 1988-2002, and provide data on within-patch dynamics and scale of movement between patches for black bears.

2. Methods

2.1. Study area

Field work was conducted in Big Bend National Park, Texas, USA. The Park encompasses 320,000 ha of northern Chihuahuan Desert in the Trans-Pecos of western Texas (Fig. 1). Climate of the Big Bend ecosystem is arid. Annual precipitation averages 30.5 cm, with most falling during thunderstorms in July, August, and September. Rainfall accumulations generally increase with elevation in the Park (Powell, 1998). Wauer (1971) recognized 6 habitat associations in the Park region: arroyo-mesquite (*Prosopis* spp.)-Acacia (*Acacia* spp.); lechuguilla (*Agave lechuguilla*)-creosote (*Larrea divaricata*) - cactus; sotol (*Dasyliirion leiophyllum*)-grass; deciduous woodland;

pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.)-oak (*Quercus* spp.) woodland; and cypress (*Cupressus* spp.)-pine-oak.

2.2. Visitor observations

Staff at Big Bend National Park maintain a computer database of all bear observation records by visitors or staff (Skiles, 1995). That database included 14 records from 1901 to 1941, and >3,000 records since Park establishment in 1944. We limited our analysis to records of > 1 bear (i.e., family groups or mating associations) between 1901 and 2002. We examined information in these records (i.e., location, time, date, number of bears observed, age composition of group, and comments) and attempted to estimate the minimum number of adult females with cubs present in any given year. Clusters of observations of family groups in the same general area (e.g., drainage, road mileage marker) were considered to be a single female with cubs. We acknowledge that multiple observations of the same family group were the rule. We report descriptive statistics on visitor observations of multiple bears. Knight et al. (1985) used similar methods for grizzly bears (*Ursus arctos*) in Yellowstone National Park.

2.3. Field methods

Black bears were captured from October 1998 to August 2000 using barrel traps baited with sardines and fish oil. We concentrated efforts in the Chisos Mountains and surrounding terrain at elevations >1,000 m. We used 2 major trapping zones: a low-country trapping zone that encompassed elevations from 1,000 to 1,800 m and a high-country trapping zone that included sites in the high Chisos > 1,800 m. Because it was not feasible to trap in both zones simultaneously, trapping was conducted in either zone, depending on time of year, bear sightings, and weather.

Handling procedures were described in Onorato et al. (2003). All adult bears and subadult bears with body mass >40 kg were fitted with radiotransmitter collars possessing a mortality switch

and breakaway cotton spaces (Hellgren et al., 1988) or expandable rubber tubing inserted between the ends of the collars. Age was estimated via cementum annuli analysis (Willey, 1974) of an extracted premolar by a commercial laboratory (Matson's Laboratory, Milltown, Montana, USA). Subadult bears were considered to be 2- or 3-years old; adults were ≥ 4 -years old. Ear tags were not attached to captured bears.

Trapping data were analyzed to determine trapping success, assess composition of the population, and estimate population size. We estimated population size using a census of the number of bears known alive in 1999 and 2000 (hence, no variance estimates were calculated). We estimated density for males and females, respectively, by dividing the estimates of minimum number known alive by the area that contained the home ranges of all radiotransmitted male and female bears. This area, also known as the composite home range, was 322.9 km² and 78.4 km² for males and females, respectively (Onorato 2003),

Reproductive rate was based on litter size, proportion of female cubs, and reproductive interval (Eberhardt, 1990). Annual and study-period (October 1998–June 2001) survival rates were estimated for each sex using the Kaplan-Meier method with the staggered entry design (Pollock et al., 1989). Because of small samples, all bears ≥ 2 -years old were included in survival rate estimates. Rates were estimated for 2 intervals: denning/summer (January-August) and autumn (September-December). Those intervals were multiplied to provide an annual rate (September-August). Due to the unknown fate of several bears that moved into Mexico in autumn 2000, we calculated survival rates in 2 different ways. Bears that moved to Mexico and whose fate was unknown were considered alive and, alternatively, considered dead. Bears with collars switched to mortality mode were assumed dead. We define migration as movement of an animal from its

resident range in the study area followed by subsequent return to the study area, and dispersal as one-way movement of an animal from its resident range in the study area.

