CONSERVATION ECOLOGY OF THE METAPOPULATION OF BLACK BEARS IN THE BIG BEND ECOSYSTEM

By

DAVID PAUL ONORATO

Bachelor of Science
Eckerd College
St. Petersburg, Florida
1991

Master of Science
University of Alabama at Birmingham
Birmingham, Alabama
1997

Submitted to the Faculty of the
Graduate College of
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
May, 2003

CONSERVATION ECOLOGY OF THE METAPOPULATION OF BLACK BEARS IN THE BIG BEND ECOSYSTEM

Thesis Approved:

Thesis Advisor

Dean of the Graduate College

ACKNOWLEDGMENTS

I would like to express my sincere appreciation to my major advisor, Dr. Eric C. Hellgren. Five years ago, he rewarded me with the opportunity of a lifetime. My lifelong ambition to conduct conservation research on a large carnivore has truly been an enjoyable experience. I am indebted to him for having taken a chance hiring a one-time fisheries biologist to complete this research in one of the most unique ecosystems in North America. He has been influential on my development as a scientist which will ultimately permit me to succeed in whatever employment opportunity I obtain.

Additionally, I thank Dr. Ronald A. Van Den Bussche for his mentoring and insight into the field of conservation genetics. He has basically served as a co-advisor on my committee due to his knowledge of the topic that comprised a major portion of my dissertation. I am thankful for the assistance and experience that he has imparted to me, and the interest the he instilled in me with regards to a field that I was initially hesitant to tackle.

I would also like to thank Drs. David M. Leslie Jr. and Samuel D. Fuhlendorf. As committee members they have been very helpful with manuscript edits and suggestions that have made my dissertation more robust. Additional gratitude is imparted to the Oklahoma Cooperative Fish and Wildlife Research Unit (OCFWRU) at Oklahoma State including staff members Judy Gray, Sheryl Lyon, and Helen Murray. Without their administrative skills and pleasant demeanor, my extensive field time would have been much more difficult and likely impossible. The field vehicle that I used extensively during my field tenure was invaluable and additional gratitude to the OCFWRU must be duly noted. The Department of Zoology at Oklahoma State University has also been instrumental in helping me complete my dissertation research in a variety of facets. I thank Dr. Shaw and the entire administrative staff for the assistance given over the past 5 years.

Two people that were influential to my field research in Big Bend National Park (BIBE) were Raymond Skiles (NPS) and Scott Mitchell (SRSU). Raymond served as my park liaison in BIBE and provided an immense amount of local knowledge and insight into the Chihuahuan desert ecosystem and life in general in the Trans-Pecos. His persistence in helping obtain funding for this project with Dr. Hellgren ultimately provided the opportunity for me to obtain this degree. I am most appreciative for everything he as done. Scott and I worked together on the field portion of this project for the first two years (1998-2000) while he completed his master degree at Sul Ross State University in Alpine. Scott, my first introduction to a true Texan, was very influential in helping me gain a better understanding of bears, trapping, telemetry, den searches, and numerous other skills. We enjoyed so many unforgettable and varied experiences during our treks throughout the park in search of bears, bear sign etc. I will always remember our experiences in the fondest way. Raymond and Scott are truly lifelong friends.

I would also like to thank Bonnie and Billy Pat McKinney. They were both instrumental in helping me learn more about west Texas, and the history of black bears in the region. Numerous discussions on black bears, especially with Bonnie, helped both of our projects. Also, introducing me to the populations of black bears in the Black Gap

Wildlife Management Area and the Rancho los Pilares in Coahuila broadened my perspective in terms of understanding the range of habitats that desert black bears inhabit and in turn are capable of surviving in. I am indebted to them for these experiences and look forward to the continuation of our friendships in the years to come.

Diana Doan-Crider provided additional tissue samples from the Serranias del Burro in Coahuila Mexico. Without these samples, a large part of my dissertation would be incomplete. I thank her and all of her assistants for providing me with these samples. Additionally, Diana has been very helpful in helping me gain a better understanding of the sociopolitical challenges facing ranchers and black bears on ranches in northern Mexico. Thanks for sharing your knowledge.

The field component of my research could not have been completed were it not for the help of numerous field volunteers, park employees, and others. I note my sincere appreciation to all of the following: Betty Alex, Vidal Davila, Jessica Erickson, Nick Herring, Meghan Hicks, Maral Kasparian, Patricia Luce, Kent Miller, John Morlock, Dan Muntean, Jon Rodman, Eric Stroker, Catherine Tredick, Eric Walker, Dave Yim, Mark Yuhaus, Jon Zubia, BIBE-NPS Trail Crew and the pack mules, Big Bend Natural History Association, and numerous other field technicians.

The friendships that I have forged during my tenure in the department of Zoology have been instrumental in helping me develop as a scientist and person. I thank the all of the graduate students from years past and present for their informative discussions and our enjoyable experiences. I am extensively indebted to members of Ron Van Den Bussche's lab whom answered my plethora of questions during many late nights working in the lab. Included among these are: Derrick Chappell, Sara Weyandt, Greg Wilson, Russell Pfau, Sara Moore, Eric Hansen, Raymond Ary, and Steve Hoofer. Without their assistance and camaraderie, my initial trials and tribulations in the lab would have been much more difficult to endure.

Special thanks go to George Vose and Marc Criffield. George was our primary pilot for radiotelemetry data collection during the duration of this project. The rest of the field crew and I enjoyed our flights with George and the recounting of his extensive travels and wildlife experiences. He is a truly generous man as demonstrated through his continuation of data collection for us, long after our funding has been depleted. Our flights over the mountains of Mexico and Chihuahuan Desert lowlands gave me the necessary perspective to interpret the challenges faced by black bears in this ecosystem. Marc Criffield, whom served as a field technician for a year (2000-2001), was instrumental in finding dens in the winter of 2000 and helped obtain additional data during the extensive migration-dispersal event that we were fortunate to witness during our last complete field season. His effort, always above and beyond the call of duty, was truly appreciated and his friendship made my final field season in BIBE a true experience.

There are several personal relationships that have been influential in the completion of my dissertation. Shauna Ginger became an important part of my life during my time at OSU and was helpful with support in the field, at school and in our personal relationship. Our time and experiences together is something that I will always cherish and look back to fondly. I could not have done this without her.

I express my sincere thanks to my deceased Grandparents (Onorato and Gatto) whom instilled values and a work ethic that has helped me forge ahead when situations appeared discouraging. Additionally, my experiences with naturalist Herbert Zim and my grandmother Grace Zim in the Florida Keys during my childhood and teenage years were influential in molding my interest in nature and ultimately lead me to the field that I presently pursue. You are all in my thoughts.

Lastly I would like to thank my Mom and Dad (Louise Showe and Frederick Onorato) and family members Michael Showe, Jennifer Showe, Cheryl Onorato, Jennifer Onorato and Gregory Onorato. They of course have been the most influential figures in my life. Without their assistance through the many trials and tribulations that we have faced over the years, I would have not been able to complete this degree. Their support has been Herculean from day 1. I cherish all of my lifelong experiences with you and look forward to spending more of them in the years to come.

TABLE OF CONTENTS

Chapter Page

LIST OF TABLES

Table Page

Chapter II

Chapter III

Table Page

Chapter IV

Chapter V

LIST OF FIGURES

Figure Page

Chapter I

Chapter II

Chapter III

Chapter IV

Chapter V

CHAPTER I

FROM EXTIRPATION TO RECOLONIZATION: A HISTORICAL PERSPECTIVE ON THE RETURN OF THE BLACK BEAR TO THE TRANS-PECOS REGION OF TEXAS

DAVID P. ONORATO

Introduction

Natural recolonization of historical range (defined as natural reestablishment by a species in an area of past extirpation) by large carnivores is rare in part because of habitat fragmentation, disturbance, and destruction. Recolonization by gray wolves (*Canis lupus*) has been documented in 8 areas in North America and Europe, but wolves crossed extensive areas of farmland to recolonize wildlands in only 2 of these cases (Wydeven et al. 1998). Smith and Clark (1994) described the reintroduction of American black bears (*Ursus americanus*) to Arkansas as one of the most successful translocations of a large carnivore. This effort led to recolonization of large tracts of forest far from reintroduction sites (Smith and Clark 1994). Populations of black bear are increasing in most parts of their geographic range (Brown 1993; Pelton and van Manen 1994), and this increase is associated with an expanding distribution (Pelton and van Manen 1994). However, as with wolves, black bears can more effectively expand their range through contiguous forest and riparian corridors, and not across extensive areas of unsuitable matrix, such as agricultural lands or desert (Brody and Pelton 1989; Mladenoff et al. 1995; Mollohan and LeCount 1989).

The return of black bear populations to the borderlands of western Texas has occurred during the last decade. This recolonization has resulted from the coalescing of biogeographic, ecological, and sociological factors. In this paper, we discuss the history of the black bear in the Trans-Pecos region, summarize available data on its natural recolonization, and explore factors that have facilitated recolonization. We propose that the black bear in the western Texas-Mexico border zone provides a useful case study for modeling the spatio-temporal patterns of large carnivore recolonization in a naturally patchy landscape.

The Landscape

The Trans-Pecos region of Texas is dominated by Chihuahuan desert vegetation and scattered mountain ranges that occasionally reach elevations high enough (1,500-2,000 m) to support woodlands and black bear. Four ranges have elevations that exceed 2,000 m, and support coniferous, oak, and mixed forests: the Chisos, Davis, Chinati, and Guadalupe ranges (Figure 1). Several other lower-elevation mountain ranges also occur across the region, including the Glass, Del Norte, Dead Horse (northern extension of the Sierra del Carmen of Coahuila Mexico), Sierra Diablo, and Rosillos Mountains. The result is a landscape of mountain islands of bear habitat amid a sea of Chihuahuan desert scrub and grassland (Figure 1).

Historical Background

Much of the information on the history of black bear in the Trans-Pecos is only available via conversations with local ranchers and other residents in the area. Two individuals who have pursued a personal interest in such information are Dr. James F. Scudday and Billy Pat McKinney. Dr. Scudday is a Distinguished Professor Emeritus in Biology at Sul Ross State University in Alpine, Texas. His family settled in this small west Texas town in 1926. During the last 70 years he has developed a good rapport with the local ranchers and hunters of the Trans-Pecos region and frequently served as a link between state agencies and ranchers when bear incidents have arisen. He has compiled a vast amount of descriptive and anecdotal information on black bears, so he is an invaluable source for a historical perspective on black bear in this region.

The McKinney family initially settled the Big Bend region of Texas in 1878. Five generations of McKinney's have remained in the area and have witnessed many of the changes that have occurred in this region in the last 120 years. Billy Pat McKinney is a wildlife specialist for the Texas Parks and Wildlife Department at the Black Gap Wildlife Management Area (BGWMA) in Brewster County, Texas. His grandfather was a federal predator control agent in the early 1900's involved with the control program for the Mexican wolf (*Canis lupus baileyi*). His father was involved with predator control as well, mostly dealing with golden eagle (*Aquila chrysaetos*) control. The vast oral library compiled over the generations combined with Mr. McKinney's more recent personal experiences provide unique insight on the fate of large carnivores, including black bears, in the Trans-Pecos.

The black bear was prevalent throughout most of western Texas (Davis and Schmidly 1994) in pre-Columbian times, but were rarely hunted by indigenous peoples. However, bears were hunted in western Texas with firearms in the late 1800's (J. Scudday, Department of Biology, Sul Ross State University, personal communication, Skiles 1995). At the turn of the century, naturalist Vernon Bailey (1905) described bears as common in the Chisos, Davis, and Guadalupe Mountains. Black bears also were common in the adjacent mountain ranges of Mexico, such as the Sierra del Carmen and the Serranias del Burro (Figure 1). Predator control and intense hunting in the first half of the 20th century led to the near extirpation of black bear from the region (Doan-Crider and Hellgren 1995; J. Scudday, Department of Biology, Sul Ross State University, personal communication).

By 1918, federal predator control agents were using poison bait to control the Mexican wolf in the Trans-Pecos. Such bait was usually a cow or horse carcass laced with strychnine (J. Scudday, Department of Biology, Sul Ross State University, personal communication). This technique, although effective, was not species-specific and contributed to the decline of other southwestern carnivores, including the grizzly bear (*Ursus arctos*, Brown 1985) and the black bear in the Trans-Pecos. Use of poisoned bait continued until the 1950's (J. Scudday, Department of Biology, Sul Ross State University, personal communication).

Bear populations in Mexico and the United States were subject to intensive hunting during the late 19th and early 20th centuries. Organized bear hunts that coincided with family outings were common in the Trans-Pecos during the early 20th century, particularly in the Davis Mountains (J. Scudday, Department of Biology, Sul

Ross State University, personal communication). During this time, bears were particularly prized for their meat and lard. Sport hunters continued to take a toll on the black bear in Texas during the 30's and 40's. Groups of hunters would make their way to western Texas from as far as Austin and Houston in search of black bear (J. Scudday, Department of Biology, Sul Ross State University, personal communication).

Populations of black bear in the United States and Mexico were characterized by differing dynamics in the 1930's. With the nationalization of Mexico, American ranchers were evicted. Many new Mexican landowners and ranchers did not have the same hunting technology as their American predecessors, and therefore were not able to locate and kill bears as effectively. Mexican ranchers also have historically developed a tolerance for predators and are willing to accept some stock loss (Doan-Crider 1995). Some ranchers in Mexico even view presence of bears on their ranch as a status symbol (B. P. McKinney, Texas Parks and Wildlife Department, personal communication). The combination of generally positive rancher attitudes and low hunting pressure allowed viable bear populations to persist in the Sierra del Carmen and Serranias del Burro mountains (Figure 1). Conversely, American ranchers were fervent in their negative attitudes toward predators. Sheep ranchers were particularly ardent when it came to predator control. The sheep industry in Texas was very powerful and produced more wool than any other state in the country during the 1930's and 40's (Carlson 1982). That disposition, combined with pressure to produce wool for the war effort during World War II, sped the decline of large carnivores not only in western Texas but the entire southwestern United States (Brown 1985, B. P. McKinney, Texas Parks and Wildlife Department, personal communication).

In our interview with B. P. McKinney, he recounted the story told to him by his grandfather concerning two prospectors who hunted in the Big Bend region. Bud Kimble, an experienced hunter from the Big Thicket region of eastern Texas, and John Moss reported the harvest of a grizzly bear on Pulliam Ridge in what is now Big Bend National Park (BIBE) during 1902 or 1903 (B. P. McKinney, Texas Parks and Wildlife Department, personal communication). Kimble noted that this exceptionally large bear (estimated at 275 kg) had silver-tipped hair, a characteristic noted in other grizzly reports from the southern extent of its range (Schmidly 1977). Kimble also noted that the packhorse was unable to carry the carcass of this bear. The only confirmed record of a grizzly bear in Texas was a large male killed in the Davis Mountains in 1890 (Brown 1985).

The combined factors of sport hunting, federal predator control programs, and persecution by ranchers noticeably reduced the black bear population in western Texas by the middle of the 20th century. Livestock overgrazing also contributed to habitat degradation (Schmidly 1977). Many of the bear hunts that took place in the 1940's and 1950's were unsuccessful (B. P. McKinney, Texas Parks and Wildlife Department, personal communication). By the 1940's, the black bear was extirpated from the Del Norte and Glass Mountains, and remnant populations survived in the Chisos (Borell and Bryant 1942) and Davis Mountains (B. P. McKinney, Texas Parks and Wildlife Department, personal communication). Those populations disappeared by the 1950's.

During the 1950's, the sheep industry in the Trans-Pecos region of Texas began to falter (Carlson 1982). The end of World War II, combined with a severe drought, caused many ranchers to abandon wool production (Carlson 1982; B. P. McKinney, Texas Parks and Wildlife Department, personal communication). This economic change provided the opportunity for black bears to recolonize the Big Bend region of Texas. When BIBE was established in 1944, bears rarely were seen (Figure 2; Big Bend National Park black bear sightings database), and those that were observed were likely transient males. During the 1960's, several yearling-sized bears were killed on the Adams Ranch northeast of BIBE. These were likely young males migrating from the Sierra del Carmen Mountains (B. P. McKinney, Texas Parks and Wildlife Department, personal communication).

Schmidly (1977) reported no evidence of resident black bears anywhere in the Trans-Pecos during the late 1970's. Although populations in the adjacent mountains of Mexico had been reduced (Baker and Greer 1962; Hall 1981; Leopold 1959), a reproductively viable population remained (Doan-Crider and Hellgren 1996). After Mexico declared a moratorium on black bear hunts in 1986 (Doan-Crider and Hellgren 1996), the stage was set for local population recovery and recolonization of vacant habitat in the Chisos Mountains.

The Recolonization Process

When discussing the recolonization of black bear in the Big Bend region, it is interesting to compare this event with the factors that inhibited grizzly bear recolonization in the southwestern United States and northern Mexico. Records denote that southwestern grizzly bears once ranged from the San Juan Mountains in southern Colorado to mountain ranges in southern Chihuahua, Mexico (Brown 1985). Unlike the situation with black bear in the Trans-Pecos, grizzly bear populations in the southwest were separated by longer distances and were smaller in size. Therefore, when anthropogenic pressures reduced grizzly numbers during the late 1800's and early 1900's, populations were so disjunct and separated by such great distances that recolonization of vacant historic habitat could not proceed. The result was isolation of the remaining populations and eventual extirpation of the species within this geographic region of the United States (Brown 1985). In contrast, the proximity of a large population of black bears in Mexico allowed the black bear to return to the Big Bend ecosystem in the Trans-Pecos.

The recolonization of the Trans-Pecos by black bear was a slow process that took many decades to complete. Infrequent black bear sightings in the park occurred from 1950 through the 1970's (Figure 2; Big Bend National Park black bear sightings database 1999). Two observations in 1969 and 1978 involved females with cubs, but park wildlife specialists believed that a resident breeding population did not exist in the park during that period (Skiles 1995). Over the next 10 years, bears made occasional appearances in the park. Again, those bears were likely young males dispersing from their natal home range in Serranias del Burro and Sierra del Carmen mountain ranges in Mexico (Doan-Crider 1995; Skiles 1995). The continued observation of such bears would later confirm that the Chisos Mountains of BIBE contained suitable habitat for black bear (LeCount and Mollohan 1995). This habitat was similar in some respects to that occupied by black bears in central Arizona (LeCount et al. 1984). The minimal requirement for a resident population to be established in BIBE was for a female to become resident in the Chisos Mountains.

Increasing black bear observations in the park during the late 1980s gave credence to the plausibility of a resident population in BIBE. In 1988, Park employees recorded 26 observations of bears. Over the next 10 years, employees recorded 2,127 observations

(Figure 2; Big Bend National Park black bear sightings database 1999), including numerous sightings of females with cubs and yearlings. The Park presently maintains a resident, breeding black bear population in the Chisos Mountains (Davis and Schmidly 1994).

The metapopulation approach (Hanski and Simberloff 1997) provides a useful conceptual structure to understand the recolonization process in the Trans-Pecos. Metapopulations are populations spatially structured into local breeding populations whose dynamics are influenced by migration among the local units (Hanski and Simberloff 1997). Several possible metapopulation systems may be applicable to the Big Bend Ecosystem, including the source-sink, rescue effect, and mainland-island metapopulation systems. The black bear population in the Chisos Mountains may have once been part of a source-sink metapopulation, with the larger population in Mexico serving as a source. Sinks are described as populations that typically have a reproductive rate (R_0) that is <1 (Stacey et al. 1997) and would go extinct without immigration. Due to the human pressures in the early 20th century discussed above, the entire Trans-Pecos region became a sink for Mexican bears. The key characteristic to this type of metapopulation is that the direction of migration is invariable over time (Stacey et al. 1997). The presence of a growing population in BIBE (Davis and Schmidly 1994) and the migration of bears from the Trans-Pecos back into Mexico (Onorato et al. 2002; Bonnie R. McKinney, Texas Parks and Wildlife Department, unpublished data) demonstrate that the source-sink model is no longer at work in this region.

The rescue-effect metapopulation system entails migration that helps avert local population extinctions. This system is characterized by stochastic deviation within the direction and rate of migration (Stacey et al. 1997). Consequently, the population that is designated as either the source or the sink can be variable through time (Harrison 1991; Stacey and Taper 1992). At present, there is little doubt that Mexico continues to be the source of immigrating black bears for the Trans-Pecos region of Texas. Therefore, we believe that the mainland-island metapopulation model is the most appropriate for this particular region. Small, suitable habitat patches (e.g., BIBE and BGWMA) are located within dispersal distance from a very large habitat patch (e.g., Mexico) that supports a perennial population (Hanski and Simberloff 1997). A large, reproductively viable bear population resides in the Sierra del Carmen and Serranias del Burro Mountain ranges of Mexico (Doan-Crider and Hellgren 1996). As those populations have grown, bears have dispersed across the Rio Grande River to BIBE and the BGWMA (Figure 1). These 2 habitat patches may serve as stepping-stones for future colonizations.

Mountain ranges of the Trans-Pecos that once supported black bear are the next likely recolonization sites. These include the Davis, Del Norte, and Glass Mountains located north of the Chisos (Figure. 1). Other regions of potential recolonization include the Chinati and Housetop Mountains (B. P. McKinney, Texas Parks and Wildlife Department, personal communication), and Val Verde County near Amistad National Recreational Area (J. Scudday, Department of Biology, Sul Ross State University, personal communication). Black bears are returning to western Texas, but whether they will be tolerated or persecuted as they venture from public land into private lands remains to be seen.

Conservation and Research Implications

What does our review of historical records on recolonization of black bears mean from regional and global perspectives? Regionally, the temporal scale at which black bears will recolonize disjunct mountain ranges in Trans-Pecos Texas is likely to require multiple decades. This process could be shortened, however, by translocating females to suitable habitat that is within male dispersal distance. In contiguous habitat, black bear populations expand their distribution by incremental range expansion by related females (Rogers 1987). Possible translocation sites include the Chinati, Davis, and Glass Mountains, which have supported bears in post-Columbian times. Bears have been sighted in the latter 2 of these ranges in the past few years (B. McKinney, Texas Parks and Wildlife Department, personal communication). Restoration through translocation in these areas would enlarge and stabilize the functional mainland-island black bear metapopulation presently found in the Trans-Pecos.

Natural recolonization by black bears provides an opportunity to investigate conservation genetics, metapopulation theory, and social organization in the species. For example, Rogers (1987) demonstrated female philopatry and a female land-tenure system in a regional black bear population in northern Minnesota. His work predicts that the distribution of female bears in a recolonized area will expand as a series of partially overlapping ranges composed of female offspring of the original resident(s). Conversely, male offspring should either disperse or become residents during the early periods of the recolonization process. Females may exhibit very high relatedness if a single founder is responsible for an extant breeding population. The spatial relationships among females of known genetic relationships would also prove interesting. These data could test Roger's

(1987) observations that female philopatry should be expressed in genetic relatedness among females found in adjacent home ranges. Initial work on this question in a bear population in contiguous habitat showed no relationship between female relatedness and range overlap (Schenk et al. 1998). A newly re-established population may produce a different result due to the specific metapopulation factors involved.

Natural recolonization by black bear will also shed light on what constitutes a barrier to dispersal in this and other ursids, thanks to genetic analyses. For example, analysis of maternally and biparentally inherited genetic markers can affirm the identity of a source population. Among brown bears, nuclear microsatellite markers showed that water barriers of 2-4 km were adequate to reduce or eliminate female dispersal, whereas 7 km was adequate to similarly affect male dispersal (Paetkau et al. 1998). These barriers led to genetic differences among insular and continental populations. Similarly, recolonization of the Trans-Pecos by black bear has occurred in spite of a 35-km terrestrial barrier (i.e., Chihuahuan desert). Techniques involving the analyses of the mtDNA control region (maternal) and microsatellites (biparental) also have been used for studies of regional genetic variation (Paetkau and Strobeck 1994) and phylogeography (Paetkau and Strobeck 1996) in black bears.