3. Results

3.1. Visitor observations

A total of 576 observations of > 1 bear was made by visitors to Big Bend National Park from 1901 to 2002. Of these observations, females with cubs or yearlings were observed only in 4 years prior to 1988: 1901, 1936, 1969, and 1978. None of those observations was followed by evidence of residency. In 1988, 4 sightings of 2 bears together were made in July. We interpreted these observations to be of breeding associations and evidence of a minimum of 2 adult bears in the population (1M, 1F). After 1988, family groups were observed every year through 2002 (Fig. 2). The minimum number of adult females increased from 1 in 1988 to 6 in 2000, followed by a decline in 2001 to 2 (Fig. 2). Simple correlation analysis revealed a strong association ($r = 0.79$, $P < 0.001$) between visitor observations and estimated minimum number of adult females.

3.2. Population characteristics

Trapping success in Big Bend National Park during the entire study was low (42 captures in 1,763 trapnights; 2.4% success). Trapping success in the low-country zone (35 captures in 1,502 trapnights) and the high-country zone (7 captures in 261 trapnights) were similar. Eleven cubs were marked in dens, and 23 bears were captured in traps (including 2 marked cubs). Thirty bears were marked in the Park, whereas 2 captured bears were not marked. In addition, the skeletal remains of a yearling were found.

Twenty-two bears were known alive in August 1999: 9 females ≥ 1 -yr old, 8 males ≥ 1 -yr-old, and 5 cubs (3M, 1F, and 1 unknown). By March 2000, 29 bears were known alive: 10 females, 11 males, and 8 cubs (Table 1). In the final year of trapping (2000), only 1 new adult (>3-years old)

bear was captured. We also captured 2 yearlings and 3 subadults (2F, 1M) in 2000. All other captures in 2000 ($n = 8$) were either recaptures of adult females or of yearlings previously marked as cubs. Based on this evidence, we believe that we captured $\geq 90\%$ of the bear population that resided in the Chisos Mountains during 1998-2000. A small number of bears may have remained uncaptured, particularly subadult (≤ 3 -years old) males roaming in nearby desert vegetation associations, because our trapping effort was limited at low elevations. However, the only bear captured below 1,300 m was an adult male.

The increase in minimum population size from 2 to 29 individuals from 1988 to 2000 represents an average annual finite growth rate (λ/yr) of 1.25. We estimated population density (including cubs) in the Chisos Mountains to be 5 male and 18 female bears/100 km² in 2000, or 23/100 km² overall in spring 2000. Within the entire Park (3,200 km²), male and female densities were 0.5 and 0.4 bears/100 km², respectively.

Litter size averaged 2.2 ($n = 5$) in dens and 2.0 ($n = 4$) in summer-fall observations. Based on nipple measurements and appearance, 3 bears had their first litters at ages 4, 5, and 6, respectively. Three females that had cubs in 1998 also had litters in 2000. Of 2 bears that had cubs in 1999, 1 did not have cubs in 2000 or 2001, and monitoring of the other bear ended in autumn 2000.

3.3. Migration and Dispersal

We observed movement to Mexico by a large portion (67%-86%) of the population during autumn 2000. Bears exhibited both migration and dispersal movements relative to their resident range in the Big Bend study area. During 17-20 August 2000, 15 collared bears (9 females, 6 males) were accounted for in Big Bend National Park. Between late August and December 2000, 10 of these bears left the Park for areas within Chihuahua and Coahuila, Mexico (Table 2). Three

additional bears were never relocated after August 2000, even with extensive aerial telemetry (Table 2). Our aerial telemetry sessions covered $> 55,000 \text{ km}^2$ to the south (Sierra la Mula), north (Davis Mountains), and east (Serranias del Burro) of the study area. The remaining 2 bears (both males) stayed within Big Bend National Park. No movements to Mexico by radiocollared bears were observed during 1998 and 1999.