Black bear recolonization in the Trans-Pecos provides a useful case study for modeling the spatio-temporal rate of unassisted large carnivore recolonization in a naturally fragmented landscape. The historical evidence in the Trans-Pecos supports Avise's (1995) contention that large carnivores with limited female dispersal will be slow to recolonize disjunct portions of their range from which they have been extirpated. Species with common female dispersal, such as gray wolves (Boyd-Heger and Pletscher

1999) or mountain lions (*Felis concolor,* Sweanor et al. 2000) are more likely to recolonize vacant range, even if that range is fragmented by natural or anthropogenic forces. However, female dispersal in geographically expanding populations of bears may be greater than previously believed, as observed for brown bears in Sweden (Swenson et al. 1998). Swenson et al. (1998) suggests that dispersal behavior in large mammals in continuous populations may be different than along the periphery of populations expanding into vacant habitat. Increased female dispersal in the latter situation obviously would benefit the conservation and restoration of these species, and help maintain metapopulations (Swenson et al. 1998). Meta-analysis of dispersal data from the periphery and cores of expanding populations of large mammals are needed to test this hypothesis.

Acknowledgments

We thank R. K. Skiles for his persistence in supporting the fieldwork that will form the supplement to this paper. We thank D. L. D. Crider and B. R. McKinney, who have contributed samples to the genetic analyses, and B. P. McKinney and J. Scudday for sharing their historical experience on black bears in the region. This paper was supported by funding from the Natural Resources Preservation Program, through the U.S. Geological Survey and the National Park Service, and logistical support from the Oklahoma Cooperative Fish and Wildlife Research Unit (U.S. Geological Survey-Biological Resources Division, Oklahoma State University, Oklahoma Department of Wildlife Conservation, and Wildlife Management Institute, cooperating).

Literature Cited

AVISE, J. C. 1995. Mitochondrial DNA polymorphism and a connection between genetics and demography of relevance to conservation. Conservation Biology 9:686-690.

BAILEY, V. 1905. Biological Survey of Texas. Department of Agriculture, Bureau of Biological Survey, Vol. 25.

BAKER, R. H., and J. K. GREER. 1962. Mammals of the Mexican state of Durango. Publications of the Museum, Michigan State University. Biological series 2:25-154.

BORELL, A. E., and M. D. BRYANT. 1942. Mammals of the Big Bend area of Texas. University of California Publication of Zoology 48:1-62.

BOYD-HEGER, D. K., and D. H. PLETSCHER. 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. Journal of Wildlife Management 63:1094-1108.

BRODY, A. J., and M. R. PELTON. 1989. Effects of roads on black bear movements in western North Carolina. Wildlife Society Bulletin 17:5-10.

BROWN, D. E. 1985. The grizzly in the southwest. University of Oklahoma Press, Norman, Oklahoma.

BROWN, G. 1993. The Great Bear Almanac. Lyons and Burford Publishers, New York.

CARLSON, P. H. 1982. Texas woolybacks. Texas A&M University Press, College Station, Texas.

DAVIS, W. B., and D. J. SCHMIDLY. 1994. The mammals of Texas. Texas Parks and Wildlife Press, Austin, Texas.

DOAN-CRIDER, D. L. 1995. Population characteristics and home range dynamics of the black bear in northern Coahuila, Mexico. Masters thesis, Texas A&M University-Kingsville, Kingsville, Texas.

DOAN-CRIDER, D. L., and E. C. HELLGREN. 1996. Population characteristics and winter ecology of black bears in Coahuila, Mexico. Journal of Wildlife Management 60:398-407.

HALL, E. R. 1981. The mammals of North America. 2nd ed. John Wiley and Sons, New York.

HANSKI, I. A., and D. SIMBERLOFF. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation, Pp. 5-26 in Metapopulation biology: ecology, genetics, and evolution (I. A. Hanski and M. E. Gilpin, eds.). Academic Press, San Diego, California.

HARRISON, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnaen Society 42:73-88.

LECOUNT, A. L., and C. MOLLOHAN. 1995. Big Bend National Park bear reconnaissance. National Park Service, 29pp.

LECOUNT, A. L., R. H. SMITH, and J. R. WEGGE. 1984. Black bear habitat requirements in Central Arizona. Arizona Game and Fish Department, Report No.14.

LEOPOLD, A. S. 1959. Wildlife of México. University of California Press, Berkeley.

MLADENOFF, D. J., T. A. SICKLEY, R. G. HAIGHT, and A. P. WYDEVEN. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conservation Biology 9:279-294.

MOLLOHAN, C. M., and A. L. LECOUNT. 1989. Problems of maintaining a viable black bear population in a fragmented forest, Pp. 149-159 in Conference on Multiresource Management of Ponderosa Pine Forests. Northern Arizona University.

ONORATO, D. P., E. C. HELLGREN, R. A. VAN DEN BUSSCHE, and D. M. LESLIE, JR. 2002. Conservation ecology of an isolated population of black bears in the Big Bend Ecosystem. National Park Service, Final Report, Project 97-08: 1-54.

PAETKAU, D., G. F. SHIELDS, and C. STROBECK. 1998. Gene flow between insular, coastal and interior populations of brown bears in Alaska. Molecular Ecology 7:1283-1292.

PAETKAU, D., and C. STROBECK. 1994. Microsatellite analysis of genetic variation in black bear populations. Molecular Ecology 3:489-495.

PAETKAU, D., and C. STROBECK. 1996. Mitochondrial DNA and the phylogeography of Newfoundland black bears. Canadian Journal of Zoology 74:192-196.

PELTON, M. R., and F. T. VAN MANEN. 1994. Distribution of black bears in North America. Eastern Workshop on Black Bear Research and Management 12:133-138.

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.

SCHENK, A., M. E. OBBARD, and K. M. KOVACS. 1998. Genetic relatedness and home-range overlap among female black bears (*Ursus americanus*) in northern Ontario, Canada. Canadian Journal of Zoology 76:1511-1519.

SCHMIDLY, D. J. 1977. The mammals of Trans-Pecos Texas: including Big Bend National Park and Guadalupe Mountains National Park. Texas A&M University Press, College Station, Texas.

SKILES, J. R. 1995. Black bears in Big Bend National Park–the Tex-Mex connection. Proceedings of the Western Black Bear Workshop 5:67-73.

SMITH, K. G., and J. D. CLARK. 1994. Black bears in Arkansas - characteristics of a successful translocation. Journal of Mammalogy 75:309-320.

STACEY, P. B., and M. TAPER. 1992. Environmental variation and the persistence of small populations. Ecological Applications 2:18-29.

STACEY, P. B., M. L. TAPER, and V. A. JOHNSON. 1997. Migration within metapopulations: the impact upon local population dynamics, Pp. 267-291 in Metapopulation biology: ecology, genetics and evolution (I. A. Hanksi and M. E. Gilpin, eds.). Academic Press, San Diego, California.

SWEANOR, L. L., K. A. LOGAN, and M. G. HORNOCKER. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798-808.

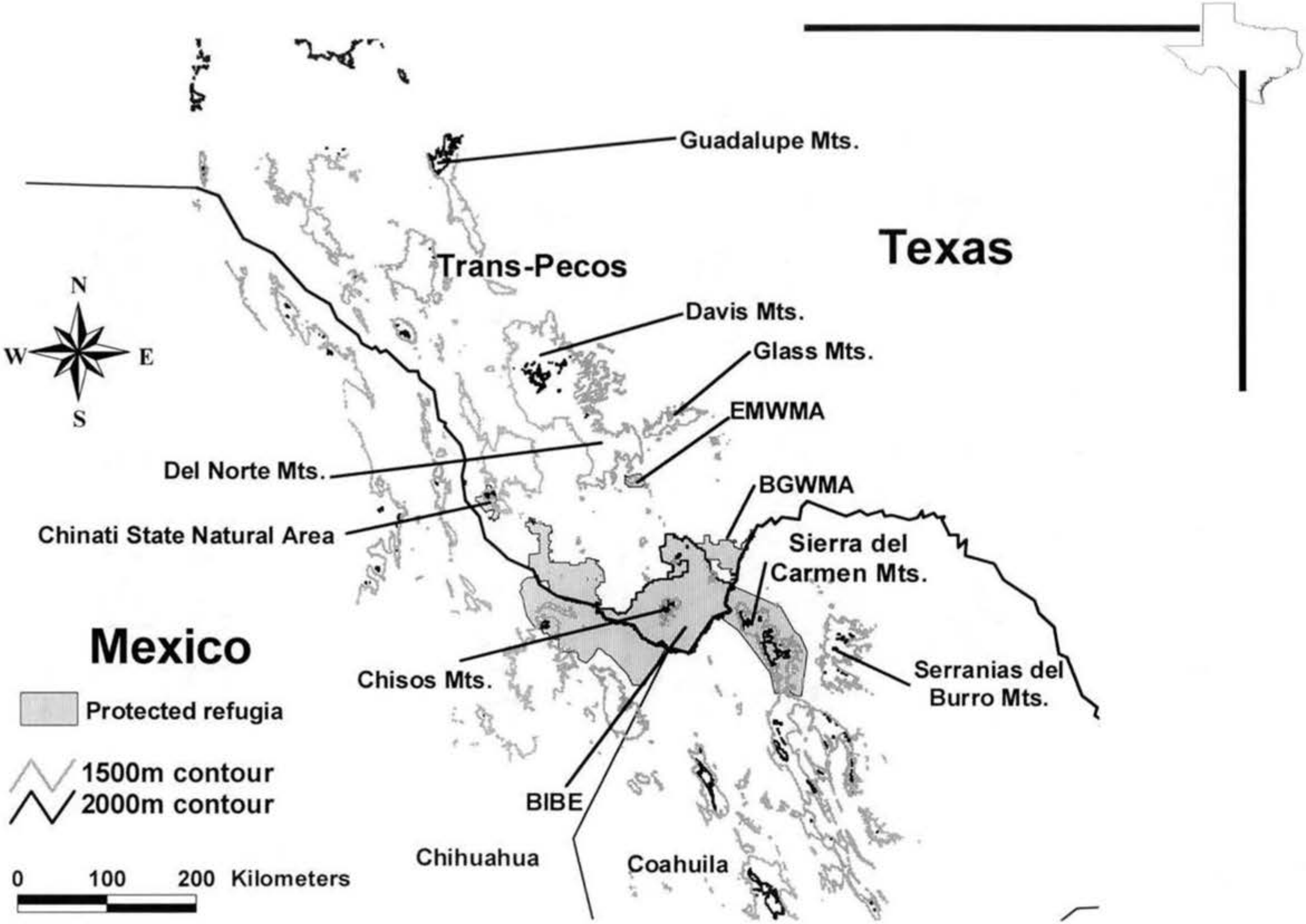
SWENSON, J. E., F. SANDERSON, AND A. SODERBERG. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. Journal of Animal Ecology 67:819-826.

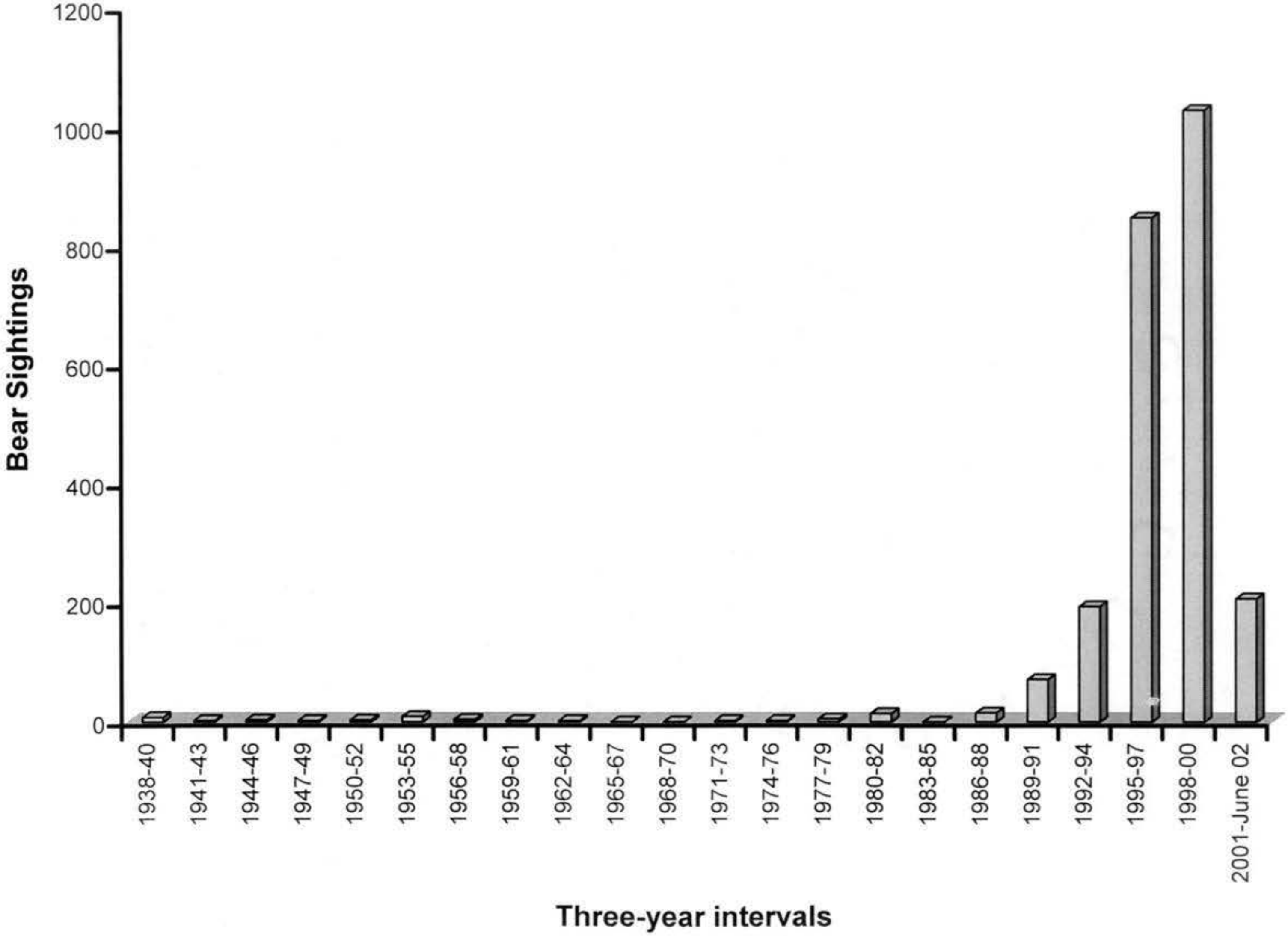
WYDEVEN, A. P., T. K. FULLER, W. WEBER, and K. MACDONALD. 1998. The potential for wolf recovery in the northeastern United States via dispersal from southeastern Canada. Wildlife Society Bulletin 26:776-784.

FIGURE LEGENDS

Figure 1.— Depiction of mainland (Serranias del Burro and Sierra del Carmen ranges) and island (Chisos Mountains, Glass Mountains, Del Norte, Davis Mountains, Black Gap Wildlife Management Area) patches available to American black bears in the Trans-Pecos region of Texas and Mexico. Acronym definitions are as follows: Big Bend National Park (BIBE), Big Bend Ranch State Park (BBRSP), Black Gap Wildlife Management Area (BGWMA), and Elephant Mountain Wildlife Management Area (EMWMA). The 1500-m isocline approximates the distribution of woodland habitats in the Chihuahuan desert matrix.

Figure 2.—Frequency of American black bear observations made over 3-year intervals in Big Bend National Park, Texas, USA (1938-1998).


Texas
Guadalupe Mts.
Trans-Pecos
Davis Mts.
Glass Mts.
EMWMA
BGWMA
Del Norte Mts.
Chinati State Natural Area
Sierra del Carmen Mts.
Serranias del Burro Mts.
Chisos Mts.
BIBE
Mexico
Chihuahua
Coahuila
N
S
E
W
Protected refugia
1500m contour
2000m contour
0
100
200
Kilometers


Bear Sightings
0
200
400
600
800
1000
1200
1938-40
1941-43
1944-46
1947-49
1950-52
1953-55
1956-58
1959-61
1962-64
1965-67
1968-70
1971-73
1974-76
1977-79
1980-82
1983-85
1986-88
1989-91
1992-94
1995-97
1998-00
2001-June 02
Three-year intervals

CHAPTER II

ECOLOGY OF AMERICAN BLACK BEARS ON A DESERT MONTANE ISLAND: HOME RANGE, HABITAT USE, AND MANAGEMENT APPLICATIONS

DAVID P. ONORATO

Abstract

American black bears (*Ursus americanus*) have recolonized Big Bend National Park (BIBE), Texas in the past 15 years from adjacent habitat in northern Mexico. Range expansion by the Big Bend bear population across the Chihuahuan desert landscape has considerable consequences for the recolonization of areas north of BIBE in western Texas (Glass, Del Norte and Davis Mountains). We studied black bear ecology from 1998 to 2001 in BIBE. Thirty bears were marked (15 with radiocollars) during the study, including newborn cubs. Home ranges of bears (males: $\overline{X} = 97.7 \pm 35.8$ km^2, females: $\overline{X} = 32.1 \pm 4.3$ km^2) were larger than in southwestern populations in Arizona and northern Mexico, but smaller than those in the nearby Black Gap Wildlife Management Area (BGMWA). Bears were mainly restricted to the Chisos Mountains and their foothills, with 65% of radiolocations in the pinyon (*Pinus cembroides*)-oak (*Quercus* spp.)-juniper (*Juniperus* spp.)-talus-meadow-grass vegetation association. Habitat selection analyses indicated that bears used oak-dominated vegetation types more than expected based upon availability. Bears were more likely than random to be <100 m from anthropogenic features (e.g., roads, trails), but that effect was much stronger in summer when visitor use was low. These data provide predictive capability to managers regarding recolonization of other montane islands north of BIBE and provide information that will help managers ensure the persistence of the small island population of black bears in BIBE.

Key words: American black bear, Big Bend National Park, Chihuahuan Desert, habitat selection, home range, metapopulation, Mexico, recolonization, Texas, *Ursus americanus*

Introduction

American black bears were once prevalent throughout parts of the Trans-Pecos region of western Texas (see Onorato and Hellgren 2001). Bears in the Chihuahuan Desert landscape have historically survived on chains of montane islands surrounded by a sea of inhospitable desert. As anthropogenic activity (cattle and goat ranching) increased in western Texas during the late 1800's and early 1900's, extermination of several large carnivores became a top priority. By the 1940's, black bear and Mexican wolf (*Canis lupus baileyi*) were extirpated from the Trans-Pecos due to predator control regimes and unregulated hunting (Onorato and Hellgren 2001).

Black bears survived in large remnant populations in the mountain ranges of northern Coahuila, Mexico (Figure 1). Populations in the Sierra del Carmen and Serranias del Burro Mountains apparently served as reservoirs for bear reproduction and dispersal into the Trans-Pecos region (Doan-Crider and Hellgren 1996; Onorato and Hellgren 2001; Onorato et al. 2003). Dispersal events from these ranges into the Chisos Mountains of Big Bend National Park (BIBE) Texas resulted in natural recolonization during the mid-1980's and reproduction within BIBE was verified in 1988 (Skiles 1995).

This recolonization process was corroborated by historical records of visitor observations of black bears in BIBE from the early 1900's until 2000 (Onorato and Hellgren 2001).

Range expansion as the BIBE population of black bears grows has important consequences for resource managers in BIBE and for assessing prospects for recolonization of other habitats formerly occupied by black bear north of BIBE. The Glass, Del Norte, and Davis Mountains (Figure 1) are known to have supported bear populations in Post-Columbian times. Knowledge of seasonal bear distribution and spatio-temporal range use can facilitate management and conservation initiatives.

We collected data on black bears in BIBE between September 1998 and December 2001. Our objectives included describing landscape use and home range characteristics for the species in a portion of their distribution that has not been intensively sampled. Additionally, we compared bear range use to visitor use and the associated effect of human-related landscape features. These data will be instrumental in preventing negative aspects of bear-human interactions frequently observed in other National Parks. They also will allow park managers to implement appropriate measures to ensure that natural recolonization can proceed in the Chisos Mountains.

Study area

We conducted fieldwork in Big Bend National Park, Texas, which encompasses 320,000 ha of northern Chihuahuan Desert in the Trans-Pecos of western Texas (Figure 1). Climate of the Big Bend Ecosystem is arid and elevation ranges from 550 m to 2385 m. Average annual precipitation totals 30.5 cm, with most falling during thunderstorms in July, August, and September. Rainfall accumulations generally increase with elevation within BIBE (Powell 1998). Plumb (1987) described 28 vegetation associations in BIBE and subsequently digitized them into a GIS data layer. We reclassified these 28 associations into 10 based on recommendations from specialists in BIBE (Table 1).

Methods

We captured black bears using barrel traps baited with sardines and fish oil. Traps were composed of 2 55-gal drums bolted together and outfitted with a sliding door at one end and heavy wire mesh at the other. A trigger arm, on which the bait was placed, served as the activator of the sliding door. These traps can capture bears ≤ 140 kg (H. Black, Department of Zoology, Brigham Young University, Utah, USA, personal communication), which was likely to be the upper extent of the mass range of BIBE black bears (Maehr et al. 2001).

We concentrated trapping effort in 2 major zones. The low-country trapping zone (LCZ) encompassed elevations from 1,000 to 1,800 m and the high-country trapping zone (HCZ) included sites in the high Chisos > 1,800 m. Trapping in both zones simultaneously was not feasible due to logistical constraints; therefore trapping was conducted in either zone depending on time of year, bear sightings, and weather.

We used Telazol (tiletamine hydrochloride and zolazepam hydrochloride, A. H. Robins Company, Richmond, Virginia, USA) to anesthetize bears at a dosage of 5.5 mg/kg via jabstick following visual estimation of weight in barrel traps. Upon immobilization, we recorded vital signs (heart rate, respiration, rectal temperature) immediately while ophthalmic ointment was applied to the eyes. We rechecked vital signs periodically during the immobilization period.

We fitted all adult bears and selected subadults with radiotransmitter collars possessing a mortality switch and breakaway cotton spacers (Hellgren et al. 1988) or expandable rubber tubing inserted between the ends of the collars (Telonics, Mesa, Arizona, USA). We extracted the first upper premolar of each bear with dental elevator and extractor tools. A commercial laboratory (Matson's Laboratory, Milltown, Montana, USA) was used to estimate age via cementum annuli analysis (Willey 1974). Each bear also was implanted with a passive integrated transponder (PIT) tag to provide permanent identification. The PIT tags were serially identified via an alpha-numeric code that can be read utilizing a Destron-Fearing mini-portable reader (Destron-Fearing Corporation, St. Paul, Minnesota, USA). After aseptically treating the injection site, PIT tags were implanted subcutaneously with a large gauge syringe into the area between to the scapulas. Ear tags were not attached to captured bears.

We attempted to locate radiocollared bears opportunistically using either aerial or ground telemetry. A majority (92%) of telemetry locations were collected during daylight hours (0700-1900 hrs). We obtained ≥ 2 azimuths in ≤ 20 minutes to estimate bear locations. Estimated locations of collared bears were assigned UTM coordinates via triangulation on 7.5-minute topographic maps. We formatted data for compatibility with GIS databases in use by Park researchers. Telemetry error was estimated using triangulations for test collars (*n* = 13) at known locations that resulted in a mean error distance of 172.6 m ± 107.7 (SD).

We estimated home ranges using 95% minimum convex polygon (MCP) and 50% fixed kernel estimator models with the Animal Movement extension (Hooge and Eichenlaub 1997) in ArcView 3.3 (Environmental Systems Research Institute, Redlands, California, USA). We used the least squares cross validation (Silverman 1986) smoothing parameter when calculating the 50% fixed kernel core areas. A nonparametric

Wilcoxon rank-sum test was used to compare MCP home ranges between sexes and age (adults vs. subadults/yearlings) groups. Animals included in the home-range analyses were monitored for > 50 days and had ≥ 25 relocations. We compared MCP home ranges of bears in BIBE to bears from the low-elevation population in the BGWMA (McKinney and Pittman 2000) using the same nonparametric analysis.

We determined variation in the spatial use of the landscape by merging UTM coordinates of bear radiolocations with digitized vegetation data for BIBE (Plumb 1987). Habitat selection by black bears was assessed at second- and third-order levels (Johnson 1980) using the compositional analysis technique (Aebischer et al. 1993) and 11 previously described vegetation associations (Table 1). If habitats were used in a nonrandom manner (i.e., selection occurred), they were ranked according to use. Differences between ranks were assessed to qualify habitat selection. Second-order selection was determined by comparing proportions of vegetative associations within a bear's 95% MCP (use) to proportions found within a composite 95% MCP calculated for all bears (availability). Third-order selection was determined by comparing proportions of vegetative associations found at radiolocation points within a bears 95% MCP (use) to proportions of vegetative associations found within the entire 95% MCP for that specific bear (availability).

We examined the effect of human activity on bear distribution using bear locations (*n* = 711) in the North Chisos and High Chisos Management use-areas. We determined the frequency of bear relocations that were within 0-100 m, 100-250 m, and 251-500 m buffers of areas with anthropogenic activity (dirt and paved roads, trails, backcountry and campground campsites, housing areas, waste dump sites). Those values were compared to the frequency of an equal number of randomly distributed points that were contained in the same buffers. Comparisons between observed and randomly generated data were completed using Chi-square analysis to determine if bears were avoiding areas with anthropogenic activity. Comparisons were made for time periods in which visitor use of BIBE was heavy (Nov-May) and light (Jun-Oct). We also tested for a difference in the distribution of bear locations across buffer zones for high- and low-use seasons ($n = 335$ and $n = 376$, respectively)

Results

Trapping success in BIBE during the entire study was low (2.4%; 42 captures in 1,763 trapnights), and capture rates were similar between the LCZ (2.3%; 35 in 1,502) and HCZ (2.7%; 7 in 261) trapping zones. We marked eleven cubs in dens, and 23 bears were captured in traps (including 2 marked cubs). Thirty bears were marked in BIBE, whereas 2 bears were captured but not marked. In addition, the skeletal remains of a yearling were found.

We radiotracked fourteen bears from October 1998 to December 2001. A total 866 location estimates was recorded. Minimum convex polygon home-range sizes varied from 5.1 km^2 to 288.5 km^2. Average home-range size for males was larger than for females (Table 2), although that difference was not significant (Wilcoxon rank sum, $S = 41.0$, $P = 0.165$). Average adult home ranges were larger than subadults, but this difference also was not significant ($S = 36.0$, $P = 0.282$). Average home-range size for black bears in BGWMA was larger ($S = 21.0$, $P = 0.017$) than those recorded in BIBE. There was a high degree of overlap in MCP home ranges for both sexes and age groups

(Figure 2). At the 50% level, overlap in core areas occurred in males and females although, some separation was evident (Figure 3).

Female bears clearly restricted their use to the Chisos Mountains and its foothills. For example, second-order selection revealed that only 12.3% of the overall composite 95% MCP was classified as pinyon-oak-juniper-talus-meadow-grass, yet 60.3% of the female composite home range contained this association (Table 3). Males made more frequent use of low-country areas, especially the creosote (*Larrea divaricata*)-lechuguilla (*Agave lecheguilla*)-prickly pear (*Opuntia* spp.)-grass-mesquite (*Prosopis* spp.) and sotol (*Dasylirion leiophyllum*)-yucca (*Yucca* spp.)-lechuguilla-grass associations (Table 3, 2nd order selection). Analyses at the third-order level show 65.1% of all bear relocations occurring in the pinyon-oak-juniper-talus-meadow-grass association.

Compositional analysis of habitat use by black bears via second-order selection was nonrandom ($\chi^2 = 48.43$, $P<0.001$). Black bears selected pinyon-oak-juniper-talus-meadow-grass more frequently than would be expected according to availability (Table 3 footnote). The oak-ponderosa pine (*P. ponderosa*)-cypress (*Cupressus* spp.) association was also used significantly more than expected, although this is a result of the small proportion of BIBE comprised of this vegetation class. The most prominent desert vegetation associations (classes 3 and 4) were used less within bear home ranges than all habitats except water (10). Third-order selection also illustrated that bears did not use home ranges in a random manner ($\chi^2 = 44.41$, $P < 0.001$). Based on radiolocations, the mixed scrub-oak scrub and pinyon-oak-juniper-talus-meadow-grass associations ranked the highest (Table 3 footnote).

Frequencies of bear relocations within buffer zones encircling anthropogenic sources of disturbance differed from random points during low-use ($\chi^2 = 32.87$, *df* = 3, $P < 0.001$) and high-use ($\chi^2 = 17.57$, *df* = 3, $P < 0.001$) periods (Table 4). During both periods, bears were found more often than expected in the buffer zone ≤ 100 m of anthropogenic features. However, during the low-use period, bears were less likely to be found > 500 m from anthropogenic features, whereas during the high-use period, bears were less likely than random to be in the 251-500-m zone. Frequencies of bear locations relative to anthropogenic features also differed ($\chi^2 = 35.98$, *df* = 3, $P < 0.001$) between the 2 periods, with bears more likely to be close (<100 m) to those features during the low-use period (Table 4).

Discussion

We preface our discussion with comments about our sampling regime. Three bears (2 males and 1 female) were captured below 1,300 m in elevation and it could be argued that our analyses and results are biased toward the habitats of the Chisos Mountains in BIBE. Most traps in the LCZ were in the foothills and lower slopes of the Chisos. Our trapping effort in low-elevation desert habitats was minimal, and more effort in these areas may have resulted in capture of additional males that were dispersing or moving across the desert from other montane islands. Several visual reports of uncollared bears in 1999 and 2000 attested to the fact that not all bears were collared, but the high number of visitor sightings of collared animals indicated that we had captured most resident bears (J. R. Skiles, National Park Service, unpublished data). In addition, visitor sightings of bears and observations of bear sign in desert habitats were rare, and we believed that trapping efficiency in these areas would be too low to be warranted given other objectives of our work. Therefore, although we recognize that our sampling was biased toward high-elevation habitats, we believe that we sampled bears where they occurred and avoided sampling where they did not.

Our telemetry monitoring revealed that resident bears, especially males, made forays into the Sierra Quemada south of the Chisos and other low-country areas. Use of these non-woodland areas (which were not included as suitable habitat by Hellgren 1993) indicated the presence of seasonally important areas away from the Chisos and likely a higher carrying capacity of the area than the 16-22 estimated by Hellgren (1993). The density estimate for bears based on the entire area of BIBE (0.9 bears/ 100 km^2; Onorato et al. 2002) was as low as any reported in the literature (Garshelis 1994) and illustrated the vast amount of desert habitat in BIBE that is unsuitable for black bears. Bear density in the Chisos Mountains alone was much greater (23 bears/100 km^2; Onorato et al. 2002)

Estimates of home range size based on MCPs for adult females in BIBE were in the middle of estimates for other areas in southwestern North America. Our estimates were larger than those observed in Arizona chaparral ($\overline{X} = 17.9$ km^2, $n = 5$; LeCount et al. 1984) and northern Coahuila, Mexico ($\overline{X} = 19.6$ km^2, $n = 12$; Doan-Crider 1995), similar to south-central New Mexico ($\overline{X} = 43.1$ km^2, $n = 25$; Costello et al. 2001), and much smaller than those in the BGWMA ($\overline{X} = 89.8$ km^2, $n = 3$; B. R. McKinney, Texas Parks and Wildlife, unpublished data). Larger home ranges in BGWMA may be indicative of a lower diversity of food resources (i.e., it is necessary for bears to cover large areas to obtain necessary food supplies). The smaller home ranges of bears in BIBE and New Mexico were due to the concentration of good bear habitat at higher elevations that were not present in BGWMA.

Differences in range dynamics of American black bears residing in BIBE compared to those in BGWMA are important to predicting the progression of bear recolonization in this region. Due to the higher availability of water and quality food sources in the higher elevations of the Chisos, we believe that black bears will achieve higher densities with smaller home ranges in BIBE. Important mast-producing species such as Texas madrone (*Arbutus xalapensis*) weeping juniper (*J. flaccida*), alligator juniper (*J. deppeana*) and nine species of oaks are prevalent in the Chisos Mountains (Powell 1998). Conversely, these species are either rare or do not occur in the lower elevations of the Chihuahuan Desert in BGWMA. The BGWMA contains over 42,800 hectares of predominantly xerophytic desert scrub-grassland associations (McKinney and Pittman 2000). In turn, larger areas must be traversed in BGWMA to obtain the necessary resources to survive. Consequently, as bears move north to other low-elevation ranges, they will require greater expanses of habitat to be successful. Any proposed reintroduction of black bears in western Texas should take this into account.

The presence of a small black bear population in the BGWMA indicates that other low-elevation ranges (with few peaks > 1,500 m) such as the Glass and Del Norte mountains could be recolonized. Reproduction has been documented in BGWMA and 3 females denned in the area in 2000 (McKinney and Pittman 2000). Two bears translocated to BGWMA (a male and female) have subsequently traveled north or northeast in an attempt to return to the areas from which they were removed. One male dispersed > 120 km in 3 days from BGWMA to the Del Norte Mountains from which he had been removed. Such movements by both sexes demonstrate the potential for BIBE and BGWMA to serve as sources of recolonizers to other ranges in western Texas.

The Davis Mountains, which are > 170 km northwest of the Chisos Mountains, contain vegetation associations similar to the Chisos. Most importantly, this range contains about ten times as much high-elevation (≥ 1,800 m) habitat as BIBE. The Davis Mountains have the potential to serve as an important island habitat for black bear in western Texas and would function as a critical subpopulation within the northern portion of the black bear metapopulation in the Big Bend Ecosystem.

Analyses at both second- and third-order scales demonstrated strong selection of the pinyon-oak-juniper-talus-meadow-grass association by black bears. Some of the primary autumnal foods upon which bears heavily depend--oak acorns, juniper berries, pinyon pine nuts, and berries of Texas madrone and littleleaf sumac (*Rhus microphylla*)--were found within this association. LeCount (1984) recorded similar habitat selection by black bears in the Four Peaks region of central Arizona. Bears in this southwestern population preferred Emory oak (*Q. emoryi*)-scrub oak (*Q. turbinella*), ponderosa pine-manzanita (*Arctostaphylus pungens*)-oak, and scrub oak-mountain mahogany (*Cercocarpus montanus*)-sugar sumac (*R. ovata*) vegetation associations. Even within these similarities, there was a difference between the Arizona population and bears in BIBE. Sixty-five percent of bear relocations in BIBE were the pinyon-oak-juniper-tallus-meadow-grass association that composed only 1.7% of BIBE. Conversely, the Emory oak-scrub oak vegetation association in Arizona contained a seasonal average of 38% (males) and 53.4% (females) relocations while comprising > 38% of the Four Peaks study area (LeCount et al. 1984). The strong selection for montane vegetation associations in the Chisos Mountains of BIBE demonstrated their importance to bears recolonizing BIBE.

Rankings for low-elevation desert associations (e.g., creosote-lechuguilla-prickly pear-grass-mesquite and sotol-yucca-lechuguilla-grass) in BIBE were low at the second-order level but fairly high at the third-order selection level. If bears had these associations in their individual home ranges, they used them, especially during summer when prickly pear and Texas persimmon (*Diospyros texana*) fruits began to ripen. Although more prevalent in the composite home range of males, female bears also utilized these associations periodically, especially the sotol-yucca-lechuguilla-grass association. A caveat to the notion that black bears used these lowland associations less than expected according to their distribution in BIBE could be made. As previously noted, our trapping was concentrated in the higher elevations of the Chisos, and the observation of selection of high-elevation vegetation associations by black bears could be a result of sampling bias. Nevertheless, we trapped at 8 locations that were considered low-elevation trapping sites (< 1,300 m). Only 1 of 3 bears captured in these traps during > 160 trap nights was not previously captured at higher elevations. Additionally, we frequently surveyed the lowland areas of BIBE during the evening and nighttime hours and continually monitored the area during these forays with telemetry equipment. Although bears were sporadically located in the lowland vegetation associations, we do not believe that our results were under representing the use of these regions of BIBE (D. P. Onorato, unpublished data).

Comparisons of our data with the nearby population in BGWMA were revealing. Bears in BGWMA were reliant on low-elevation (500-1,500 m) plant assemblages for survival. Food sources used by bears in this region included sotol, Spanish dagger (*Y. torreyi*), and mesquite beans (McKinney and Pittman 2000). Mesquite beans are comparable to sandpaper oak (*Q. pungens*) in percent fat, fiber and protein (McKinney and Pittman 2000), indicating the possibility that they may serve as a supplement for sparse acorn patches in low-elevation areas of the Chihuahuan Desert. Although these food items have been found in some scat samples in BIBE, they appear to be used far less frequently by BIBE bears than bears in BGWMA (Onorato et al. 2001). Nevertheless, bears in BGWMA concentrated in scattered oak groves and persimmon patches at higher elevations (1,500-1,700 m) during the autumn to take advantage of those food sources (McKinney and Pittman 2000).

We think that a regular autumn mast source (e.g., acorns, juniper, Texas madrone) is necessary to maintain small populations in low-elevation ranges in western Texas. Studies of food habits of black bears in BGWMA and BIBE have demonstrated the importance of mast in both habitats (Hellgren 1993; McKinney and Pittman 2000; Mitchell 2001). Mitchell (2001) found that acorns were present in > 60% of the scats analyzed in that study in BIBE, yet acorns may have been underrepresented in the diet due to low levels of precipitation in 1998 and 2000. We think mast failures in 1999–2000 and subsequent infestation by variable oakleaf caterpillars (*Lochmaeus manteo*) resulted in a large-scale migration-dispersal event in which 13 of 15 collared bears left the Chisos for portions of northern Mexico (Mitchell 2001; Onorato et al. 2002).

Analyses of bear locations within buffer zones surrounding anthropogenic disturbances in the Chisos Mountains provided 2 findings of management interest. First, throughout the year, bears were more likely than chance to be located close (≤ 100 m) to human-related features. Second, during summer, the period of relatively low visitor use, bears were more likely to be close to these features than during the period of high visitor use. Whether this shift was caused by human disturbance is difficult to interpret. Similar findings have been noted in relation to bear habitat use and roads (traffic volumes and location) in the Pisgah National Forest in North Carolina and central Cascades of Oregon (Brody and Pelton 1989; Heyden and Meslow 1999). Chi and Gilbert (1999) reported that a higher proportion of black bears restricted their fishing activities to 2 waterfalls on Anan Creek with lower human activity as compared to falls that were open to the general public. We suggest that visitor use in BIBE may reduce use of these areas (trails, roads, campsites) by bears during the late autumn and winter, which may negatively impact bears in the Chisos Basin. Many trails and campsites in this area are encircled by or adjacent to stands of pinyon pines, Texas madrone, juniper and a variety of oak species. The mast and berries from these trees make up a majority of the diet of BIBE black bears during autumn (Mitchell 2001). From October to December, bears are trying to gain mass to survive winter hibernation (or limited movement).

A majority of our relocations were obtained during daylight hours and may have biased our disturbance analyses. Modified environments with readily available food sources (e.g. garbage dumps and orchards) have been suspected to result in behavior modification by black bears and increase nocturnal activity (Ayres et al. 1986). However, data collected during 6-hour monitoring sessions (day or night) within the developed region of the Basin in the Chisos Mountains demonstrated that bears rarely ventured into campgrounds or housing developments (D. P. Onorato, unpublished data). Even in nocturnal monitoring sessions, bears typically avoided close contacts with these human features. Although bears in BIBE were active during portions of the night, we believe that the population in BIBE generally follows a diurnal pattern of activity noted in other natural environments in North America (Lariviere et al. 1994). The staff at BIBE has been pro-active in preventing bear-human conflicts with visitors by implementing camper awareness programs, bear-proof waste containers and food storage boxes, and by supporting research. Big Bend National Park has benefited from the nuisance bear lessons learned in other, more heavily visited national parks (Yosemite and Great Smoky Mountains) and in turn has not experienced any major problems to this date.

Due to the limitations of our data, conclusions concerning avoidance and use could be considered speculative. Additional studies are necessary to determine the exact impacts that these anthropogenic disturbances are having on BIBE bears. Park officials should be vigilant in noting bear activity near development during these months and respond appropriately. Managers should also be aware of these potential impacts when planning future hiking trails or other development in the Chisos.

The black bear in the Trans-Pecos of Texas has endured periods of persecution, extirpation, and recolonization in the last century (Onorato and Hellgren 2001). Data presented herein and collected during concurrent research using genetic markers (Onorato et al. 2003) has established a link between black bears in BIBE and Coahuila, Mexico. The black bear population in BIBE always will be limited by the amount of suitable bear habitat available (<100 km^2, primarily in the Chisos Mountains) because preferred foods in adequate quantities only occur at high elevations. Nevertheless, this population is an important stepping-stone to natural recolonization of other areas of western Texas from Mexico. An increase in the number of complaints by private landowners to the Texas Parks and Wildlife Department involving black bears (B. R. McKinney, Technical

Wildlife Coordinator, El Carmen Project, CEMEX, Coahuila, Mexico, personal communication; Taylor 1999) attest to the fact that the recolonization process is slowly progressing. Several ranges north of BIBE, including the Del Norte, Glass and Davis mountains, once harbored populations of black bears (Onorato and Hellgren 2001). Most of this habitat is still undeveloped and could support small bear populations.

We recommend that managers use these data to predict effects of management decisions involving new development on bears in BIBE and other areas in western Texas with suitable habitat for recolonization. Our data also can be used to select suitable sites for, and predict trajectories of, future reintroductions and natural recolonizations of black bears to montane islands in the desert southwest.

Acknowledgments

This study was supported by funding from the Natural Resource Preservation Program of the U.S. National Park Service and U.S. Geological Survey. We thank D. M. Leslie, Jr. and the Oklahoma Cooperative Fish and Wildlife Research Unit (U.S. Geological Survey-Biological Resources Division, Oklahoma State University, Oklahoma Department of Wildlife Conservation, and Wildlife Management Institute, cooperating) for administrative and logistical support. We acknowledge additional funding granted by the Wyoming Chapter of the Wildlife Society (Memorial Bear Grant), and the American Museum of Natural History (Theodore Roosevelt Memorial Fund). We conducted this work under the auspices of Scientific Permit SPR-290-015 from the Texas Parks and Wildlife Department and Protocol 628 of the Institutional Animal Care and Use Committee of Oklahoma State University. We are indebted to pilots George Vose (Wildlife Surveillance Services) and Nick Herring (NPS), the staff of the Science

and Resource Management Division at BIBE, mechanics Dan Muntean and Mark Yuhas (NPS), and numerous field technicians and volunteers that helped collect the data that made this study feasible.

Literature Cited

AEBISCHER, N. J., P. A. ROBERTSON, and R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.

AYRES, L. A., L. S. CHOW, and D. M. GRABER. 1986. Black bear activity patterns and human induced modifications in Sequoia National Park. International Conference of Bear Research and Management 6:151-154.

BRODY, A. J., and M. R. PELTON. 1989. Effects of roads on black bear movements in western North Carolina. Wildlife Society Bulletin 17:5-10.

CHI, D. K., and B. K. GILBERT. 1999. Habitat security for Alaskan black bears at key foraging sites: are there thresholds for human disturbance? Ursus 11:225-238.

COSTELLO, C. M., ET AL. 2001. A study of black bear ecology in New Mexico with models for population dynamics and habitat suitability. New Mexico Department of Game and Fish, W-131-R, Federal Aid in Wildlife Restoration Project.

DOAN-CRIDER, D. L. 1995. Population characteristics and home range dynamics of the black bear in northern Coahuila, Mexico. Masters thesis, Texas A&M University-Kingsville, Kingsville, Texas USA.

DOAN-CRIDER, D. L., and E. C. HELLGREN. 1996. Population characteristics and winter ecology of black bears in Coahuila, Mexico. Journal of Wildlife Management 60:398-407.

GARSHELIS, D. L. 1994. Density-dependent population regulation of black bears, Pp. 3-14 in Density-dependent population regulation of black, brown and polar bears (M. Taylor, ed.). International Association for Bear Research and Management, Monograph Series No. 3, Missoula, Montana, USA.

HELLGREN, E. C. 1993. Status, distribution, and summer food habits of black bears in Big Bend National Park. The Southwestern Naturalist 38:77-80.

HELLGREN, E. C., D. W. CARNEY, N. P. GARNER, and M. R. VAUGHAN. 1988. Use of breakaway cotton spacers on radio collars. Wildlife Society Bulletin 16:216-218.

HEYDEN, M. V., and E. C. MESLOW. 1999. Habitat selection by female black bears in the central Cascades of Oregon. Northwest Science 73:283-294.

HOOGE, P. N., and B. EICHENLAUB. 1997. Animal movement extension to ArcView. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska, USA.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

LARIVIÈRE, S., J. HUOT, and C. SAMSON. 1994. Daily Activity Patterns of Female Black Bears in a Northern Mixed-Forest Environment. Journal of Mammalogy 75:613-620.

LECOUNT, A. L., R. H. SMITH, and J. R. WEGGE. 1984. Black bear habitat requirements in Central Arizona. Arizona Game and Fish Department, Report No.14.

MAEHR, D. S., E. C. HELLGREN, R. L. BINGHAM, and D. L. DOAN-CRIDER. 2001. Body mass of black bears from Mexico and Florida. The Southwestern Naturalist 46:129-133.

McKinney, B. R., and M. T. Pittman. 2000. Habitat, diet, home range, and seasonal movement of resident and relocated black bears in west Texas. Texas Parks and Wildlife Department, Project WER57-STATE.

Mitchell, F. S. 2001. Winter ecology and food habits of black bears in Big Bend National Park. Masters thesis, Sul Ross State University, Alpine, Texas USA.

Onorato, D. P., and E. C. Hellgren. 2001. Black bear at the border: the recolonization of the Trans-Pecos. Pp. 245-259 in Large mammal restoration: ecological and sociological challenges in the 21st Century (D. S. Maehr, R. F. Noss and J. L. Larkin, eds.). Island Press, Washington D.C., USA.

Onorato, D. P., E. C. Hellgren, R. A. Van Den Bussche, and D. L. Doan-Crider. 2003. Phylogeographic patterns within a metapopulation of black bears (*Ursus americanus*) in the American Southwest. Journal of Mammalogy 84:000-000.

Onorato, D. P., E. C. Hellgren, R. A. Van Den Bussche, and D. M. Leslie, Jr. 2002. Conservation ecology of an isolated population of black bears in the Big Bend Ecosystem. National Park Service, Final Report, Project 97-08: 1-54.