Bears traveled 47-128 km from the Chisos Mountains to areas within Mexico during August-December 2000 (Table 2, Fig. 3). Dispersal movements averaged (\pm SD) 76.1 ± 33.9 km for females ($n = 7$) and 92.0 ± 15.4 km for males ($n = 4$). One adult female (bear 7) moved southeast to the Sierra del Carmen in Mexico, returned to Big Bend National Park, then headed west to Chihuahua before her collar went in mortality mode (Table 2, Fig. 3). We believe that bear 7 either slipped her collar (which she had done previously in the Park) or died of natural causes because her collar was remote from any anthropogenic activity. We also documented 3 cases in which bear radiocollars in mortality mode were located in or near ejido towns (bears 8, 9, 16; Table 2) in Mexico. Ejidos are communities that rely on agriculture for subsistence and were initially started as communes for city dwellers that wished to work the land in the 1950s. We suspected poaching loss, although black bears are protected by Mexican law and we could not verify this suspicion. Of the 4 radiocollars of monitored bears located on mortality mode in Mexico during autumn 2000, only 1 (in May 2003) was recovered due to logistical and political constraints. We believe that we should have found most of the bears that were not relocated after August-September 2000 (Table 2; bears 3, 5, 6, 27) based on our extensive telemetry surveying. Because we never obtained signals from those bears, we believe that they may have ventured farther into Mexico than we could reach by aerial telemetry.

Only 2 females and 1 male were known to have returned by spring 2001, making migrations of at least 154, 214, and 178 km (Table 2, Fig. 3). Based on telemetry of collared bears and their cubs, we estimate that only 5-7 bears (3 of which were collared) were in the Park by December 2000. A large decrease (82%) in visitor observations of multiple bears from 2000 to 2001 corroborated our field data (Fig. 2).

Survival over the entire study period was high for the first 2 years of field work but dropped precipitously with the migration and dispersal event (Fig. 4). Estimates of annual survival (September-August) in 1998-99, 1999-2000, and 2000-2001 were 1.0, 1.0 and 0.43 for males, and 1.0, 1.0, and 0.73, respectively, for females when missing bears were considered alive. When bears with unknown fates (emigrants to Mexico) were considered dead, male rates did not change but the female rate dropped to 0.22 in the last year of the study.

4. Discussion

Our findings illustrate the scale of movements made by black bears in a naturally fragmented environment such as the Chihuahuan desert, which contains woodland patches interspersed within a desert matrix. Density estimates based on the entire area of Big Bend National Park were as low as any reported in the literature for black bears (Garshelis, 1994) and underscored the vast amount of desert habitat in the Park that is unsuitable for black bears. In addition, the migration and dispersal event was a clear example of the effects of environmental stochasticity on a small island population. These data documenting movement between bear populations support genetic inferences that black bears in northern Mexico and western Texas exist in a metapopulation structure linked by dispersal (Onorato, 2003). Data from mitochondrial DNA sequences indicated that extant differentiation among these populations is maintained by a single female disperser approximately every 12 years (Onorato et al., 2004). This rate is closely matched

by separate observations of family groups made in Big Bend in 1969, 1978, and 1989, and the migration and dispersal event in 2000 reported here. We acknowledge that data obtained from visitor observations are incomplete and problematic due to lack of verification, variability in Park visitation and data collection since Park establishment in 1944, and fortuitous data collection before Park establishment. However, the regular presence of black bears in the Park since 1988 has led to increased effort by Park staff to improve and standardize reporting of bear sightings.

Excursions by black bears from spring-summer ranges to clumped and abundant food supplies in autumn are well-described (Garshelis and Pelton, 1981; LeCount et al., 1984; Smith, 1985; Rogers, 1987; Hellgren and Vaughan, 1990). These movements were considered seasonal migrations because bears typically returned to their resident ranges. However, the migration and dispersal event observed in Big Bend National Park was remarkable in its magnitude, including the longest recorded movement by a female black bear (Table 2: 128 km). In Minnesota, 4 movements > 90 km, including female movements of 92 and 107 km, were recorded in years of widespread food scarcity (Rogers, 1987).

Proximate causes for the movement to Mexico by bears during autumn 2000 were unclear. Dispersal as a density-dependent response to high density was a possibility, but density estimates for bears in the Chisos Mountains were in the mid-range of densities (7-162 bears/100 km²) described for 23 populations of black bears (Garshelis, 1994). They also were similar or slightly lower than populations in similar vegetation associations in Arizona (24-33 bears/100 km²; LeCount, 1982; Waddell and Brown, 1984) and northern Mexico (35-56/100 km²; Doan-Crider and Hellgren, 1996; Doan-Crider, 2003).

We believe that the main impetus to the movements was a combination of drought and mast failure leading to an imbalance between bear density and resource availability. Distances between

suitable bear habitat in the Chihuahuan desert landscape likely amplified the scale of movement. In Big Bend, defoliation of oak by variable oakleaf caterpillars (*Lochmaeus manteo*) during the previous 2 years (D. P. Onorato, unpublished observations) may have contributed to mast failure. Crops of juniper berries, a major alternative food, in Big Bend also appeared low during these 2 years (D. P. Onorato, unpublished observations). Perhaps insufficient alternative foods led to bears migrating to areas in Mexico with higher food availability in autumn. However, quantitative mast surveys were not conducted in the study area. A mast failure was documented in the nearby Serranias del Burro range in Mexico (Fig. 1) in autumn 2000, but bears enlarged their home ranges within this larger mountain range rather than embark on lengthy migratory movements to ancillary ranges (Doan-Crider, 2003).

The effect of the autumnal migration and dispersal on viability of the population is evident in low annual survival rates of females that more closely correspond to rates observed in hunted populations (Kasworm and Thier, 1994). In addition, female survival in Big Bend was characterized by high interannual variability as a result of environmental stochasticity. Estimates of annual survival rates for adult females in our study (0.22-1.00) were lower and more variable than in other unhunted areas (0.89-0.96; Smith, 1985; Beck, 1991; Kasbohm et al., 1996), including Coahuila (Doan-Crider and Hellgren, 1996; Doan-Crider, 2003). Growth rates of bear populations are sensitive to changes in survival of adult females (Eberhardt, 1990), and this parameter is arguably the most important vital rate in the demography of black bears and other large carnivores. The rates that we observed are not likely to lead to a sustainable population (Eberhardt, 1990).

Our data substantiate the genetic (Onorato et al., 2004) and ecological links between black bears in Big Bend National Park and Coahuila, Mexico, as well as the tenuous viability of this montane island population within the larger metapopulation. It is likely that the population in Big

Bend always will be limited because preferred foods in adequate quantities only occur at high elevations (>1,500 m) and suitable habitat covers <100 km² in the Chisos Mountains. The small area increases the probability of mast failure affecting the entire population. However, populations in the ranges of northern Coahuila are less vulnerable to food failure because of larger habitat patch size (Doan-Crider, 2003) and can provide a steady supply of dispersers to western Texas. Nevertheless, the Big Bend population is an important stepping-stone for natural recolonization of other patches of western Texas that once harbored populations of black bears (Onorato and Hellgren, 2001).

5. Implications to Carnivore Conservation

Restoration of large carnivores, either by natural recolonization as described here or by human intervention, is a conservation issue of considerable interest (Maehr et al., 2001). Regional restoration of large carnivores to the montane islands of southwestern North America requires consideration of social, cultural, political, and ecological concerns (Dugelby et al., 2001). Our observations on this island population of black bears were useful to the ecological context. First, we provided an empirical reminder of the vulnerability of small populations to stochastic events. Large carnivores are especially prone to extinction in small populations because their top-level trophic position constrains them to live at low densities (Woodroffe and Ginsberg, 1998) and leaves them vulnerable to demographic and environmental stochasticity (Beier, 1996). Lande (2002) argued that incorporating stochastic dynamics of local populations into models is important in assessing metapopulation viability.