Onorato, D. P., B. R. McKinney, F. S. Mitchell, J. R. Skiles, Jr., M. T. Pittman, and E. C. Hellgren. 2001. Home range and diet of two naturally recolonizing black bear populations in the Chihuahuan Desert of southwestern Texas, P. 202 in Abstracts from the 13th International Conference on Bear Research and Management. Snow King Resort, Jackson, Wyoming, USA.

Plumb, G. A. 1987. An algorithmic approach to automated vegetation mapping of Big Bend National Park, Texas. Dissertation, University of Kansas, Lawrence, Kansas, USA.

POWELL, A. M. 1998. Trees and shrubs of the Trans-Pecos and adjacent areas. University of Texas Press, Austin, Texas, USA.

SILVERMAN, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London, United Kingdom.

SKILES, J. R. 1995. Black bears in Big Bend National Park–the Tex-Mex connection. Proceedings of the Western Black Bear Workshop 5:67-73.

TAYLOR, R. B. 1999. Black bear status report. Texas Parks and Wildlife Department, Project 19: 1-11.

WILLEY, C. H. 1974. Aging black bears from first premolar tooth sections. Journal of Wildlife Management 38:97-100.

Table 1. —Reclassification scheme used for vegetation associations derived by Plumb (1987) in Big Bend National Park. Vegetation classifications were combined according to criteria relating to botanical and bear natural history. Numbers designate codes that are periodically used for simplicity.

Plumb (1987)	Onorato et al. (2002)
Bare	Bare (1)
Cottonwood grove	Cottonwood-desert willow (2)
Desert willow	
Creosote flats	Creosote-lechuguilla-prickly pear-grass-mesquite (3)
Creosote grass	
Creosote-lechuguilla-prickly pear	
Creosote-lechuguilla	
Creosote-tarbush	
Creosote-yucca-grass	
Lechuguilla-grass	
Lechuguilla-grass-candelilla	
Lechuguilla-grass-hechtia	
Lechuguilla-grass-viguiera	
Mesquite thicket	
Sotol-lechuguilla-grass	Sotol-yucca-lechuguilla-grass (4)
Sotol-nolina-grass	
Yucca-sotol	
Pinyon-juniper-grass	Pinyon-oak-juniper-talus-meadow-grass (5)
Pinyon-oak-juniper	
Pinyon-talus	
Forest meadow	
Mixed scrub	Mixed scrub-oak scrub (6)
Oak scrub	
Oak-ponderosa pine-cypress	Oak-ponderosa pine-cypress (7)
Mixed riparian	Mixed riparian-reed grass (8)
Reed grass	
Mixed oak	Mixed oak (9)
Water	Water (10)
No data	No data (11)

Table 2.—Comparison of 95% minimum convex polygon home range sizes for American black bears in Big Bend National Park. Testing for statistical significance (* for $P < 0.05$) was completed using a Wilcoxon rank-sum test. The sample of bears from BGWMA was comprised of 5 males (3 adults and 2 subadults) and 3 females (2 adults and 1 subadult).

Group	n	Mean (km^2)	P
Males	7	97.7	0.165
Females	7	32.1	
Adults	8	86.5	0.282
Subadults	6	36.2	
BIBE	14	64.9	0.017*
BGWMA	8	152.7	

Table 3.—Proportion of vegetation associations available in Big Bend National Park, Texas (1998-2001) within the composite home range (95% minimum convex polygon) of all black bears, male and female black bears, and at relocations (*n* = 866) of monitored bears. Home range data were collected between October 1998 and December 2001. Results of rankings of habitat selection (using vegetation codes in column 1) via compositional analysis at the second- and third-order scales are described in footnote ♦. A >>> denotes significant differences ($P < 0.05$) between ranked habitats left and right of the symbol.

		2nd Order selection			3rd Order selection
Vegetation associations	Proportion of BIBE	Proportion within composite 95% MCP	Mean proportion within male 95% MCP	Mean proportion within female 95% MCP	Proportion of relocation points
Bare (1)	0.015	0.003	0.004	0.010	<0.001
Cottonwood-desert willow (2)	0.017	<<0.001	0.000	0.000	0.000
Creosote-lechuguilla-prickly pear -grass-mesquite (3)	0.773	0.472	0.202	0.034	0.062
Sotol-yucca-lechuguilla-grass (4)	0.156	0.351	0.331	0.243	0.180
Pinyon-oak-juniper-talus-meadow -grass (5)	0.017	0.123	0.389	0.603	0.651
Mixed scrub-oak scrub (6)	0.018	0.048	0.067	0.096	0.089
Oak-ponderosa pine-cypress (7)	<0.001	<0.001	0.001	0.002	<0.001
Mixed riparian-reedgrass (8)	0.003	0.000	0.000	0.000	0.000
Mixed oak (9)	<0.001	0.003	0.005	0.009	0.010
Water (10)	0.001	<0.001	0.000	<0.001	0.000
No data (11)	<0.001	<0.001	<0.001	0.002	<0.001

♦ Second-order selection 7 > 5 >>> 1 > 11 > 6 > 9 > 4 >>> 10 > 3

Third-order selection 5 > 6 >>> 4 > 3 > 10 > 9 > 7 > 11 > 1

Table 4.—Comparison of observed bear relocations to random points within buffer zones that encircle sources of anthropogenic disturbance (dirt and paved roads, trails, campsites, housing developments, dump) in Big Bend National Park, 1998-2001. Random points were derived by obtaining a similar number of randomly located points in the 2 most heavily used management zones during periods of low use (Jun-Oct) and high use (Nov-May) within the Park.

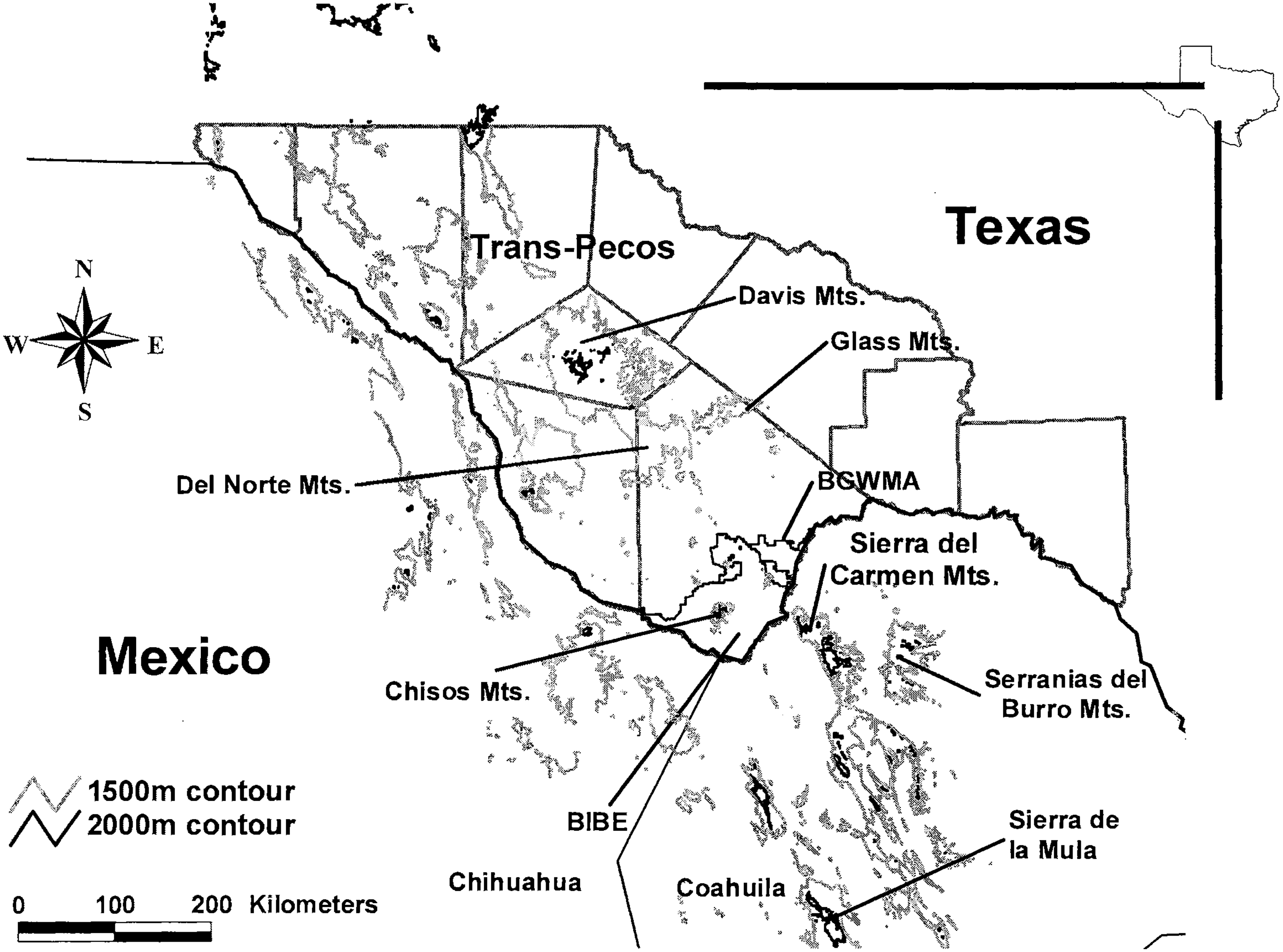
Use period	Buffer zone	Observed locations	Random locations
Low	≤100 m	109	55
	101-250 m	71	66
	251-500 m	79	70
	>500 m	117	185
High	≤100 m	60	41
	101-250 m	63	48
	251-500 m	39	77
	>500 m	173	169

FIGURE LEGENDS

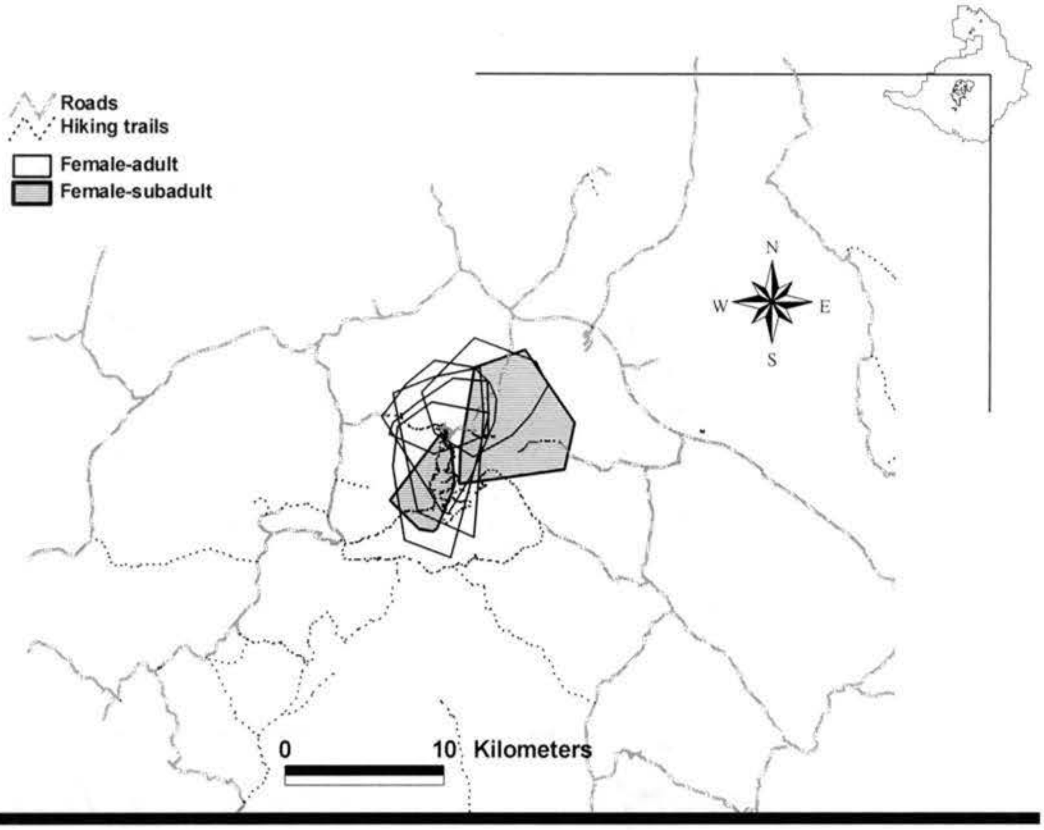
Figure 1.—Location of Big Bend National Park (BIBE) within the Big Bend Ecosystem. American black bears residing in the Chisos Mountains were the primary focus of our field research. The Serranias del Burro and Sierra del Carmen ranges in northern Coahuila, Mexico, constitute large, contiguous areas of black bear habitat. BGWMA = Black Gap Wildlife Management Area, Texas, USA.

Figure 2.—Home ranges (95% minimum convex polygon) of subadult (≤ 3-yr-old) and adult black bears in the Chisos Mountains of Big Bend National Park 1998-2001. Diagram A contains female home ranges and diagram B male home ranges.

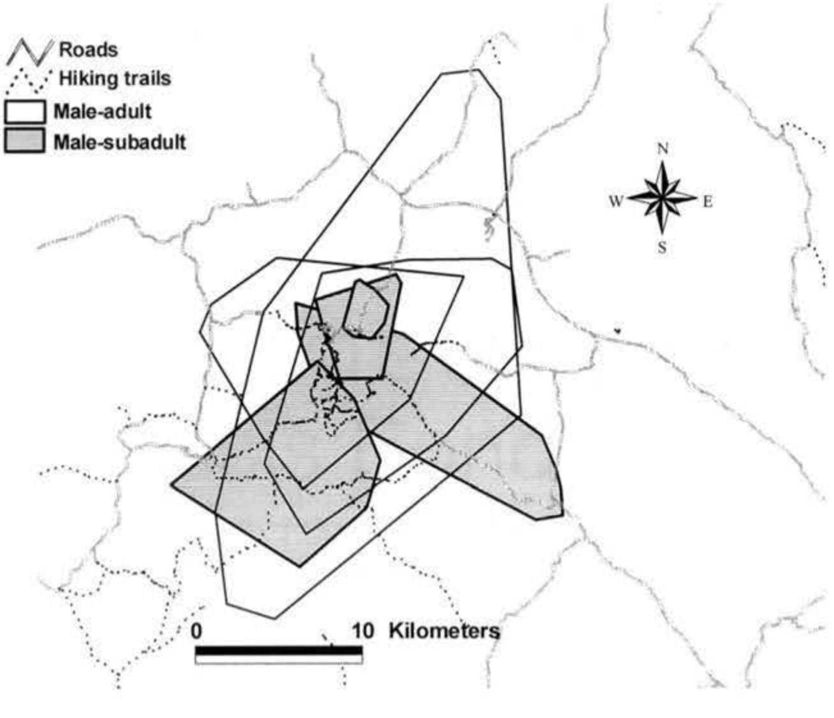
Figure 3.—Core areas (50% fixed kernel) of subadult (≤ 3-yr-old) and adult black bears in the Chisos Mountains of Big Bend National Park, 1998-2001. Diagram A contains female core areas and diagram B male core areas. Note the differences in scale between A and B.


Texas
Trans-Pecos
Davis Mts.
Glass Mts.
Del Norte Mts.
BGWMA
Sierra del Carmen Mts.
Mexico
Chisos Mts.
Serranias del Burro Mts.
BIBE
Sierra de la Mula
Chihuahua
Coahuila
N
S
W
E
1500m contour
2000m contour
0
100
200
Kilometers

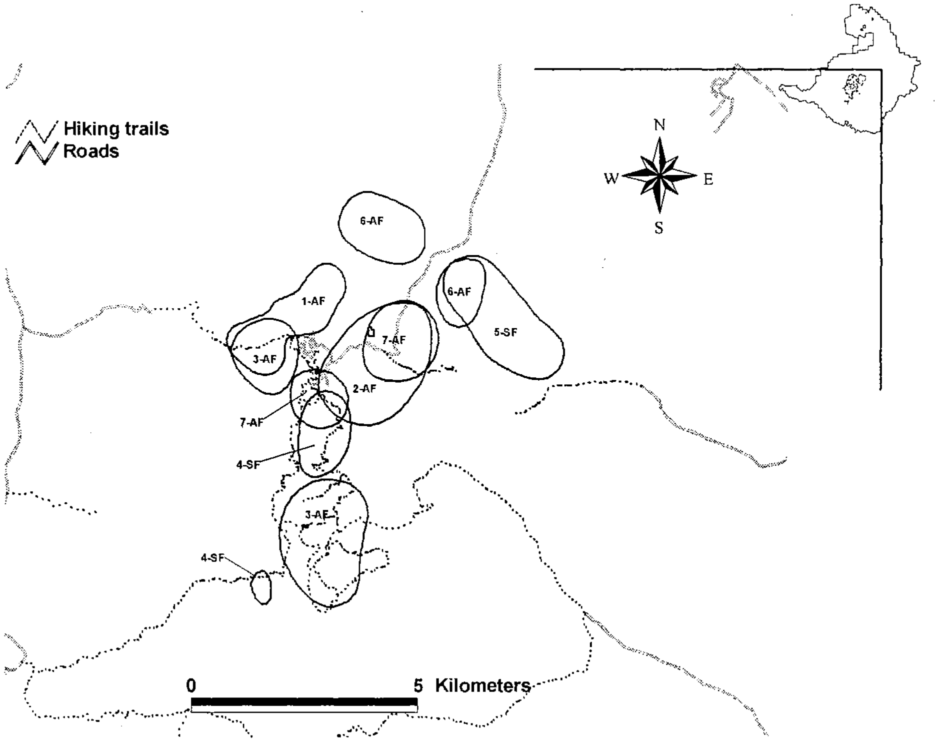
A


Roads
Hiking trails
Female-adult
Female-subadult
N
W
E
S
0
10 Kilometers

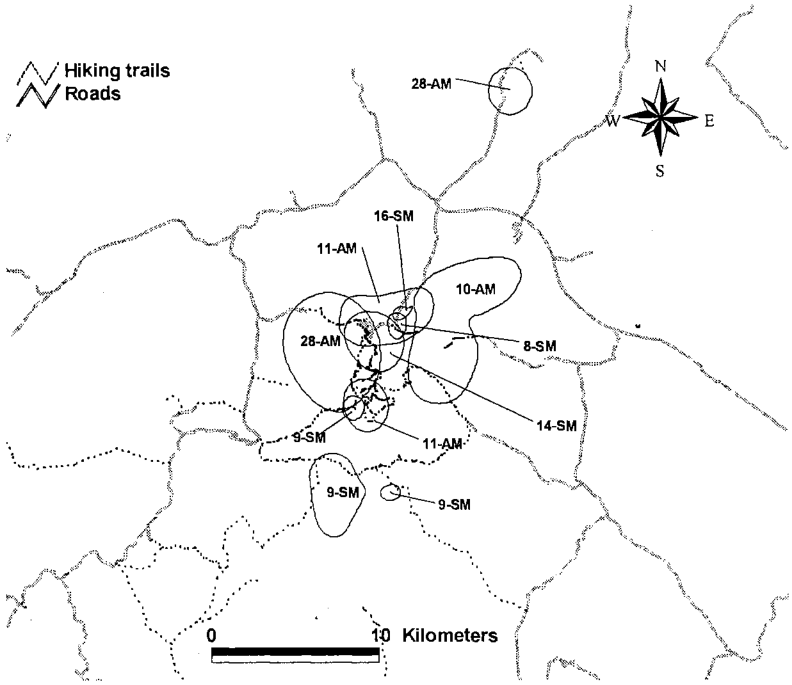
B


Roads
Hiking trails
Male-adult
Male-subadult
N
W
E
S
0
10 Kilometers

A


Hiking trails
Roads
N
W
E
S
6-AF
1-AF
6-AF
5-SF
7-AF
3-AF
2-AF
7-AF
4-SF
3-AF
4-SF
0
5 Kilometers

B


Hiking trails
Roads
28-AM
N
W
E
S
16-SM
11-AM
10-AM
28-AM
8-SM
14-SM
9-SM
11-AM
9-SM
9-SM
0
10 Kilometers

CHAPTER III

PHYLOGEOGRAPHIC PATTERNS WITHIN A METAPOPULATION OF AMERICAN BLACK BEARS (*URSUS AMERICANUS*) IN SOUTHWESTERN NORTH AMERICA

DAVID P. ONORATO

Abstract

Natural recolonization by large carnivores has rarely been documented. American black bears (*Ursus americanus*) recently (1988-present) recolonized part of their former range in western Texas. We utilized mtDNA sequence data (n = 144) from 7 populations of southwestern black bears in New Mexico, Texas and northern Mexico to test predictions regarding metapopulation structure of the species in this region and the source of recolonization in western Texas. Six variable nucleotides were detected, resulting in 5 mtDNA haplotypes. Although within-site diversity of haplotypes (h) and nucleotides (π) was low, a high degree of genetic partitioning among sites was detected ($\phi_{ST} = 0.6301$). Analyses pinpointed northern Mexico as the source of black bears for western Texas. Female-mediated gene flow is proceeding slowly in this system ($N_fm = 0.4961$ individuals/generation), but its occurrence was inferred via field observations. Nested clade analyses indicated that populations of bears in the Mex-Tex region (area that encompasses mountain ranges within Nuevo Leon and Coahuila Mexico northward to smaller ranges located in the Trans-Pecos region of western Texas) were connected via restricted gene flow due to isolation by distance. Long-distance colonization is the likely cause of extant geographical associations between New Mexican and Mex-Tex populations. The naturally fragmented, xeric environment of the Chihuahuan Desert impedes colonization, but is not a complete barrier to this process. Conservation initiatives concerning recolonization by black bears within the Mex-Tex mainland-island metapopulation should focus on preventing human-bear interactions and maintaining corridors for dispersal between the mainland populations in Mexico and the island populations in western Texas.

Keywords: black bear, Chihuahuan Desert, genetic structuring, gene flow, metapopulation, mtDNA, *Ursus americanus*

Introduction

Natural recolonizations are rarely documented in large terrestrial mammals, especially carnivores (Forbes and Boyd 1996; Mladenoff et al. 1995). With ever-increasing anthropogenic fragmentation of wild habitats, political policy hopscotching, and negative attitudes frequently associated with predators, it is imperative that researchers gain knowledge from recolonization events that did not require direct anthropogenic catalysts.

A limiting factor concerning the recolonization of former range by a species is the proximity of suitable habitat to a reproductively viable population. Additionally, females must be capable of dispersing to the former range and be reproductively successful. Documented natural recolonizations by gray wolves (*Canis lupus*) in the northern Rocky Mountains and northern Minnesota have been facilitated by the behavior of female wolves that disperse long distances (Boyd-Heger and Pletscher 1999), and habitat corridors between Canada and the United States containing suitable and contiguous habitat (Forbes and Boyd 1996; Mladenoff et al. 1995). Although female black bears (*Ursus americanus*) rarely (7%) disperse from their natal area (Elowe and Dodge 1989; Rogers 1987a; Schwartz and Franzmann 1992), with only 1 documented dispersal event > 15 km (Maehr 1997), they have recently recolonized fragments of their former range in the western Texas portion of the Big Bend Ecosystem (Onorato and Hellgren 2001). This ecosystem spans the Texas-Mexican border, and black bears appear to be organized as a metapopulation in the region (Onorato and Hellgren 2001). Dispersal events between populations are not facilitated by contiguous habitat or hospitable corridors. Instead, island populations in western Texas occur in a matrix of Chihuahuan Desert that inhibits dispersal by black bears. Environmental barriers within the Big Bend ecosystem coupled with the low intrinsic rate of female dispersal by black bears highlights the unlikely nature of a natural recolonization.