We have provided data to parameterize models of metapopulations of black bears in fragmented systems by documenting the scale of movement across inhospitable matrix habitat that bears can make to maintain linkages among populations. A recent report of extensive movements

(25-104 km) by translocated male black bears across desert basins in Nevada (Beckmann and Lackey, 2004) supports our work. We emphasize the need to incorporate 2 different survival rates in such a model, a high rate of 0.90-1.00 in normal years and a low rate of < 0.50 (e.g., 0.22 in 2000) in drought or mast failure years. The model could be designed to select these 2 survival rates with a probability equal to their likelihood of occurring over time. We do not advise using the average survival rate from our 3-year study because we suspect that the frequency of catastrophic years is less than 1 in 3 years. Although we do not know the periodicity of mast failures in this system, we speculate that they occur on the scale of ≥ 10 years. Thus, the probability of using the lower survival rate could be set at 0.1. We caution that field estimates of annual variation in survival rates reflect sampling and temporal variability. Gould and Nichols (1998) discussed how to separate sampling variation from total variation to obtain an adjusted estimate of temporal variation in survival rates. Beier (1996) further explored methods of distinguishing demographic from environmental stochasticity in survival estimates.

Our data also offer a cautionary tale about the use of dispersal data in modeling efforts. The spatial scale of metapopulations is set by the scale of recolonization of empty patches, which in turn is set by dispersal distances (Hanski, 2002). Empirical data on dispersal are thus very important for modeling metapopulation viability of other large carnivores. Dispersal distances may be larger in naturally fragmented systems than in contiguous habitat or habitat constrained by anthropogenic development. For example, dispersal of black bears on the Kenai Peninsula in Alaska, which contains contiguous habitat and is constrained by oceanic barriers, did not exceed 30 km (Schwartz and Franzmann, 1992), which is 3 times shorter than the movement distances that we observed. Dispersal by male mountain lions in the anthropogenically-constrained regions of southern California ($\bar{x} = 63$ km; Beier, 1995) and southern Florida ($\bar{x} = 68$ km; Maehr et al., 2002) is

approximately 50% of that reported for the species in the naturally fragmented Chihuahuan desert ($\bar{x} = 116$ km; Sweanor et al., 2000). Similarly, Boyd and Pletscher (1999) stated variability in wolf (*Canis lupus*) dispersal may be a function of human density and landscape patchiness, among other factors. Blundell et al. (2002) added the caution that dispersal distances and immigration rates of river otters (*Lontra canadensis*) may vary due to occupancy of habitat. We recommend that the landscape context under which dispersal data for large carnivores were collected be considered if those data are used for model parameterization.

Strategies in conservation planning for large carnivores typically involve core areas, buffer zones, and landscape linkages (Noss et al. 1996). We believe that this approach is appropriate for carnivores that occur in islands of forest and woodland habitat surrounded by xeric matrix habitat that occur throughout southwestern North America. Indeed, it is being proposed for the sky islands of the Madrean Archipelago (Dugelby et al., 2001). In areas of low human density ($<1/\text{km}^2$) and few high-speed highways, the main barrier to dispersal is simply distance across the desert or grassland matrix. Indeed, Beckmann and Lackey (2004) concluded that desert matrix was not an effective barrier to bear movement in the Great Basin of Nevada. We found for black bears in our study region, as observed for cougars in other Chihuahuan desert habitats (Sweanor et al., 2000), that we could not identify distinct corridors for dispersal between insular mountain ranges. However, with increasing human density and road construction, dispersal of large carnivores among suitable habitat patches will be curtailed and narrowed (Beier, 1995). Maintaining broad landscape linkages that are zoned to control human development and road construction in the desert matrix between montane islands will facilitate continued dispersal among populations by individuals in a carnivore metapopulation.

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References

- Beck, T.D.I., 1991. Black bears of west-central Colorado. Colorado Division of Wildlife Technical Publication Number 39: 1-86.
- Beckmann, J.P., Lackey, C. W., 2004. Are desert basins effective barriers to movements of relocated black bears (*Ursus americanus*)? *Western North American Naturalist* 64, 269-272.

- Beier, P., 1995. Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management* 59, 228-237.
- Beier, P., 1996. Metapopulation models, tenacious tracking, and cougar conservation. In: McCullough, D. R. *Metapopulations and Wildlife Conservation*, Island Press, Washington, D.C., pp. 293-323.
- Beissinger, S.R., Westphal, M.I., 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62, 821-841.
- Blundell, G.M., Ben-David, M., Groves, P., Bowyer, R.T., Geffen, E., 2002. Characteristics of sex-biased dispersal and gene flow in coastal river otters: implications for natural recolonization of extirpated populations. *Molecular Ecology* 11, 289-303.
- Boyd, D.K., Pletscher, D.H., 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. *Journal of Wildlife Management* 63, 1094-1108.
- Brown, J. H., 1971. Mammals on mountaintops: non-equilibrium insular biogeography. *American Naturalist* 105, 467-478.
- Brown, J. H., 1978. The theory of island biogeography and the distribution of boreal birds and mammals. *Great Basin Naturalist Memoirs* 2, 209-227.
- Doan-Crider, D.L., 2003. Movements and spatiotemporal variation in relation to food productivity and distribution, and population dynamics of the Mexican black bear in the Serranias del Burro, Coahuila, Mexico. Ph.D. Dissertation, Texas A&M University-Kingsville, USA.
- Doan-Crider, D.L., Hellgren, E.C., 1996. Population characteristics and winter ecology of black bears in Coahuila, Mexico. *Journal of Wildlife Management* 60, 398-407.
- Dugelby, B.L., Foreman, D., List, R., Miller, B., Humphrey, J., Seidman, M., Howard, R., 2001. Rewilding the sky islands region of the Southwest. In: Maehr, D.S., Noss, R.F., Larkin, J.L.,

- eds. *Large Mammal Restoration: Ecological and Sociological Challenges in the 21st Century*. Island Press, Washington D. C., pp. 65-81.
- Eberhardt, L.L., 1990. Survival rates required to sustain bear populations. *Journal of Wildlife Management* 54, 587-590.
- Garshelis, D.L., 1994. Density-dependent population regulation of black bears. In: Taylor, M., ed. *Density-Dependent Population Regulation of Black, Brown and Polar Bears*. International Association for Bear Research and Management, Missoula, Montana, USA, pp.3-14.
- Garshelis, D.L., Pelton, M. R., 1981. Movements of black bears in the Great Smoky Mountains National Park. *Journal of Wildlife Management* 45, 912-925.
- Gould, W. R., Nichols, J. D., 1998. Estimation of temporal variability of survival in animal populations. *Ecology* 79, 2531-2538.
- Hanski, I.A., 2002. Metapopulations of animals in highly fragmented landscapes and population viability analysis. In: Beissinger, S.R., McCullough, D. R., eds. *Population Viability Analysis*. University of Chicago Press, Chicago, Illinois, USA, pp. 86-108.
- Hanski, I.A., Simberloff, D., 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. In: Hanski, I.A., Gilpin, M.E., eds. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, California, USA, pp. 5-26.
- Hellgren, E.C., Carney, D. W., Garner, N.P., Vaughan, M.R., 1988. Use of breakaway cotton spacers on radio collars. *Wildlife Society Bulletin* 16, 216-218.
- Hellgren, E.C., Vaughan, M.R., 1990. Range dynamics of black bears in Great Dismal Swamp, Virginia-North Carolina. *Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies* 44, 268-278.