We hypothesized that black bears in the Big Bend Ecosystem were organized as a mainland-island metapopulation (Hanski and Simberloff 1997) with populations in western Texas recolonizing from Mexico. We tested 2 predictions of this hypothesis: (1) black bears in Big Bend National Park are more closely related to putative source populations in Mexico than more distant populations in New Mexico; and (2) black bears in the metapopulation show evidence of genetic structuring. We assessed levels of genetic differentiation and female mediated gene flow among 7 populations of southwestern black bears. To address this objective, we sequenced approximately 555 bp of the mitochondrial genome encompassing the 3' portion of the cytochrome-*b* gene and the 5' end of the control region. We also used nested clade analyses to evaluate mechanics behind the natural recolonization process within this metapopulation and decipher the source of recolonizers. The significance of this study relates to the increasing difficulty associated with the reintroduction of large carnivores in the United States (Federal Register 2001). If the present political climate concerning the reintroduction of large carnivores continues, natural recolonizations may become the only means by which such reintroductions occur. Therefore, a better understanding of the metapopulation dynamics, genetic structure, and processes responsible for successful natural recolonizations should provide insight into the effective management of ecosystems to facilitate recolonizations and conservation initiatives for black bears and other large carnivores.

Materials and Methods

Sampling sites.—All samples were collected between 1991 and 2001. Concurrent fieldwork and tissue collection (*n* = 31) were conducted in Big Bend National Park (BIBE in Figure 1), Texas between September 1998 and July 2001. The Park encompasses approximately 320,000 ha of northern Chihuahuan Desert in the Trans-Pecos region of western Texas (Figure 1). The primary habitat for black bears in the Park is located within a 100-km^2 area comprising the Chisos Mountains (elevation 1400-2385 m) where abundant food sources such as oak (*Quercus*), juniper (*Juniperus*), and madrone (*Arbutus xalapensis*) can be found. Nine samples were obtained from a small population of black bears recolonizing the adjacent Black Gap Wildlife Management Area (BGWMA in Figure 1). This region contains suitable habitat at lower elevations (900-1,400 m) approximately 40 km northeast of the Chisos Mountains of BIBE. Most of the terrain between BIBE and the BGWMA is lowland desert that could serve as a deterrent to migration between the 2 populations. No migrations or dispersals by radiocollared animals were documented between these study areas between 1998 and 2001 (Onorato and Hellgren, unpublished data)

Tissue samples (*n* = 65) also were obtained from larger, more contiguous ranges found in northern Coahuila, Mexico. Two mountain ranges known to support large populations of black bears are the Serranias del Burro (SDB) and Sierra del Carmen Mountains (SDC). Elevations can exceed 2,400 m in the del Carmen range. Additionally, we obtained tissue samples (*n* = 4) from the Sierra Madre Mountains near Monterey, Mexico (SMM). Six samples were collected throughout the Trans-Pecos region of Texas (⊡ in Figure 1). These individuals were sampled after vehicle collisions or during relocation after nuisance complaints. Although this may make the delineation of these individuals as a "population" suspect, we feel that these animals should be grouped together because reproductively viable populations are not currently present in the habitats where these samples were collected (Taylor 1999). This notion is further supported because only 1 of the 6 bears assigned to this "population" was a reproductive female. Therefore, these samples can be categorized as dispersing or colonizing animals in historic habitat within western Texas. No samples were collected from the northern portion of the Trans-Pecos because of logistical constraints and the lack of evidence for the presence of black bear populations in that region. A very small (6-8 bears) population may reside in the Guadalupe Mountains along the border of southeastern New Mexico (Taylor 1999) but this is likely a result of recent migrations or dispersal of bears from larger populations in the Lincoln National Forest of New Mexico. Populations BIBE, BGWMA, SDB, SDC, SMM, and the Trans-Pecos samples compose what will hereby be referred to as the Mex-Tex populations.

Samples ($n = 29$) collected from the Mogollon Mountains (MM in Fig. 1) of west-central New Mexico during a long-term black bear study by the Hornocker Wildlife Institute (Costello et al. 2001) were analyzed for comparative purposes to determine how closely related bears from this region are to those found in the Mex-Tex ecosystem. In terms of available habitat, this ecoregion is more similar to the larger ranges found in Mexico. The study area is primarily in the Gila National Forest and elevations range from 1750 m to > 3000 m.

DNA sequencing.—Blood and tissue samples were either stored frozen (-20°C) or in lysis buffer (Longmire et al. 1997). Whole genomic DNA was extracted using the phenol extraction method described by Longmire et al. (1997). An approximately 555 bp mtDNA fragment containing a portion of the 3' end of the cytochrome *b* gene (nucleotides 1-111) and 5' end of the d-loop (nucleotides 247-555) was amplified via the polymerase chain reaction (PCR) using primers L15774 and H16498 (Shields and Kocher 1991). Amplifications were performed in 50 μl reactions using 0.44 μM of each primer, 2 mM $MgCl_2$, 0.8 mg/ml Bovine Serum Albumin, Perkin-Elmer 10X PCR buffer (10 mM Tris-HCl pH 9.0, 50 mM KCl and 0.1% Triton® X-100), 140 μM each dNTP, 1.25 units of Perkin-Elmer AmpliTaq DNA polymerase and ~250-500 ng of DNA. Cycling parameters were: 1 cycle of 95°C for 10 min.; 30 cycles of denaturing at 94°C for 60 s, annealing at 50°C for 60 s, extension at 72°C for 60 s, followed by a single 30 min final extension. Resulting amplicons were electrophoresed through a 1.5% Tris-boric acid-EDTA(TBE) agarose gel stained with ethidium bromide and visualized with exposure to ultraviolet light.

Amplicons were purified using the Wizard PCR Prep DNA Purification System (Promega, Madison, Wisconsin). Both strands of the amplified products were sequenced using flanking primers and cycle sequencing according to manufacturers instructions (BigDye™, Perkin-Elmer Applied Biosystems, Foster City, California). Cycling parameters were as follows: 25 cycles at 96°C for 10 s, 50°C for 5 s, and 60°C for 4 min. Sequence products were electrophoresed on a Perkin-Elmer Applied Biosystems 377 Automated Sequencer. The computer program AssemblyLIGN™ 1.0.9 (Oxford Molecular Group PLC, 1998) was used to assemble contiguous, overlapping fragments within individuals and a multiple sequence alignment of all individuals was performed using CLUSTALX (Jeanmougin et al. 1998). The multiple sequence alignment was subsequently imported into MacClade (Maddison and Maddison 2000) for visual inspection and to group sequences into unique haplotypes using the REDUNDANT TAXA option.

Data analysis.—Estimates of haplotype (h) and nucleotide (π) diversity, the extent of sequence variation partitioned among sites and among groups (analyzed via a hierarchical examination of ϕ_{ST} using a grouped analysis of molecular variance or AMOVA), population comparisons (pairwise difference ϕ_{ST}), and overall ϕ_{ST} were calculated using ARLEQUIN version 2.0 (Schneider et al. 2000). Deletions were treated as a 5th character state. Transitions and deletions were weighted equally in analyses. Number of estimated female migrants (N_fm) per generation was determined from the approximation $N_fm = ((1/\phi_{ST})-1)/2$. These data were used in conjunction with life table parameters (Hellgren and Vaughan 2000) to estimate a generation time (Akçakaya et al. 1999) and recolonization rates within this metapopulation.

Nested phylogeographical analyses were applied to nucleotide sequence data using the method of Templeton (1998). The program TCS, version 1.13 (Clement et al. 2000) was used to generate a haplotype genealogy following the algorithm of Templeton et al. (1992). Any ambiguities concerning tip or interior status in the resulting genealogy were resolved using haplotype frequency data. Rare haplotypes typically occur at the tips of cladograms, while more common haplotypes are found preferentially at the interior position (Crandall and Templeton 1993; Templeton and Sing 1993). The haplotype network was then manually nested into successional clades, with haplotypes representing 0-step clades, and adjacent haplotypes joined by a single mutation event considered 1-step clades etc. (Templeton et al. 1995).

The resulting nested clade design and geographic distance between all pairs of populations were analyzed using the GeoDis 2.0 (Posada et al. 2000) software package. Following the protocol of Templeton et al. (1995), sample locations were treated as categorical variables that are analyzed via exact permutational contingency tests calculated in a nested routine for each clade. Chi-square analyses were completed on the contingency tables comparing clades and geographical locations. More intricate analyses using actual geographic distances between populations were completed within GeoDis (Posada et al. 2000). Distance statistics produced included within clade (D_c: represents the geographical distribution of the haplotypes within a clade) and between clade (D_n: represents the distance between haplotypes in a clade relative to those within the nested clade) distances (Templeton et al. 1995). A Monte Carlo procedure was utilized to determine if D_n and D_c were larger or smaller than expected at each level within the nested clade, thereby rejecting the null hypothesis of no geographical association. A thousand random permutations were completed in GeoDis to make statistical conclusions at the 5% level (Posada et al. 2000). Significance of values for geographic distances within clades and nested clades (whether greater or smaller than expected) were interpreted in a biological perspective via an inference key (Posada et al. 2000; http://bioag.byu.edu/zoology/crandall_lab/dposada/documents/NCA-key (24Oct01).pdf).

Results

Haplotype distribution.—Mitochondrial DNA sequence data were obtained from 144 black bears collected from 7 different southwestern populations. Sequences are deposited in GenBank under accession nos ######-######. Six variable nucleotide positions out of 555 bp resulted in the delineation of 5 haplotypes. Variable sites included 4 transitions and 2 insertion-deletion events (Table 1). Two transitions occurred within the cytochrome *b* gene (base pairs 1-111) while the remaining variation was located within the control region (base pairs 247-555).

Haplotype distribution was variable within and among the 7 analyzed populations (Figure 2). The B haplotype was dominant in the Mexican populations, whereas the A haplotype predominated in BIBE. All females, their offspring, and males < 2 years old in BIBE expressed haplotype A. The New Mexico population contained only the D and E haplotypes. Trans-Pecos specimens contained all haplotypes except E. Haplotype and nucleotide diversities were low for all populations analyzed except those specimens within the Trans-Pecos population (Table 2). The AMOVA depicted a high level of genetic structuring (ϕ_{ST}), with 63.01% of the genetic differentiation being ascribed to differences among sampling localities.

Pairwise ϕ_{ST} comparisons revealed that bears from BIBE and the Mogollon Mountains (MM) exhibited a higher ($P < 0.002$) degree of genetic differentiation when compared to the other 5 sampled localities (Table 3). Proportion of genetic variation attributable to within-site variation (27.95%) and among sites within regions (28.45%) was lower than the variation between New Mexico and the Mex-Tex populations (43.60%).

The number of female migrants per generation necessary to maintain the current degree of genetic structuring among populations ranged from 0.11 to ∞ (Table 3). The number of dispersing females per generation necessary to maintain the overall ϕ_{ST} (0.6301) was 0.294.

Nested clade analysis.—The haplotype network and nested design developed using TCS and manual techniques resulted in a simple cladogram (Figure 3i) that depicted haplotypes A, C, and E as tip clades, whereas D and B were classified as interior clades. An ambiguous relationship between clades 1-1 and 1-2 (Figure 3ii) was resolved using haplotype frequency data (see methods). Since haplotype C was found in only 1 animal (this sample was sequenced 3 times to check the validity of the haplotype), it has a very low probability of being designated an interior haplotype. Therefore, the connection between haplotype C and E is not strongly supported while the alternate connection between haplotype B and D is. The resulting figure demonstrates the most parsimonious network of 10 steps or fewer that has a > 95% probability of being correct (Figure 3).

Nested contingency analyses of geographical associations deciphered using GeoDis were significant for 2 of the 3 clades analyzed. Results incorporating geographic distances for the nested clade analyses (Figure 4) and their interpretation using the most recent inference key suggested a process of restricted gene flow with isolation by distance in the Mex-Tex populations and panmixia within the population in New Mexico (Table 4).

Discussion

Our results supported both of our predictions regarding organization and mechanics of the putative metapopulation of black bears in the Mex-Tex border region. We documented low overall genetic variation, but a high degree of differentiation among these populations of southwestern black bears. This differentiation was a result of restricted gene flow among populations, likely due to the harsh desert environment surrounding montane habitats. Our analyses also have demonstrated that the larger, mainland populations in northern Coahuila, Mexico are the probable sources of colonizers for areas of Texas in the Big Bend Ecosystem.

Only 5 haplotypes were identified among 144 black bear samples for a 555 bp portion of the mtDNA control and cytochrome-*b* regions. Similar studies conducted on the mtDNA genome typically exhibited more haplotypes (7-8) even with smaller (n = 18-37) sample sizes (Paetkau and Strobeck 1996; Wooding and Ward 1998). Nucleotide variability also was lower in our study than others from the literature (Paetkau and Strobeck 1996; Stone and Cook 2000; Wooding and Ward 1998). These differences can partly be attributed to the fact that samples in these previous studies included bears collected over a large geographic region (eastern to western Canada, Paetkau and

Strobeck 1996; Oregon to Alaska, Stone and Cook 2000; east to west coast of North America, Wooding and Ward 1997). Nevertheless, we believe this paucity of genetic variation observed in our study is a product of 2 factors; the isolated nature of black bear populations in the southwestern U.S. and northern Mexico and the low effective population sizes of recently recolonized populations in BIBE and BGWMA. The harsh environment and natural fragmentation of suitable bear habitat in the arid southwest impedes high levels of gene flow. Conversely, gene flow may be more extensive and less inhibited in areas of more contiguous populations such as northwestern Montana and the northwestern portions of the U.S. and Canada (Larivière 2001; Pelton and van Manen 1994). Additionally, the recent recolonizations by black bears within BIBE and BGWMA (Onorato and Hellgren 2001) were likely initiated by single, dispersing females from northern Mexico. These matriarch females and their offspring would comprise a majority of these small populations and result in a high level of relatedness within these regions. The combination of high levels of relatedness and small population sizes would ultimately result in low effective sizes in these 2 Mex-Tex populations.

Southwestern black bears exhibited an overall high level of genetic structuring among sampling localities ($\phi_{ST} = 0.6301$). Comparably, large mammals such as jaguars (*Panthera onca*) and right whales (*Eubalaena australis*) exhibited much lower levels of genetic differentiation ($\phi_{ST} = 0.3000$ and 0.1570 respectively) among subpopulations (Baker et al. 1999; Eizirik et al. 2001). Wolverines (*Gulo gulo*) exhibited a similarly high degree of genetic structuring ($\phi_{ST} = 0.5360$) in part of their range in northern Canada (Wilson et al. 2000). The genetic partitioning among populations of black bears in the Mex-Tex region and New Mexico suggested a pattern of male-mediated gene flow that has resulted in the structuring among populations. This conclusion is supported by the dominance of the A haplotype in BIBE (all females and all males <2 years old), with the B haplotype present only in males > 2 years old.

Pairwise comparisons of ϕ_{ST} values for the 7 populations analyzed demonstrated the uniqueness of the BIBE and New Mexican populations. These 2 populations were genetically differentiated from all other analyzed populations of southwestern bears except the Trans-Pecos group. From a conservation perspective, these analyses indicate the importance of these 2 populations in maintaining genetic variation within this region of the distribution of black bears in North America.

The recolonization of the Chisos Mountains in BIBE by black bears required > 40 years to occur (Onorato and Hellgren 2001). Using a generation time of 6.27 years (see methods) and estimates of average female-mediated gene flow, we estimate that 1 reproductive female migrant occurs between populations every 20 years. Because this calculation utilized data from New Mexico, this rate is underestimated when considering the metapopulation dynamics solely at work in the Mex-Tex populations (because we failed to observe exchange of female migrants between the New Mexico and Mex-Tex regions). Therefore, the ϕ_{ST} value was calculated for the Mex-Tex populations separately. The resulting value (0.4961) indicates that it will require 1 reproductive female migrant among Mex-Tex populations every 12 years (or 2 bear generations) to maintain currently observed levels of genetic differentiation.

Whether reproductive females move among Mex-Tex populations at such a temporal scale is difficult to verify, but historical evidence suggests that it is possible. During the > 40-year absence of a reproductively viable population of black bears from

BIBE, 2 observations of females with cubs were recorded (autumn 1969 and autumn 1978; Skiles 1995). Neither of these observations was followed by later evidence of residency. A female with cubs, followed by residency and subsequent reproduction was observed in 1988 (Skiles 1995). Our field observations during a probable mast failure verified movement of female bears from BIBE back into Mexico in autumn 2000 (Onorato and Hellgren, unpublished data). Factors responsible for spurring these migrations are likely fluctuations in food availability within and surrounding the Park.

There are some innate problems with estimating gene flow and migration/dispersal via indirect measures such as ϕ_{ST} (Whitlock and McCauley 1999). In translating ϕ_{ST} to $N_f m$, several of Wright's island model assumptions (1931) can be violated. Among these is the assumption that all populations in an island model contribute equally to the pool of dispersing animals between populations. Such a violation may lead to the underestimation of migration/dispersal rates (Whitlock and McCauley 1999). Nevertheless, assessment of direct measures of gene flow (recorded dispersal events via telemetry, direct observation of migrating/dispersing individuals) may help substantiate the use of indirect measures to predict $N_f m$ (Whitlock and McCauley 1999). We believe that our historical and recent direct observational data (described above) ascribe to these criteria and give credence to our $N_f m$ estimate.

Nested clade analyses imply that the clade of Mex-Tex populations (clade 1-1) has been impacted by restricted gene flow due to isolation by distance. This conclusion accurately describes the circumstances that are presently at work in this system. As discussed previously, ecological and genetic data lead us to deduce that gene flow occurs between Texas and populations in northern Mexico. However, the 40 km distance between patches of suitable bear habitat and the intervening matrix of unsuitable desert limits dispersal and gene flow, resulting in the genetic structuring presently observed in the Mex-Tex region.

Nested clade analysis denotes an inconclusive outcome in regards to analyses between the Mex-Tex and New Mexico populations. This conclusion demonstrates 1 of the weaknesses of parameter estimation methods such as the nested clade analysis. Although this method is considered to be statistically robust, it does not assess the error associated with the derived inferences and provides minimal consideration of more complex phylogeographic accounts (Knowles and Maddison 2002). Nevertheless, interpreting the haplotype network and its association with the geographical distribution of haplotypes can lead to 2 interesting hypotheses involving long-distance colonization. Long-distance colonization during the Pleistocene epoch was likely facilitated during periods of glaciation that occurred on several occasions. Cooler climates and more suitable habitat in the southwestern United States would have increased the prospect of long-distance colonization from New Mexico into western Texas (Elias 1997). Today, such a colonization event is unlikely due to the desert conditions between the montane islands of New Mexico and the Mex-Tex region. However, male bears appear to be capable of extensive dispersal. An individual killed in a vehicle collision in Fort Hancock, Hudspeth County, Texas was a male with haplotype D (⊙ in Figure 2). This individual was > 300 km from the Mogollon Mountains of New Mexico, but proximal to some lower-elevation ranges in northeastern Chihuahua. Another scenario could involve the colonization of western Texas and Mexico from populations of black bears from eastern North America. Our analyses do not permit us to eliminate 1 of these hypotheses.

This will require additional phylogenetic analyses using sequence data from across the distribution of black bears to decipher whether Mex-Tex populations are more closely related to bears from the western or eastern United States.

The importance of intraspecific genetic variation can not be overlooked when dealing with conservation issues, especially when involving species that typically maintain low population levels and have low fecundities. This variation is even more important when pertaining to small island populations within metapopulations. The recolonization of island populations of black bears in western Texas is dependent upon dispersing individuals from the larger mountain ranges in northern Coahuila. Such movements across a naturally fragmented desert environment are uncommon events, but they do occur. To maintain the smaller populations in western Texas, dispersal must not be impeded by anthropogenic factors (hunting, poaching, development, high-speed highway construction). Black bears are classified as threatened in Texas and are protected from hunting. In Mexico, a hunting moratorium for black bears was declared in 1986 (Doan-Crider and Hellgren 1996) and they were consequently listed as an endangered species. Development in Chihuahuan Desert habitat is not occurring at a rapid pace and does not pose a threat at this time. Continued educational efforts of state and federal agencies will hopefully demonstrate to private landowners that these animals can coexist with livestock in the area.

Our designation of the Trans-Pecos group as a "population" may be problematic as previously described. The fact that only 1 of the 6 bears allocated to this population was a female agrees well with the accepted pattern of male-mediated dispersal in black bears and the lack of a reproductively viable population in this region. Nevertheless, bears collected over this broad area expose interesting conservation perspectives for black bears in the southwestern United States and Northern Mexico. Although the sample size was very low, this region contained bears that exhibited 4 different haplotypes. Bears appear to be attempting to disperse into western Texas from the north (New Mexico) and the south (Coahuila, Mexico) as evidenced by the presence of haplotypes A, B, and D. Although no reproductively viable population is presently known to exist in the Trans-Pecos region north of BIBE, it appears that if/when such a population is established (with the residency of reproductively active female black bears into the area), there is the likelihood for a high amount of haplotypic variation within such a new population.

Poaching may occur in Mexico and to a lesser degree on private land in the Trans-Pecos northeast of BIBE (Sylvester H. Sorola, Texas Parks and Wildlife Department, personal communication). Prevention of poaching in Mexico will be difficult due to the remote nature of ejidos (communities that rely on agriculture for subsistence and were initiated in the 1950's as communes for city dwellers that wished to work the land) and the economic plight of the people in this region. Several governmental agencies in Mexico are working with ejido landowners to educate residents of the values of black bears to their natural heritage and of the laws that must be upheld in that region. The prospects from these efforts appear good, especially with the recent designation of large tracts of the Sierra del Carmen range as a private wildlife refuge (El Carmen Refuge) and the continued cooperation of area ranchers in providing habitat for bears on their lands (B. R. McKinney, Technical Wildlife Coordinator, El Carmen Project, CEMEX, Coahuila, Mexico, personal communication).

Our research has indicated that long-distance colonization may be responsible for the extant genetic differentiation within these southwestern populations of black bears. We speculate that dispersal of bears from either New Mexico or the eastern United States was responsible for the colonization of this species within this portion of their distribution. The divergence between New Mexico and Mex-Tex populations is a consequence of the changing climates that impacted present-day xeric systems from this region. The endemic qualities of the A, B and C haplotypes to the Mex-Tex region may have conservation implications for southwestern black bears and measures should be taken to insure that these haplotypes are preserved.

Acknowledgements

We thank B. R. McKinney (TPWD & CEMEX), and Cecily Costello (Hornocker Wildlife Institute) for contributing samples for genetic analyses. Additional thanks go J. R. Skiles (NPS), F. S. Mitchell, S. Ginger, P. Luce, M. Kasparian, M. Criffield, C. Tredick, G. Vose, N. Herring, numerous BIBE employees and field volunteers, and the RAVDB lab crew for their assistance in making the collection of these data feasible. This study was supported by funding from the Natural Resource Preservation Program (through the U.S. Geological Survey and USDI National Park Service, and Big Bend National Park). We thank D. M. Leslie, Jr. and the Oklahoma Cooperative Fish and Wildlife Research Unit (U.S. Geological Survey-Biological Resources Division, Oklahoma State University, Oklahoma Department of Wildlife Conservation, and Wildlife Management Institute, cooperating) for administrative and logistic support. We acknowledge additional funding granted by the Wyoming Chapter of the Wildlife Society

(Memorial Bear Grant), the American Museum of Natural History (Theodore Roosevelt Memorial Fund), and the Robert L. Lochmiller II Endowed Scholarship.

Literature Cited

AKÇAKAYA, H. R., M. A. BURGMAN, and L. R. GINZBURG. 1999. Applied population ecology. Sinauer Associates Inc., Sunderland, Massachusetts.