- Kasbohm, J.W., Vaughan, M.R., Kraus, J.G., 1996. Effects of gypsy moth infestation on black bear reproduction and survival. *Journal of Wildlife Management* 60, 408-416.
- Kasworm, W.F., Thier, T.J., 1994. Adult black bear reproduction, survival, and mortality sources in northwest Montana. *International Conference on Bear Research and Management* 9, 223-230.
- Knight, R.R., Blanchard, B.M., Eberhardt, L.L., 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. *Wildlife Society Bulletin* 23, 245-248.
- Lande, R., 2002. Incorporating stochasticity in population viability analysis. In: Beissinger, S.R., McCullough, D. R., eds. *Population Viability Analysis*. University of Chicago Press, Chicago, Illinois, USA, pp. 18-40.
- Lawlor, T.E., 1998. Biogeography of Great Basin mammals: paradigm lost? *Journal of Mammalogy* 79, 1111-1130.
- LeCount, A.L., 1982. Population characteristics of Arizona black bears. *Journal of Wildlife Management* 46, 861-868.
- LeCount, A.L., Smith, R.H., Wegge, J.R., 1984. Black bear habitat requirements in Central Arizona. *Arizona Game and Fish Department Report* 14, 1-49.
- Lomolino, M.V., Brown, J.H., Davis, R., 1989. Island biogeography of montane forest mammals in the American Southwest. *Ecology* 70, 180-194.
- Maehr, D.S., Land, E.D., Shindle, D.B., Bass, O.L., Hctor, T.S., 2002. Florida panther dispersal and conservation. *Biological Conservation*. 106,187-197.
- Maehr, D.S., Noss, R. F., Larkin, J.L., eds., 2001. *Large Mammal Restoration: Ecological and Sociological Challenges in the 21st Century*. Island Press, Washington D. C.

- Noss, R.F., Quigley, H.B., Hornocker, M.G., Merrill, T., Paquet, P.C., 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* 119, 949-963.
- Onorato, D. P. 2003. Conservation ecology of the metapopulation of black bears in the Big Bend ecosystem. Ph.D. Dissertation, Oklahoma State University, Stillwater, 156pp.
- Onorato, D.P., Hellgren, E.C., 2001. Black bear at the border: the recolonization of the Trans-Pecos. In: Maehr, D.S., Noss, R.F., Larkin, J.L., eds. *Large Mammal Restoration: Ecological and Sociological Challenges in the 21st Century*. Island Press, Washington D. C., pp. 245-259.
- Onorato, D.P., Hellgren, E.C., Van Den Bussche, R.A., Crider, D.L.D., 2004. Phylogeographic patterns within a metapopulation of black bears (*Ursus americanus*) in the American Southwest. *Journal of Mammalogy* 85, 140-147.
- Onorato, D. P., Hellgren, E.C., Mitchell, F.S., Skiles, J.R., Jr., 2003. Ecology of American black bears on a desert montane island. *Ursus* 14, 120-129.
- Pelton, M. R. 2003. Black bear. In: Feldhamer, G. A., Thompson, B.C., Chapman, J. A., eds. *Wild Mammals of North America: Biology, Management, and Conservation*. Johns Hopkins University Press, Baltimore, Maryland, USA, pp. 547-555.
- Pollock, K.H., Winterstein, S.R., Bunck, C.M., Curtis, P.D., 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53, 7-15.
- Powell, A.M., 1998. *Trees and Shrubs of the Trans-Pecos and Adjacent Areas*. University of Texas Press, Austin, Texas, USA.
- Rogers, L.L., 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. *Wildlife Monographs* 97, 1-72.

- Schwartz, C.C., Franzmann, A.W., 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. *Journal of Wildlife Management* 56, 426-431.
- Skiles, J.R., 1995. Black bears in Big Bend National Park- the Tex-Mex connection. *Western Workshop on Black Bear Research and Management* 5, 67-73.
- Smith, T.R., 1985. Ecology of black bears in a bottomland hardwood forest in Arkansas. Ph.D. Dissertation, University of Tennessee, Knoxville, USA, 209pp.
- Sweaner, L.L., Logan, K.A., Hornocker, M.G., 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology* 14, 798-808.
- Waddell, T.E., Brown, D.E., 1984. Exploitation of two subpopulations of black bears in an isolated mountain range. *Journal of Wildlife Management* 48, 933-938.
- Warshall, P., 1994. The Madrean sky island archipelago: a planetary overview. In: Debano, L. F., Ffolliott, P.F., Ortega-Rubio, A., Gottfried, G.J., Hamre, R. H., Edminster, C.B., tech. coords. *Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico*. U.S. Department of Agriculture, Forest Service General Technical Report RM-GTR-264, pp.6-19.
- Wauer, R.H., 1971. Ecological distribution of birds of the Chisos Mountains, Texas. *The Southwestern Naturalist* 16, 1-29.
- Willey, C.H., 1974. Aging black bears from first premolar tooth sections. *Journal of Wildlife Management* 38, 97-100.
- Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280, 2126-2128.

Figure Captions

Figure 1. Depiction of mainland (Serranias del Burro and Sierra del Carmen) and island (Chisos Mountains, Glass Mountains, Davis Mountains, Del Norte Mountains, Chinati Mountains, Sierra la Rica) patches that have supported extant and historical populations of black bears in the Trans-Pecos region of Texas and Mexico. Boundaries of mountain ranges are defined by the 1,500-m isocline, which approximates the distribution of woodland habitats in the Chihuahuan desert matrix.

Figure 2. Annual number of visitor observations of > 1 bear (i.e., family groups or mating associations; solid squares) and estimated number of adult females (open circles) in Big Bend National Park, Texas from 1988 to 2002.

Figure 3. Geographic depiction of dispersal (missing and mortality) and migrational movements and fates of radio-collared black bears from Big Bend National Park, Texas into Mexico in autumn 2000. See Figure 1 for names of mountain ranges.

Figure 4. Survival curves for female black bears (≥ 2 -years old) in Big Bend National Park from October 1998 to May 2001. Different curves represent survival calculation assuming bears missing from migration into Mexico in fall 2000 were alive (solid line) or dead (dotted line).

Table 1. Sex and age distribution of the population of black bears in Big Bend National Park, Texas, at the time of peak population, March 2000.

Age class	Females	Males
0 (cubs)	4	4
1	1	3
2	1	3
3	2	3
4-7	3	0
8-10	2	2
> 10	1	0

Table 2. Dispersal and migration data collected on black bears that moved into northern Mexico from Big Bend National Park in summer 2000.

Bear ID	Sex	Age	Distance and direction of longest movement from the Chisos Basin (km)		Longest movement distance from U.S.-Mexican border (km)	Location of longest dispersal	Fate
1	F	7	77	SE	46	Maderas del Carmen	Returned December 2000
2	F	6 ^a	29	SE		Mariscal Mountain	Mortality in BIBE
3	F	8 ^a	47	E	6	Canyon el Diablo	Unknown
4	F	2	128	SE	92	Eutimias ejido	Unknown
5	F	5 ^a	?	?	?	?	Unknown
6	F	10 ^a	?	?	?	?	Unknown
7	F	16	80	SE	40	Maderas del Carmen	Returned 10 October 2000
7	F	16	65	W	20	19 km west of Lajitas	Unknown- collar on mortality mode
8	M	2	115	SSE	78	Eutimias ejido	Unknown- collar on mortality mode
9	M	2	87	SW	56	Rancho Los Morteros	Unknown- collar on mortality mode
10	M	3	89	SE	53	Sierra la Vasca	Returned May 2001
16	M	1	80	S	48	8 km north of Ejido Rosita	Unknown- collar on mortality mode
27	F	3	?	?	?	?	Unknown
29	F	3	107	SE	75	Sierra la Encantada	Returned April 2001

^a with cubs of the year