BAKER, C. S., N. J. PATENAUDE, J. L. BANNISTER, J. ROBINS, and H. KATO. 1999. Distribution and diversity of mtDNA lineages among southern right whales (*Eubalaena australis*) from Australia and New Zealand. Marine Biology 134:1-7.

BOYD-HEGER, D. K., and D. H. PLETSCHER. 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. Journal of Wildlife Management 63:1094-1108.

CLEMENT, M., D. POSADA, and K. A. CRANDALL. 2000. TCS: a computer program to estimate gene genealogies. Molecular Ecology 9:1657-1659.

COSTELLO, C. M., ET AL. 2001. A study of black bear ecology in New Mexico with models for population dynamics and habitat suitability. New Mexico Department of Game and Fish, W-131-R, Federal Aid in Wildlife Restoration Project.

CRANDALL, K. A., and A. R. TEMPLETON. 1993. Empirical tests of some predictions from coalescent theory with applications to intraspecific phylogeny reconstruction. Genetics 134:959-969.

DOAN-CRIDER, D. L., and E. C. HELLGREN. 1996. Population characteristics and winter ecology of black bears in Coahuila, Mexico. Journal of Wildlife Management 60:398-407.

EIZIRIK, E., J. KIM, M. MENOTTI-RAYMOND, P. G. C. JR., S. J. O'BRIEN, and W. E. JOHNSON. 2001. Phylogeography, population history and conservation genetics of jaguars (*Panthera onca*, Mammalia, Felidae). Molecular Ecology 10:65-79.

ELIAS, S. A. 1997. The Ice-Age History of Southwestern National Parks. Smithsonian Institution Press, Washington D.C.

ELOWE, K. D., and W. E. DODGE. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management 53:962-968.

FEDERAL REGISTER. 2001. Reevaluation of the record of decision for the final environmental impact statement and selection of alternative for grizzly bear recovery in the Bitterroot Ecosystem. Department of Interior-Fish and Wildlife Service, Vol. 66: 33623-33624.

FORBES, S. H., and D. K. BOYD. 1996. Genetic variation of naturally colonizing wolves in the central Rocky Mountains. Conservation Biology 10:1082-1090.

HANSKI, I. A., and D. SIMBERLOFF. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation, Pp. 5-26 in Metapopulation biology: ecology, genetics, and evolution (I. A. Hanski and M. E. Gilpin, eds.). Academic Press, San Diego, California.

HELLGREN, E. C., and M. R. VAUGHAN. 2000. Ecology, conservation, and management of black bears in the Great Dismal Swamp, Pp. 199-208 in The natural history of the Great Dismal Swamp (R. K. Rose, ed.). Omni Press, Madison, Wisconsin.

JEANMOUGIN, F., J. D. THOMPSON, M. GOUY, D. G. HIGGINS, and T. J. GIBSON. 1998. Multiple sequence alignment with Clustal X. Trends in Biochemical Science 23:403-405.

KNOWLES, L. L., and W. P. MADDISON. 2002. Statistical phylogeography. Molecular Ecology 11:2623-2635.

LARIVIÈRE, S. 2001. *Ursus americanus*. Mammalian Species 647:1-11.

LONGMIRE, J. L., M. MALTBIE, and R. J. BAKER. 1997. Use of "lysis buffer" in DNA isolation and its implication for museum collections. Occasional Papers, The Museum, Texas Tech University 163:1-3.

MADDISON, D. R., and W. P. MADDISON. 2000. MacClade 4: Analysis of Phylogeny and Character Evolution. Sinauer Associates, Sunderland, Massachusetts.

MAEHR, D. S. 1997. The comparative ecology of bobcat, black bear and Florida panther in south Florida. Bulletin of the Florida Museum of Natural History 40:1-176.

MLADENOFF, D. J., T. A. SICKLEY, R. G. HAIGHT, and A. P. WYDEVEN. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conservation Biology 9:279-294.

ONORATO, D. P., and E. C. HELLGREN. 2001. Black bear at the border: the recolonization of the Trans-Pecos, Pp. 245-259 in Large mammal restoration: ecological and sociological challenges in the 21st Century (D. S. Maehr, R. F. Noss and J. L. Larkin, eds.). Island Press, Washington D.C..

PAETKAU, D., and C. STROBECK. 1996. Mitochondrial DNA and the phylogeography of Newfoundland black bears. Canadian Journal of Zoology 74:192-196.

PELTON, M. R., and F. T. VAN MANEN. 1994. Distribution of black bears in North America. Eastern Workshop on Black Bear Research and Management 12:133-138.

POSADA, D., K. A. CRANDALL, and A. R. TEMPLETON. 2000. GeoDis: a program for the cladistic nested analysis of the geographical distribution of genetic haplotypes. Molecular Ecology 9:487-488.

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.

SCHNEIDER, S., D. ROESSLI, and L. EXCOFFIER. 2000. A software for population genetics data analysis. Genetics and Biometry Lab, Dept. of Anthropology, University of Geneva, Geneva, Switzerland.

SCHWARTZ, C. C., and A. W. FRANZMANN. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. Journal of Wildlife Management 56:426-431.

SHIELDS, G. F., and T. D. KOCHER. 1991. Phylogenetic relationships of North American Ursids based on analysis of mitochondrial DNA. Evolution 45:218-221.

SKILES, J. R. 1995. Black bears in Big Bend National Park--the Tex-Mex connection. Proceedings of the Western Black Bear Workshop 5:67-73.

STONE, K. D., and J. A. COOK. 2000. Phylogeography of black bears (*Ursus americanus*) of the Pacific Northwest. Canadian Journal of Zoology 78:1218-1223.

TAYLOR, R. B. 1999. Black bear status report. Texas Parks and Wildlife Department, Project 19: 1-11.

TEMPLETON, A. R. 1998. Nested clade analyses of phylogeographic data: testing hypotheses about gene flow and population history. Molecular Ecology 7:381-397.

TEMPLETON, A. R., K. A. CRANDALL, and C. F. SING. 1992. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. Genetics 132:619-633.

TEMPLETON, A. R., E. ROUTMAN, and C. A. PHILLIPS. 1995. Separating population structure from population history: a cladistic analysis of the geographical distribution of mitochondrial DNA haplotypes in the tiger salamander, *Ambystoma tigrinum*. Genetics 140:767-782.

TEMPLETON, A. R., and C. F. SING. 1993. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping. IV. Nested analyses with cladogram uncertainty and recombination. Genetics 134:659-669.

WHITLOCK, M. C., and D. E. MCCAULEY. 1999. Indirect measure of gene flow and migration: $F_{ST} \neq 1/(4Nm + 1)$. Heredity 82:117-125.

WILSON, G. M., R. A. VAN DEN BUSSCHE, P. K. KENNEDY, A. GUNN, and K. POOLE. 2000. Genetic variability of wolverines (*Gulo gulo*) from the Northwest Territories, Canada: conservation implications. Journal of Mammalogy 81:186-196.

WOODING, S., and R. H. WARD. 1997. Phylogeography and Pleistocene evolution in the North American black bear. Molecular Biology and Evolution 14:1096-1105.

WOODING, S., and R. H. WARD. 1998. Patterns of genetic diversity in a black bear population indicate recent immigration. Ursus 10:329-333.

WRIGHT, S. 1931. Evolution in Mendelian populations. Genetics 16:97-159.

Table 1.—Identified mtDNA haplotypes within 7 populations of black bears (*Ursus americanus*) in Texas, New Mexico, and northern Mexico. Variable nucleotide positions are denoted according to their location within the 555 bp portion of the control region and cytochrome *b* gene that were sequenced. Identical nucleotides are indicated with (•) and insertion/deletion events with (–).

Haplotype	36	93	351	352	462	466
A	T	T	T	T	A	G
B	•	•	•	–	•	•
C	•	•	–	–	•	•
D	C	C	•	–	G	A
E	C	C	–	–	G	A

Table 2.—Distribution of mtDNA haplotypes, measures of haplotype (*h*) and nucleotide (π) diversity, and standard error (SE) from 7 populations of black bears in Texas, New Mexico, and northern Mexico. Populations BIBE, BGWMA, SDB, SDC, SMM and Trans-Pecos encompass the area referred to as the Mex-Tex region in the text.

	mtDNA haplotypes									
Population	A	B	C	D	E	*n*	*h*	SE	π	SE
BIBE	26	5				31	0.2796	0.0904	0.00050	0.00062
BGWMA		9				9	0.0000	0.0000	0.00000	0.00000
SDB	12	48				60	0.3254	0.0624	0.00059	0.00067
SDC		5				5	0.0000	0.0000	0.00000	0.00000
SMM		4				4	0.0000	0.0000	0.00000	0.00000
Trans-Pecos	1	3	1	1		6	0.8000	0.1721	0.00360	0.00271
MM				25	4	29	0.2463	0.0935	0.00045	0.00058
Average							0.2359		0.00073	

Table 3.—Pairwise comparisons of mtDNA genetic structuring (ϕ_{ST}), upper portion of the triangular matrix, and estimates of female-mediated gene flow (N_fm), lower portion of the triangular matrix for 7 populations of southwestern black bears (*Ursus americanus*). Significance levels for ϕ_{ST} comparisons were determined using the Bonferroni correction for pairwise comparisons (* is significantly different from 0 at $P < 0.00238$).

Population	BIBE	BGWMA	SDB	SDC	SMM	Trans-Pecos	MM
BIBE		0.757*	0.564*	0.732*	0.724	0.438*	0.737*
BGWMA	0.161		0.070	0.000	0.000	0.287	0.819*
SDB	0.387	6.643		0.022	0.000	0.100	0.704*
SDC	0.183	∞	22.227		0.000	0.161	0.799*
SMM	0.191	∞	∞	∞		0.111	0.792*
Trans-Pecos	0.642	1.242	4.500	2.606	4.005		0.529*
MM	0.178	0.111	0.210	0.126	0.131	0.445	

Table 4.—Results of statistical testing for nonrandom geographical associations of haplotypes using a nested contingency analyses. Significant associations ($P < 0.05$) are denoted with an *. Conclusions were derived by interpreting the observed distance patterns of haplotypes with a key developed by Templeton et al. (1995).

Clade	Chi-square statistic	Probability value	Chain of Inference	Conclusion
1-1	167.663	0.000*	1-2-3-4-NO	Restricted gene flow with isolation by distance
1-2	0.159	1.000	1-NO	Panmixia
Total cladogram	144.000	0.000*	1-2-Tip interior status cannot be determined	Inconclusive outcome

FIGURE LEGENDS

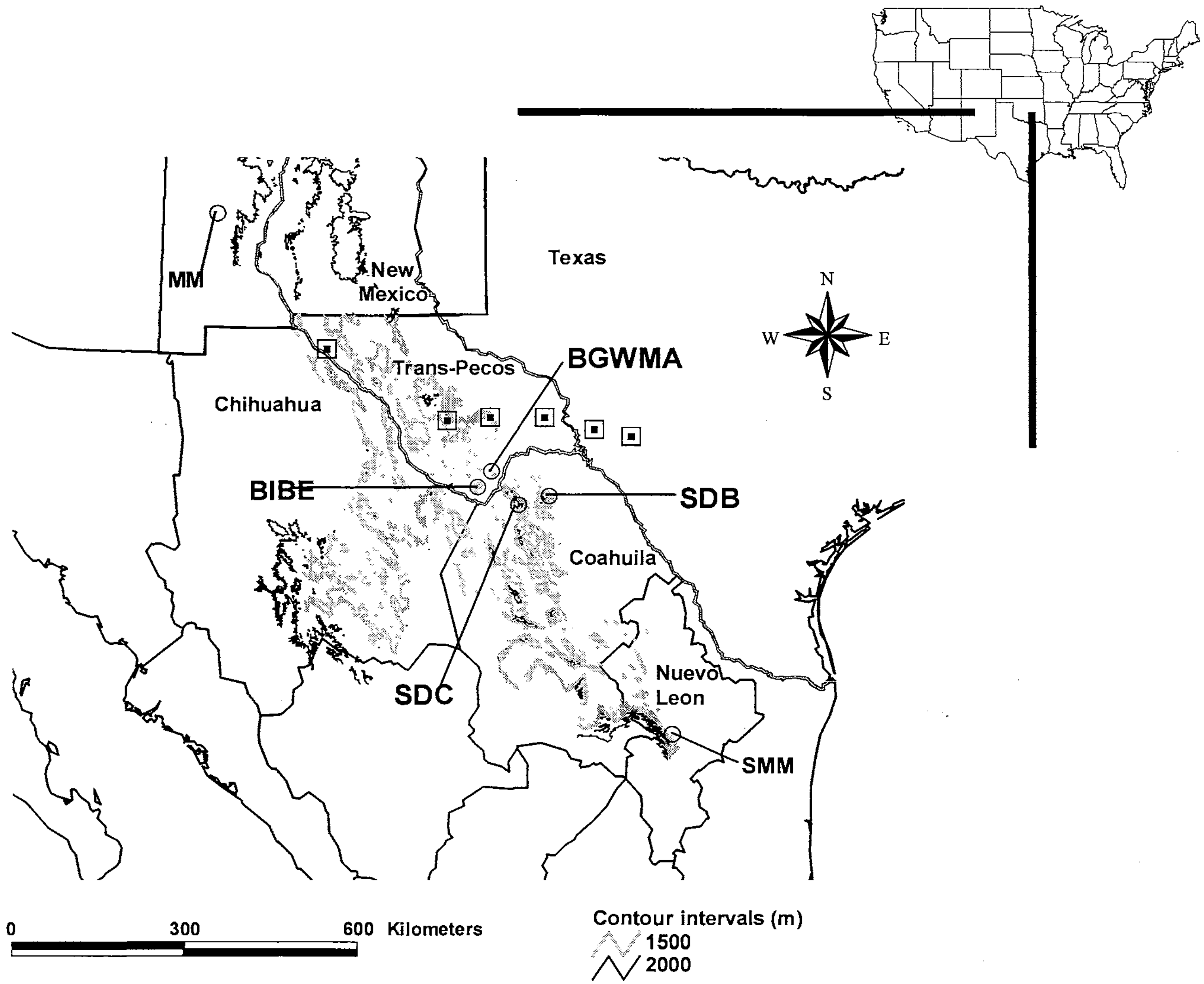
Figure 1.—Locations of the 7 collection sites for tissue samples of southwestern black bears. Collection sites include: BIBE, Big Bend National Park, Texas, U.S.A; BGWMA, Black Gap Wildlife Management Area, Texas, U.S.A; SDB, Serranias del Burro Mountains, Coahuila, Mexico; SDC, Sierra Del Carmen Mountains, Coahuila, Mexico, SMM, Sierra Madre Mountains, Nuevo Leon, Mexico; ⊡, Trans-Pecos region of western Texas, U.S.A.; MM, Mogollon Mountains, New Mexico, U.S.A. Populations BIBE, BGWMA, SDB, SDC, SMM and ⊡ were designated as the Mex-Tex metapopulation. Hierarchical analyses were completed between the Mex-Tex and New Mexico regions.

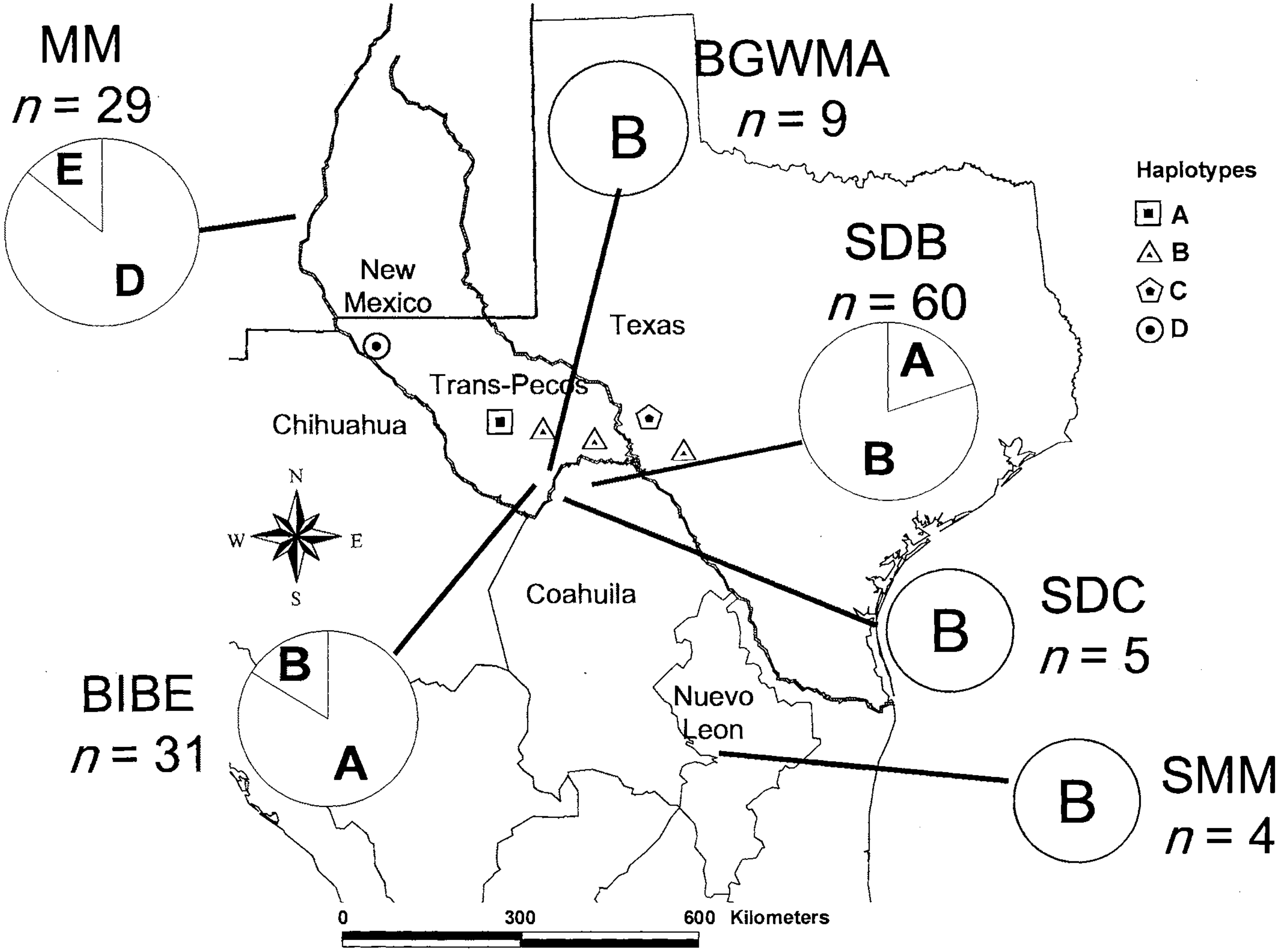
Figure 2.—Frequency distribution of the 5 haplotypes found in 7 populations of southwestern black bears (n = 144). Population abbreviations are identical to those denoted in Figure 1.

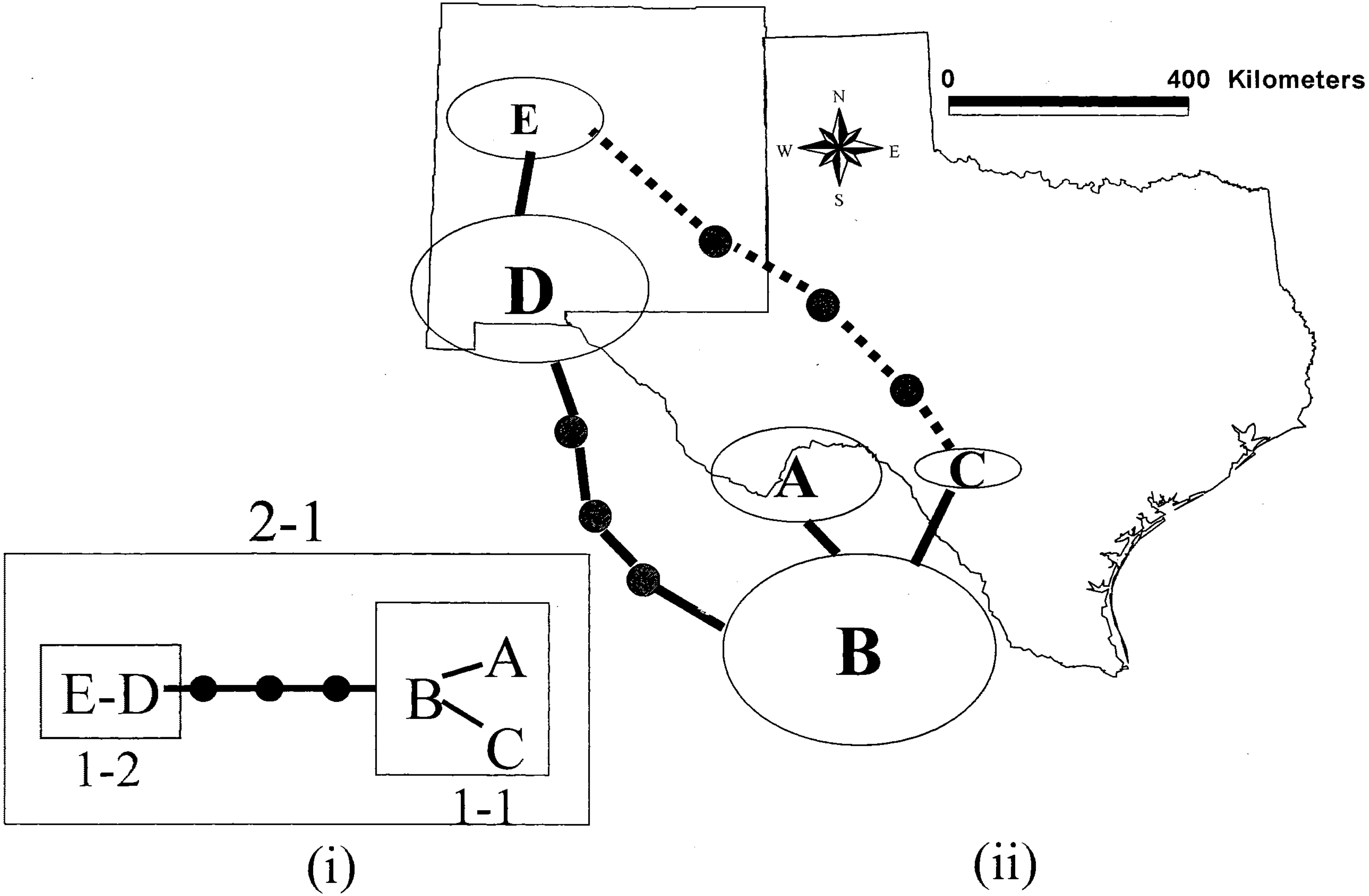
Figure 3.—Haplotype networks developed using maximum parsimony for phylogeographic comparisons of black bears. The manually derived nesting scheme (i) for the haplotype network developed using the program TCS and (ii) the representation of this network overlaid on the geography of the region. The ambiguous loop that was resolved using the protocol of Crandall and Templeton (1993) is denoted via the dashed line.

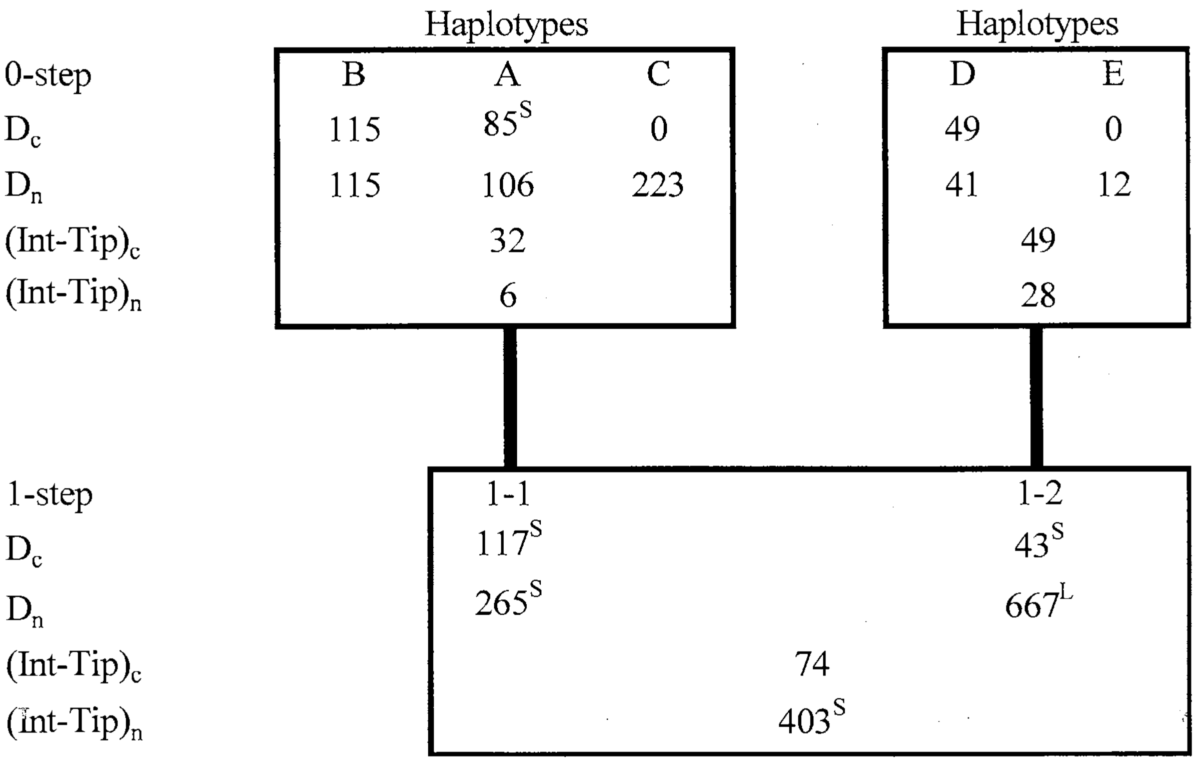
Figure 4.—Results of the nested clade analysis for 5 mtDNA haplotypes of southwestern black bears. Values for distances within clades (D_c) and within nested clades (D_n) are denoted for each level of the manually derived nested design (refer to Fig.

3). Values superscripted with (S) or (L) refer to significantly small or large clade or nested clade distance values. Average values for the difference between interior and tip D_c and D_n values are given in the Int-Tip row.


MM
New Mexico
Texas
Trans-Pecos
BGWMA
Chihuahua
BIBE
SDB
SDC
Coahuila
Nuevo Leon
SMM
N
W
E
S
0
300
600 Kilometers
Contour intervals (m)
1500
2000


MM
n = 29
E
D
BGWMA
n = 9
B
Haplotypes
A
B
C
D
SDB
n = 60
A
B
New Mexico
Texas
Trans-Pecos
Chihuahua
N
W
E
S
Coahuila
Nuevo Leon
SDC
n = 5
B
BIBE
n = 31
B
A
SMM
n = 4
B
0
300
600 Kilometers


2-1
E-D
B
A
C
1-2
1-1
(i)
E
D
A
C
B
N
W
E
S
0
400 Kilometers
(ii)



0-step	Haplotypes B	Haplotypes A	Haplotypes C	Haplotypes D	Haplotypes E
D_c	115	85^S	0	49	0
D_n	115	106	223	41	12
$(\text{Int-Tip})_c$		32		49	
$(\text{Int-Tip})_n$		6		28	

1-step	1-1	1-2
D_c	117^S	43^S
D_n	265^S	667^L
$(\text{Int-Tip})_c$	74	
$(\text{Int-Tip})_n$	403^S	

CHAPTER IV

GENETIC STRUCTURE OF AMERICAN BLACK BEARS IN THE DESERT SOUTHWEST OF NORTH AMERICA: CONSERVATION IMPLICATIONS FOR RECOLONIZATION

DAVID P. ONORATO

Abstract

American black bears (*Ursus americanus*) have recolonized parts of their former range in the Trans-Pecos region of western Texas after a 40+year absence. Assessment of genetic variation, structuring, gene flow, and dispersal among bear populations along the borderlands of Mexico and Texas is important to gain a better understanding of recolonizations of large carnivores. We evaluated aspects of genetic diversity and gene flow for 7 populations of black bears in southwestern North America using genotypic data from 7 microsatellite loci. Our results indicated that genetic diversity generally was high in the borderland metapopulation whereas levels of genetic structuring were low. Combining data from nuclear markers with previously generated mitochondrial-DNA data indicated that the borderlands metapopulation is affected by female philopatry and male-biased dispersal. Inbreeding does not appear to be occurring in the fledgling populations of bears in Big Bend National Park (BIBE) or the Black Gap Wildlife Management Area (BGWMA) at this time. Additionally, pairwise comparisons of genetic distance and structural statistics reveal that the population of bears in BIBE maintains a high level of genetic diversity for its size. Islands of habitat that once supported black bears in the Trans-Pecos of Texas will rely on periodic migration-dispersal events of female bears from northern Coahuila for recolonization to occur. The high level of genetic diversity present in BIBE makes this population an important source for male and female bears dispersing north and west of the Park.

Keywords: black bear, Chihuahuan Desert, dispersal, gene flow, metapopulation, microsatellite, recolonization, *Ursus americanus*

Introduction

Large carnivores will continue to face increasing challenges in the 21st century due to continued human population explosion and extensive loss of habitat. Maintaining viable populations of large carnivores has become increasingly difficult as human encroachment continues at a rapid pace. This struggle has been exemplified in the last several decades by such high-profile cases as the Florida panther (*Puma concolor coryi)* in southern Florida (Maehr 1997) and the Sumatran tiger (*Panthera tigris sumatrae*) in the Indonesian archipelago (Williamson et al. 2002).

Large carnivores have naturally recolonized parts of their former range in rare instances. For example, gray wolves (*Canis lupus*) have reappeared in parts of the northern Rocky Mountains, northern Minnesota, Wisconsin, and Michigan (Beyer et al. 2001; Boyd-Heger and Pletscher 1999; Forbes and Boyd 1996; Thiel et al. 1997). This recolonization process has been facilitated by long-distance dispersal of female wolves (Boyd-Heger and Pletscher 1999) and habitat corridors between Canada and the United States that contain suitable and contiguous habitat (Forbes and Boyd 1996; Mladenoff et al. 1995). Although female American black bears (*Ursus americanus*) rarely disperse from their natal area (Elowe and Dodge 1989; Rogers 1987a; Schwartz and Franzmann 1992), descendents of reintroduced black bears are dispersing from western Arkansas and have naturally recolonized parts of the Ouachita Mountains in southeastern Oklahoma (Smith and Clark 1994). This recolonization of the Ouachitas in Oklahoma is facilitated by contiguous suitable bear habitat between the border of Arkansas and southeastern Oklahoma.

Black bears recently (mid 1980's) have recolonized parts of their former range in the western Texas segment of the Big Bend Ecosystem (Onorato and Hellgren 2001). In this instance, dispersal events between large, contiguous ranges in northern Coahuila, Mexico are not facilitated by suitable habitat corridors into western Texas. The inhospitable environment of the lower Chihuahuan Desert serves as a semi-permeable barrier for black bears moving from Mexico into parts of western Texas (Fig. 1). This factor, coupled with the low intrinsic rate of female dispersal, highlights the improbable nature of a natural recolonization of black bears in this ecoregion (Onorato and Hellgren 2001). Based on mtDNA and demographic data, we described black bears in this region as existing in a mainland-island metapopulation (Onorato et al. 2003). Combining data from mtDNA with data from biparentally inherited nuclear DNA markers allows researchers to make conclusions concerning male dispersal and aspects of gene flow and genetic diversity. Data from both maternally and biparentally inherited loci ultimately result in more complete deductions concerning phylogeography, population structure, and dispersal patterns of a species.

We describe genetic relationships of black bears from 7 populations in northern Mexico and the southwestern United States using 7 hypervariable microsatellite loci. We hypothesized that populations of black bears within this mainland-island metapopulation are affected by male-biased dispersal with intermittent female migration-dispersal events that have resulted in recolonization of former range. We predicted that (1) male-biased dispersal should result in low levels of genetic structuring between mainland and island populations at biparentally inherited loci and (2) that black bears in recently recolonized parts of western Texas (island populations) are genetically more similar to populations in northern Mexico (mainland populations) than to bears in the Mogollon Mountains of southwestern New Mexico. The southwestern portion of the range of black bears has been seriously understudied and these data ultimately will permit researchers to arrive at appropriate conservation initiatives to catalyze and increase success of recolonizations.

Materials and Methods

Concurrent fieldwork and tissue collection were conducted in Big Bend National Park (BIBE in Figure 1, n = 32), Texas between September 1998 and July 2001 (Onorato et al. *Ursus*, in press). The Park encompasses about 320,000 ha of northern Chihuahuan desert in the Trans-Pecos region of western Texas. The primary habitat for black bears in the Park is located within a 100-km^2 area comprising the Chisos Mountains (elevation 1400-2385 m) where abundant food sources such as oak (*Quercus* spp.), juniper (*Juniperus* spp.), and madrone (*Arbutus xalapensis*) can be found. Tissue samples from 9 individuals also were obtained from a small population of black bears recolonizing the adjacent Black Gap Wildlife Management Area (BGWMA in Figure 1). This region contains suitable habitat at lower elevations (900-1400 m) about 40 km northeast of the Chisos Mountains of BIBE. Tissue samples from 8 individuals were collected throughout the Trans-Pecos region of Texas (Figure 1). These individuals were sampled after vehicle collisions, poaching incidents, or during relocation after nuisance complaints. Reproductively viable populations are not currently present in habitats where these samples were collected (Taylor 1999). However, we categorized these samples as a "population" of dispersing or colonizing animals in historic habitat within western Texas.

Tissue samples also were obtained from two mountain ranges known to support large populations of black bears: Serranias del Burro (SDB, $n = 58$) and Sierra del Carmen (SDC, $n = 5$) in northern Coahuila, Mexico. We also obtained tissue samples of 4 individuals from the Sierra Madre Oriental near Monterey, Mexico (SMM). Populations in BIBE, BGWMA, SDB, SDC, SMM, and the Trans-Pecos samples are referred to as the Mex-Tex populations. Reference to the borderlands metapopulation includes only BIBE, BGWMA, SDC, SDB, and Trans-Pecos, unless otherwise noted.

Samples collected from the Mogollon Mountains (MM, Figure 1, $n = 29$) of west-central New Mexico during a long-term study by the Hornocker Wildlife Institute (Costello et al. 2001) were analyzed for comparative purposes to determine how closely related bears from this region are to those found in the Mex-Tex ecosystem. In terms of available habitat, this ecoregion is more similar to the larger ranges found in northern Mexico. The study area is primarily in the Gila National Forest and elevations range from 1750 m to > 3000 m.

Samples were either stored frozen (-20°C) or in lysis buffer (Longmire et al. 1997). DNA was extracted using the phenol extraction method described by Longmire et al. (1997). Seven $(GT)_n$ microsatellite loci were amplified using the polymerase chain reaction (PCR) and primers described in Paetkau et al. (1998). Six of these loci (G1D, G10B, G10C, G10L, G10P, G10O) were cloned from an American black bear DNA library (Paetkau et al. 1995; Paetkau and Strobeck 1994), whereas CXX20 was derived from a domestic dog (*Canis familiaris*) library (Ostrander et al. 1993). One primer of each pair was synthesized with a fluorescent dye (FAM, HEX, or TET) to permit detection and sizing of microsatellite repeats on a Perkin-Elmer ABI Prism 377 Automated Sequencer.

Amplifications were performed in 15 μl reactions using 50–200 ng DNA, 0.17 μM of each primer, 9 μl True Allele PCR premix (Perkin-Elmer Applied Biosystems, Foster City, CA) and 3.8 μl double deionized water. The following thermal profile was used during amplification: 12 min at 95°C; 10 cycles of 15 s at 94°C, 1 min at 49-55°C (annealing temperatures were specific for different loci), 30 sec at 72°C; 25 cycles of 15 s at 89°C, 1 min at 55°C, 30 s at 72°C; and 30 min at 72°C. Products were diluted and combined based on the size, fluorescent dye and yield. One microliter of PCR dilutions was added to 3 μl of loading buffer containing 0.5 μl GS-400HD ROX size standard, 0.5 μl of loading-dye, and 2.5 μl of formamide. The mixture was denatured at 95°C for 5 min and loaded on a 6% Long-Ranger acrylamide gel with resulting data analyzed using GENESCAN™ version 2.1 and GENOTYPER™ version 2.4 software packages (Perkin-Elmer Applied Biosystems, Foster City, California).

Assessment of observed (H_o) and expected (H_e) heterozygosity within populations were calculated using ARLEQUIN version 2.0 (Schneider et al. 2000). The same calculations were computed on a per locus basis using Cervus 2.0 (Marshall et al. 1998). Deviations from Hardy-Weinberg equilibrium (HWE, Guo and Thompson 1992) were tested for at the locus level within each population using ARLEQUIN version 2.0 (Schneider et al. 2000).

The extent of allelic variation partitioned among populations within groups, within populations, and among groups was analyzed via hierarchical examination of F_{ST} using a grouped analysis of molecular variance or AMOVA. Groupings for analyses that involved all 7 populations included Texas populations (BIBE, BGWMA, and Trans-Pecos), Mexican populations (SDB, SDC, SMM) and New Mexico populations (MM). Groupings for the borderlands metapopulations included the Texas populations and Mexican borderlands populations (SDB, SDC). Population comparisons (pairwise F_{ST}), and overall genetic differentiation as assessed by F_{IS}, F_{IT}, and F_{ST} were calculated using ARLEQUIN version 2.0 (Schneider et al. 2000). Tests that involved multiple comparisons were corrected for the increased likelihood of making a type I error using a sequential Bonferroni adjustment. Pairwise F_{ST} values were compared with ϕ_{ST} values obtained in a previous study by Onorato et al. (2003) using mtDNA sequences.

We calculated a Mantel test (Sokal and Rohlf 1995) to determine if a correlation existed between a matrix of pairwise F_{ST} values and pairwise straight-line geographic distances between the 6 true populations and within the borderland metapopulation using Arlequin 2.0 (Schneider et al. 2000). We did not include samples collected from the Trans-Pecos "population" because designating a geographic center for these samples was not possible.

The likelihood-ratio-distance statistic D_{LR} (Paetkau et al. 1997) and a population assignment test were computed using the web-based program Doh developed by J. Brzustowski (http://www2.biology.ualberta.ca/jbrzusto/Doh.php). The assignment test utilized by Doh follows the protocol of Paetkau et al. (1995). We selected a randomization method without replacement that shuffled gene frequencies at each locus across populations. Pairwise-genetic-distance values (D_{LR}) also were used to generate a neighbor-joining tree using MEGA version 2.1 (Kumar et al. 2001).

Results

DNA from 145 black bears representing 7 populations was amplified and genotyped at 7 microsatellite loci (Table 1). In certain cases, even after repeated attempts, some individuals did not amplify at a locus and those discrepancies were tallied (Table 1). The highest H_e was observed for locus G10P and the lowest level was noted for G1D. All loci were polymorphic with an average of 9.29 alleles/locus and a range of 8 to 12. Observed heterozygosity (H_o) was lower than H_e in all sampled populations and bears in MM had the lowest level of H_e (Table 2). The two populations with the highest average number of alleles per locus were SDB and BIBE. Assessment of HWE via an exact test using the Markov chain parameters denoted that the assumptions of HWE were violated for 2-6 loci in each population (Table 3). Similarly, within loci, HWE was violated between 1 to 6 times.

Overall genetic differentiation among all 7 populations ($F_{ST} = 0.0045$) and among populations within the borderlands metapopulation ($F_{ST} = 0.0004$) was low. Levels of inbreeding in individuals relative to subpopulations (F_{IS}) and relative to all populations (F_{IT}) also were low in comparisons over all 7 sampled populations ($F_{IS} = 0.0385$, $F_{IT} = 0.0420$) and among the borderlands metapopulation ($F_{IS} = -0.0005$, $F_{IT} = -0.0001$). The proportion of genetic variation attributable to within-site variation ($V_c = 99.55\%$) was much higher than variation among sites within groups ($V_b = 0.31\%$) and among groups ($V_a = 0.14\%$). A similar pattern was noted when comparisons were made only among populations considered within the borderlands metapopulation ($V_a = 0.03\%$, $V_b = 0.01\%$,

$V_c = 99.96\%$). Pairwise comparisons of F_{ST} and ϕ_{ST} inferred significant amounts of genetic differentiation between BIBE and MM populations compared with the other 5 sampled localities (Table 4). This differentiation was more evident in the maternally inherited mtDNA data when compared with nuclear DNA. Nevertheless, the only pairwise comparisons for F_{ST} that were statistically significant were present in comparisons between MM or BIBE and the remaining populations.

Results from the Mantel test between pairwise F_{ST} and geographic distance document a high correlation ($r = 0.7205$, $P = 0.056$), denoting an increase in genetic differentiation as geographic distance between populations increased. Performing the same analysis for only populations specifically within the borderlands metapopulation, no correlation was detected between pairwise F_{ST} and geographic distance ($r = 0.2258$, $P = 0.403$).

Supporting results from *F*-statistics, the likelihood-ratio genetic distances (D_{LR}) calculated for all 7 populations revealed a high level of genetic differentiation between Mex-Tex populations and bears from the Mogollon Mountains of west-central New Mexico (Table 5). The small genetic distance ($D_{LR} = 0.259$) between the populations of bears from the two large mountain ranges in northern Coahuila (SDB and SDC) indicated that gene flow may occur frequently between these two ranges. An unrooted neighbor-joining tree of D_{LR} values illustrated the close association of bear populations in the Mex-Tex metapopulation and the divergence between bears from this region and those located in the Mogollon Mountains of west-central New Mexico (Figure 2).

The population assignment test correctly assigned individuals to the population in which they were captured in 74.5% of the cases (Table 6). Populations of bears in western Texas (BIBE, BGWMA and Trans-Pecos) contained animals that had a high probability of assignment to the larger populations in northern Coahuila. Coincidentally, the SDB population contained several individuals that were assigned to western Texas populations, potentially resulting from bidirectional migrations or dispersals between these two regions. All tissue samples collected from bears in MM were correctly assigned to that mountain range.

Discussion

Data from this study and previous work (Onorato and Hellgren 2001; Onorato et al. 2003; Onorato et al. 2002) revealed several important characteristics concerning metapopulation dynamics of American black bears in southwestern North America. Overall levels of H_e for each of the 7 southwestern populations ranged from 0.4795 to 0.8367, which is comparable to values reported by Paetkau and Strobeck (1994) for Canadian black bears (0.360–0.801) and higher than those cited by Warrillow et al. (2001) for disjunct black bear populations in the southeastern United States (0.390–0.560). Interestingly, none of the newly established populations sampled in Texas (BIBE and BGWMA) exhibited H_e values as low as those found in insular populations (0.360 in Newfoundland; Paetkau and Strobeck 1994) or other areas that may be impacted by low levels of gene flow between populations (0.33 in White River National Wildlife Refuge, Arkansas USA; Warrillow et al. 2001). In several studies conducted with large carnivores, such as brown bears (*U. arctos*) and wolverines (*Gulo gulo*), H_e values are typically < 0.60 for populations that are isolated from the effects of migration and dispersal from other populations due to anthropogenic factors or natural barriers (Kyle and Strobeck 2001; Paetkau et al. 1998; Waits et al. 2000). Although the desert ecosystem surrounding populations in BGWMA and BIBE impedes migration or dispersal, it is not a complete barrier to periodic movements from mountains in northern Coahuila to parts of western Texas. Our field observations have attested to bidirectional movement of male and female black bears between SDC and BIBE (Onorato et al. 2002) and this movement is corroborated by mtDNA analyses (Onorato *et al.*, in press).

Low levels of H_e in MM are difficult to interpret because this population resides in a mountain range that contains > 15,000 km^2 of suitable bear habitat (Costello et al. 2001). The study area where these samples were collected (Bear Wallow Mountain, New Mexico) is > 400 km^2 and is adjacent to several other large mountains that contain excellent bear habitat (Costello et al. 2001). In many ways, this area is comparable to the large, contiguous ranges in SDB and SDC. Interestingly, the estimated density of bears in this study area was 9.4 bears/100 km^2 (Costello et al. 2001), which is at the low end of the range of density estimates (7-130 bears/100 km^2) for populations of black bears (Garshelis 1994). The population density estimate for MM also is 4 times lower than the density reported for SDB (35 bears/100 km^2; Doan-Crider and Hellgren 1996). Low density may result in lower H_e within MM, but it is unlikely that population fragmentation or small sample size was problematic. The most notable difference between MM and Mex-Tex populations is that a legal hunting season is open during part of the year in New Mexico (there is no legal hunting season in Mexico). Regulated hunting pressure should not produce low levels of H_e in a stable or increasing population because it would afford opportunity for younger males to disperse into vacated home ranges from adjacent habitat or populations.

The overall high levels of H_e and the fact that many of the populations and microsatellite loci are not in HWE indicate that assumptions of HWE have been violated. Migration or dispersal between the larger populations of bears in northern Coahuila and the island refugia in western Texas would lead to deviations in HWE due to violation of the closed population assumption. The impact of gene flow on HWE was also supported by F_{ST} (low levels of structuring), assignment tests (presence of bears of Mexican descent in Texas populations and vice-versa), and D_{LR} (low genetic distance ratios between populations in Mexico and Texas). Other factors that may result in deviations from HWE include inbreeding, assortative or disassortative mating, and fragmentation of populations (Frankham et al. 2002). Inbreeding is unlikely within this region, especially in the Mex-Tex populations (see below). Conversely, natural fragmentation of populations, as exemplified in the Mex-Tex ecosystem, may produce deviations from HWE. The Wahlund Effect also could produce a false reduction in the number of heterozygotes within populations due to further population subdivision. Although further subdivision is unlikely in Texas populations due to the small size and recent recolonization, it is possible that the population in the SDB mountains is composed of > 1 population. Deviations from HWE at several of these loci were noted by Waits et al. (2000) in Scandinavian brown bears. Purported reasons for these deviations included the presence of populations of brown bears within the path of an expanding Scandinavian bear distribution affected by recent emigration and immigration (Swenson et al. 1998; Waits et al. 2000). The similar circumstance of bears recolonizing western Texas from northern Coahuila may have had an analogous impact on our results.

Combining nuclear and mitochondrial data provides a more accurate assessment of dispersal patterns of bears in the borderlands metapopulation. Previous research using maternally inherited mtDNA demonstrated a high degree of genetic structuring (ϕ_{ST} = 0.6301) among these populations (Onorato et al. 2003). However, our data indicate that levels of inbreeding relative to each subpopulation (F_{IS}) and to the total population (F_{IT}) are low in a comparison involving all 7 populations (0.0385 and 0.0420, respectively) and are negative (-0.0005 and -0.0001, respectively) when only the borderlands metapopulation is included in the analyses. Lack of any evident inbreeding problem for recolonizing populations in western Texas is an important finding concerning process and success of these fledgling populations. Our measurements of population divergence (F_{ST}) for all 7 populations and the borderlands metapopulation were low (0.0045 and 0.0004, respectively) but consistent with previous observations of female philopatry and male-biased dispersal in black bears (Rogers 1987a; Schwartz and Franzmann 1992; Smith and Clark 1994).

The Mantel test depicted a high correlation between genetic differentiation and geographical distance across the 7 populations. This test demonstrates that although periodic movements between New Mexico and Mex-Tex regions may occur, they are probably extremely rare and unlikely to involve reproductive females. Conversely, within the borderlands metapopulation, there was no geographical association with genetic structuring. This conclusion is consistent with our knowledge of recolonization of black bears in western Texas and their association with populations in northern Coahuila (Onorato and Hellgren 2001). Previous research has demonstrated the linkage between populations of black bears in western Texas and populations in northern Mexico via genetic evidence (Onorato et al. 2003) and historical narratives from local ranchers and predator control agents (Onorato and Hellgren 2001). Movement of female and male black bears between the SDC and BIBE was verified during a migration-dispersal event in autumn 2000 (Onorato et al. 2002). These data demonstrate that the Chihuahuan Desert serves as a semi-permeable barrier to dispersal by bears.

The likelihood-genetic-ratio distances (D_{LR}) exhibited a similar trend to the Mantel test and structural statistics in characterizing the difference in genotypes present in MM versus those in the Mex-Tex ecosystem. All D_{LR} values were > 12.000 in pairwise comparisons between MM and Mex-Tex populations. This high value asserts that genotypes in MM are > 12 times more likely to occur in MM than in any of the other populations sampled. Alternatively, bears in the SDB have a high probability of occurring in BIBE or the Trans-Pecos as depicted by D_{LR} values of 2.089 and 0.819, respectively. Mean D_{LR} values also showed that genotypes in BIBE were on average more distinct than genotypes found in other Mex-Tex populations, which suggests that the black bear population in BIBE is diverging from source populations in northern Coahuila. Factors resulting in the observed D_{LR} trend include restricted gene flow and low effective population sizes. The uniqueness of the BIBE population also has been implied in previous analyses with mtDNA (Onorato et al. 2003).

The level of correct population assignment (74.5%) was comparable to 78% correctly assigned in a study by Warrillow et al. (2001) that assessed the subspecific affinity of black bears in parts of the southeastern United States. Several brown bear studies exhibited higher percentages of correct assignment (92%; Paetkau et al. 1998; 84%; Waits et al. 2000). A study by Paetkau et al. (1995) on 4 populations of polar bears

(*U. maritimus*) obtained a much lower level of correct assignment (60%) and even lower levels have been described for wolverines (56%; Kyle and Strobeck 2002; 43%; Kyle and Strobeck 2001). The lower levels of correct population assignment for polar bears and wolverines may result from the biology of these animals, which requires that they maintain large home ranges and disperse greater distances (Belikov and Boltunov 1998; Garner et al. 1994; Kyle and Strobeck 2001), ultimately resulting in the increased probability of gene flow between populations. Although brown and black bears of either sex may disperse distances > 50 km (McLellan and Hovey 2001; Onorato et al. 2002), movements beyond this distance are uncommon in females.

The high percentage of correct population assignment for populations of black bears in BIBE and MM is significant. No bears from MM were assigned to a Mex-Tex population, indicating little to no current gene flow between these two regions. Only 1 bear from the Mex-Tex metapopulation was assigned to MM. This assignment is accurate and gives credence to the other population assignments in this study. The bear assigned to MM from the Trans-Pecos "population" was a road-killed specimen collected at Fort Hancock in extreme western Texas. Although the bear was > 300 km from the MM, he was located only 60 km from the New Mexico border. Fort Hancock also is adjacent to some low-elevation ranges in Chihuahua Mexico in which the status of black bears is unresolved. This dispersing individual may be an indication of the potential gene flow between New Mexico or Chihuahua and the Trans-Pecos region of Texas. Further research should involve sampling black bears in the northern and western parts of the Trans-Pecos such as Guadalupe Mountains National Park (GMNP in Figure 1), Hudspeth and El Paso counties to quantify linkages between bear populations in New Mexico and Texas.

In BIBE, 90.6% of the bears sampled were assigned correctly to the Park population. The 3 bears that were assigned to SDB included 2 adult males > 7 years old and 1 3-year old (age at time of capture). These assignments attest to gene flow occurring between mountain ranges in northern Coahuila and western Texas, especially in terms of male dispersal. Nevertheless, the high percentage of correct assignment indicates that the BIBE population maintains a degree of genotypic distinctiveness. The unrooted neighbor-joining tree further corroborated differentiation of BIBE from other Mex-Tex populations. This diagram clusters the Mex-Tex populations at one end, but BIBE is extended out on its own branch (Figure 2). This result is another indication of the uniqueness of the black bear population within BIBE and the fact that it could serve as a genetically diverse source of male and female dispersers to former range located in the Trans-Pecos to the north and northwest of BIBE.

The differentiation between New Mexico bears in MM and Mex-Tex populations has important conservation implications. Moritz (1994; 1995) describes evolutionarily significant units (ESU's) as populations in which mtDNA alleles are reciprocally monophyletic and nuclear loci demonstrate significant divergence of allele frequencies. Designating bears from these two ecoregions as separate ESU's is controversial, given the continual debate over the actual definition of an ESU (Fraser and Bernatchez 2001). Nevertheless, our nuclear and mtDNA (Onorato et al. 2003) data support the designation of two ESU's according to Moritz (1994; 1995). In following the "adaptive evolutionary conservation" perspective described by Fraser & Bernatchez (2001), these populations meet the criteria of several different ESU definitions. Populations of bears in the borderlands metapopulation and New Mexico meet the criteria of ESU's described by Crandall *et al.* (2000), Moritz (1994) and Fraser & Bernatchez (2001). Whether black bears in MM are truly a different subspecies than black bears in the Mex-Tex populations will require further investigation and analyses. The modified distribution of black bear subspecies described by Larivière (2001) denotes the possible presence of *U. a. eremicus, U. a. machetes,* and *U. a. amblyceps* within the Big Bend ecosystem. Nevertheless, from a management perspective, it appears that bears in MM should be managed separately from Mex-Tex populations. Any proposed reintroduction of black bears in southwestern North America should consider these data before proceeding.

Male dispersal among these populations is apparently frequent enough to maintain low levels of genetic structuring. However, periodic female dispersal must be maintained to continue the natural recolonization process in western Texas. Although disruption due to anthropogenic factors remains a minor impact in this region, it is imperative that this area remains disturbance-free to permit the continuation of migration-dispersal events. Additional genetic and demographic data from the population in SDC and dispersing bears in the ranges north of BIBE will have important ramifications in assessing the uniqueness of this poorly studied portion of the range of the American black bear.

Acknowledgments

We thank B. R. McKinney (TPWD & CEMEX), and Cecily Costello (Hornocker Wildlife Institute) for contributing samples for genetic analyses. Additional thanks go to F. S. Mitchell, S. M. Ginger, P. Luce, M. A. Kasparian, M. Criffield, C. Tredick, G. Vose, N. Herring, numerous BIBE employees and field volunteers, and the RAVDB lab crew for their assistance in making the collection of these data feasible. This study was supported by funding from the Natural Resource Preservation Program (through the U.S. Geological Survey and USDI National Park Service, and Big Bend National Park). We thank D. M. Leslie, Jr. and the Oklahoma Cooperative Fish and Wildlife Research Unit (U.S. Geological Survey-Biological Resources Division, Oklahoma State University, Oklahoma Department of Wildlife Conservation, and Wildlife Management Institute, cooperating) for administrative and logistic support. We acknowledge additional funding granted by the Friends of Big Bend National Park, Wyoming Chapter of the Wildlife Society (Memorial Bear Grant), the American Museum of Natural History (Theodore Roosevelt Memorial Fund), and the Robert L. Lochmiller II Endowed Scholarship.

Literature Cited

BELIKOV, S. E., and A. N. BOLTUNOV. 1998. Problems with conservation and sustainable use of polar bears in the Russian Arctic. Ursus 10:119-127.

BEYER, D. E., B. J. ROELL, J. H. HAMMILL, and R. D. EARLE. 2001. Records of Canada Lynx, *Lynx canadensis*, in the Upper Peninsula of Michigan, 1940-1997. Canadian Field-Naturalist 115:234-240.

BOYD-HEGER, D. K., and D. H. PLETSCHER. 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. Journal of Wildlife Management 63:1094-1108.

COSTELLO, C. M., ET AL. 2001. A study of black bear ecology in New Mexico with models for population dynamics and habitat suitability. New Mexico Department of Game and Fish, W-131-R, Federal Aid in Wildlife Restoration Project.

CRANDALL, K. A., O. R. P. BININDA-EMONDS, G. M. MACE, and R. K. WAYNE. 2000. Considering evolutionary processes in conservation biology. Trends in Ecology & Evolution 15:290-295.

DOAN-CRIDER, D. L., and E. C. HELLGREN. 1996. Population characteristics and winter ecology of black bears in Coahuila, Mexico. Journal of Wildlife Management 60:398-407.

ELOWE, K. D., and W. E. DODGE. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management 53:962-968.

FORBES, S. H., and D. K. BOYD. 1996. Genetic variation of naturally colonizing wolves in the central Rocky Mountains. Conservation Biology 10:1082-1090.

FRANKHAM, R., D. A. BRISCOE, and J. D. BALLOU. 2002. Introduction to conservation genetics. Cambridge University Press, Cambridge, United Kingdom.

FRASER, D. J., and L. BERNATCHEZ. 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. Molecular Ecology 10:2741-2752.

GARNER, G. W., S. E. BELIKOV, M. S. STISHOV, J. V. G. BARNES, and S. M. ARTHUR. 1994. Dispersal patterns of maternal polar bears from the denning concentration on Wrangel Island. International Conference of Bear Research and Management 9:401-410.

GARSHELIS, D. L. 1994. Density-dependent population regulation of black bears, Pp. 3-14 in Density-dependent population regulation of black, brown and polar bears (M. Taylor, ed.). International Association for Bear Research and Management, Monograph Series No. 3, Missoula, Montana, USA.

GUO, S. W., and E. A. THOMPSON. 1992. Performing the exact test of Hardy-Weinberg proportion for multiple alleles. Biometrics 48:361-372.

KUMAR, S., K. TAMURA, I. B. JAKOBSEN, and M. NEI. 2001. MEGA2: molecular evolutionary genetics analysis software. Bioinformatics 17:1244-1245.

KYLE, C. J., and C. STROBECK. 2001. Genetic structure of North American wolverine (*Gulo gulo*) populations. Molecular Ecology 10:337-347.

KYLE, C. J., and C. STROBECK. 2002. Connectivity of peripheral and core populations of North American wolverines. Journal of Mammalogy 83:1141-1150.

LARIVIÈRE, S. 2001. *Ursus americanus*. Mammalian Species 647:1-11.

LONGMIRE, J. L., M. MALTBIE, and R. J. BAKER. 1997. Use of "lysis buffer" in DNA isolation and its implication for museum collections. Occasional Papers, The Museum, Texas Tech University 163:1-3.

MAEHR, D. S. 1997. The comparative ecology of bobcat, black bear and Florida panther in south Florida. Bulletin of the Florida Museum of Natural History 40:1-176.

MARSHALL, T. C., J. SLATE, L. E. B. KRUUK, and J. M. PEMBERTON. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology 7:639-655.

MCLELLAN, B. N., and F. W. HOVEY. 2001. Natal dispersal of grizzly bears. Canadian Journal of Zoology 79:838-844.

MLADENOFF, D. J., T. A. SICKLEY, R. G. HAIGHT, and A. P. WYDEVEN. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conservation Biology 9:279-294.

MORITZ, C. 1994. Defining "evolutionarily significant units" for conservation. Trends in Ecology and Evolution 9:373-375.

MORITZ, C. 1995. Uses of Molecular Phylogenies for Conservation. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 349:113-118.

ONORATO, D. P., and E. C. HELLGREN. 2001. Black bear at the border: the recolonization of the Trans-Pecos. Pp. 245-259 in Large mammal restoration: ecological and sociological challenges in the 21st Century (D. S. Maehr, R. F. Noss and J. L. Larkin, eds.). Island Press, Washington D.C., USA.

ONORATO, D. P., E. C. HELLGREN, R. A. VAN DEN BUSSCHE, and D. L. DOAN-CRIDER. 2003. Phylogeographic patterns within a metapopulation of black bears (*Ursus americanus*) in the American Southwest. Journal of Mammalogy 84:000-000.

ONORATO, D. P., E. C. HELLGREN, R. A. VAN DEN BUSSCHE, and D. M. LESLIE, JR. 2002. Conservation ecology of an isolated population of black bears in the Big Bend Ecosystem. National Park Service, Final Report, Project 97-08: 1-54.

OSTRANDER, E. A., G. F. SPRAGUE, and J. RINE. 1993. Identification and characterization of dinucleotide repeat $(CA)_n$ markers for genetic mapping in dog. Genomics 16:207-213.

PAETKAU, D., W. CALVERT, I. STIRLING, and C. STROBECK. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4:347-354.

PAETKAU, D., G. F. SHIELDS, and C. STROBECK. 1998. Gene flow between insular, coastal and interior populations of brown bears in Alaska. Molecular Ecology 7:1283-1292.

PAETKAU, D., and C. STROBECK. 1994. Microsatellite analysis of genetic variation in black bear populations. Molecular Ecology 3:489-495.

PAETKAU, D., L. P. WAITS, P. L. CLARKSON, L. CRAIGHEAD, and C. STROBECK. 1997. An empirical evaluation of genetic distance statistics using microsatellite data from bear (Ursidae) populations. Genetics 147:1943-1957.

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.

SCHNEIDER, S., D. ROESSLI, and L. EXCOFFIER. 2000. A software for population genetics data analysis. Genetics and Biometry Lab, Dept. of Anthropology, University of Geneva, Geneva, Switzerland.

SCHWARTZ, C. C., and A. W. FRANZMANN. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. Journal of Wildlife Management 56:426-431.

SMITH, K. G., and J. D. CLARK. 1994. Black bears in Arkansas - characteristics of a successful translocation. Journal of Mammalogy 75:309-320.

SOKAL, R. R., and F. J. ROHLF. 1995. Biometry. 3rd ed. W. H. Freeman and Company, New York.

SWENSON, J. E., F. SANDEGREN, and A. SODERBERG. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. Journal of Animal Ecology 67:819-826.

TAYLOR, R. B. 1999. Black bear status report. Texas Parks and Wildlife Department, Project 19: 1-11.

THIEL, R. P., W. H. HALL, and R. N. SCHULTZ. 1997. Early den digging by Wolves, *Canis lupus*, in Wisconsin. Canadian Field-Naturalist 111:481-482.

WAITS, L., P. TABERLET, J. E. SWENSON, F. SANDEGREN, and R. FRANZEN. 2000. Nuclear DNA microsatellite analysis of genetic diversity and gene flow in the Scandinavian brown bear (*Ursus arctos*). Molecular Ecology 9:421-431.

WARRILLOW, J., M. CULVER, E. HALLERMAN, and M. VAUGHAN. 2001. Subspecific affinity of black bears in the White River National Wildlife Refuge. Journal of Heredity 92:226-233.

WILLIAMSON, J. E., R. M. HUEBINGER, J. A. SOMMER, E. E. LOUIS, and R. C. BARBER. 2002. Development and cross-species amplification of 18 microsatellite markers in the Sumatran tiger (*Panthera tigris sumatrae*). Molecular Ecology Notes 2:110-112.

Table 1.—Genetic variation assessed at 7 microsatellite loci for southwestern American black bears including the number of alleles (k), number of animals genotyped (*n*), observed (H_o) and expected (H_e) heterozygosity and the probability of identity (PID). Annealing temperatures were used for amplification during PCR.

Locus	Temp °C	k	*n*	H_o	H_e	PID
G1D	52	8	145	0.428	0.739	0.100
G10B	49	8	144	0.549	0.743	0.097
G10C	49	12	143	0.427	0.810	0.061
G10L	49	10	134	0.201	0.753	0.095
G10P	52	8	142	0.627	0.829	0.050
G10O	49	8	145	0.386	0.806	0.065
CXX20	49	11	144	0.514	0.808	0.058
Overall		9.29	142	0.447	0.784	$1.060X10^{-8}$

Table 2.—Genetic variation assessed at 7 microsatellite loci for 7 populations of American black bears in southwestern North America. Symbols are identical to those found in Table 1 with the exception that *n* is the number of animals within each sample.

Population	*n*	H_e	H_o	Average no. alleles/locus	Total no. alleles
BIBE	32	0.6819	0.5179	4.71	33
BGWMA	9	0.7143	0.5238	3.71	26
SDB	58	0.7182	0.4478	6.86	48
SDC	5	0.8095	0.5143	4.14	29
SMM	4	0.8367	0.3214	3.14	22
Trans-Pecos	8	0.7798	0.5000	4.57	32
MM	29	0.4795	0.2414	4.29	30
Overall	145	0.7171	0.4381		

Table 3.—Probability values from the exact test to assess Hardy-Weinberg equilibrium following the protocol of Guo and Thompson (1992). Exact test was performed with the Markov chain parameters set at a forecasted length of 100,000 and 1000 dememorization steps.

				Loci			
Population	G1D	G10B	G10C	G10L	G10P	G10O	CXX20
BIBE	<0.0001*	0.4291	0.0228*	0.0003*	0.0426*	0.0015*	0.1047
BGWMA	0.1715	0.0451*	0.0070*	0.0315*	1.0000	0.0860	0.5568
SDB	<0.0001*	0.0558	<0.0001*	<0.0001*	0.0090*	<0.0001*	0.0004*
SDC	0.6127	0.0487*	0.5487	0.0065*	0.3436	0.8968	0.1908
SMM	0.3160	1.0000	0.3141	0.0279*	0.0277*	0.0248*	0.1470
Trans-Pecos	0.0356*	0.1334	0.0635	0.0035*	0.1025	0.0786	0.1557
MM	0.0056*	<0.0001*	0.0011*	<0.0001*	0.0075*	1.0000	0.0657

* = $P < 0.05$

Table 4.—Pairwise comparison of mtDNA genetic structure (ϕ_{ST} from Onorato et al. 2003, above the diagonal) and microsatellite structure (F_{ST}, below the diagonal) for 7 populations of American black bears. Significance levels for both comparisons were determined using the Bonferroni correction for pairwise comparisons (* is significantly different from 0 at $P < 0.00238$).

Population	BIBE	BGWMA	SDB	SDC	SMM	Trans-Pecos	MM
BIBE		0.7570*	0.5636*	0.7323*	0.7242	0.4379*	0.7366*
BGWMA	0.0005		0.0704	0.0000	0.0000	0.2871	0.8191*
SDB	0.0006*	0.0000		0.0224	0.0000	0.0996	0.7040*
SDC	0.0005	0.0000	0.0002		0.0000	0.1608	0.7988*
SMM	0.0162	0.0165	0.0157	0.0174		0.1111	0.7925*
Trans-Pecos	0.0000	0.0000	0.0002	0.0000	0.0166		0.5290*
MM	0.0071*	0.0069	0.0067*	0.0072	0.0231	0.0070	

Table 5.—Likelihood ratio of genetic distance (D_{LR}) values obtained via genotypes from 7 microsatellite loci for 7 populations of American black bears. Mean values were calculated for each corresponding population along column 1.

Populations	BIBE	BGWMA	SDB	SDC	SMM	Trans-Pecos	MM	Mean D_{LR}
BIBE	-							5.141
BGWMA	2.484	-						4.751
SDB	2.089	1.277	-					3.664
SDC	3.125	1.562	0.259	-				3.246
SMM	4.987	5.173	2.339	0.000	-			4.743
Trans-Pecos	1.891	1.342	0.819	0.000	2.737	-		3.297
MM	16.268	16.667	15.202	14.528	13.220	12.995	-	14.813

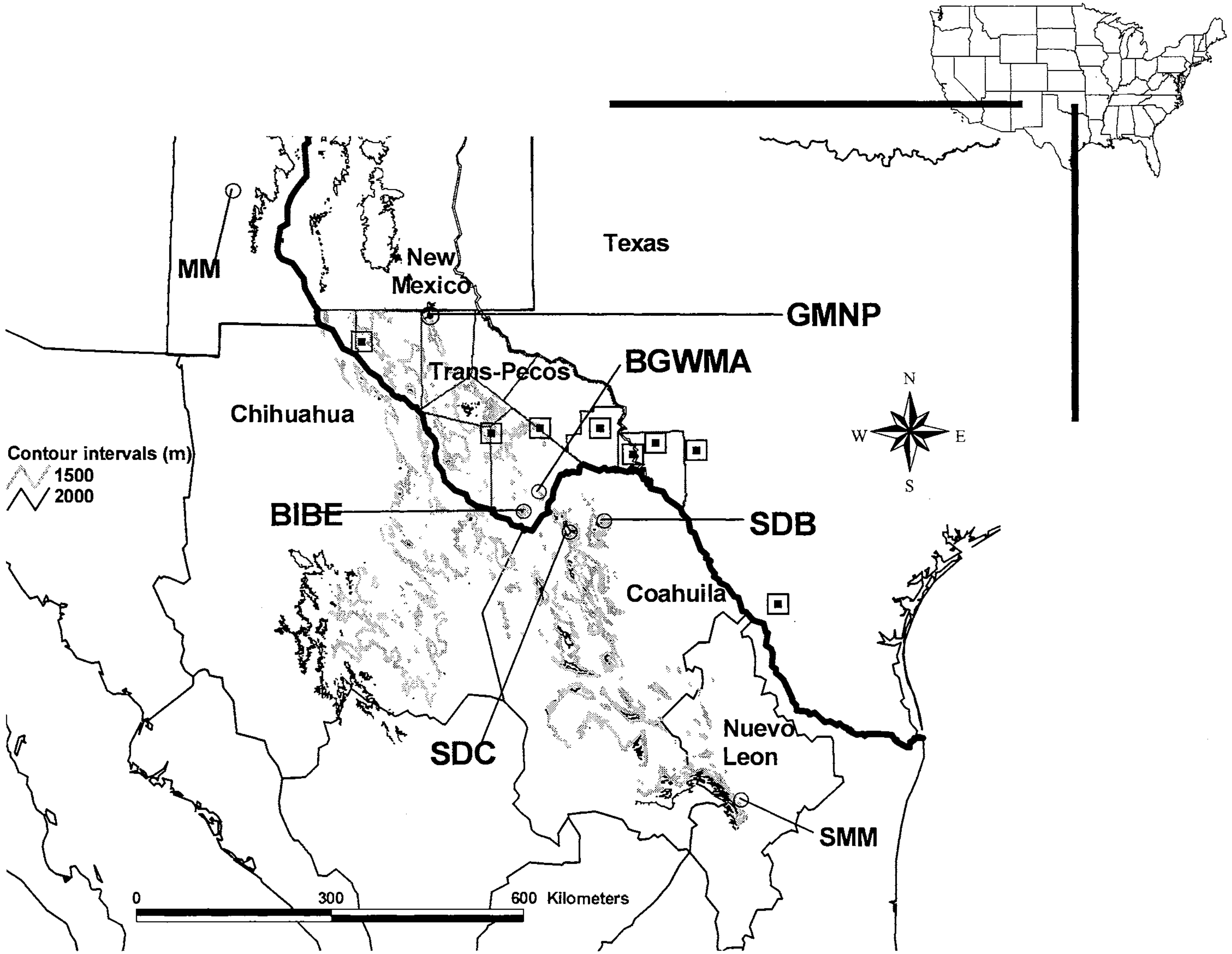
Table 6.—Population assignment test results for 7 populations of American black bears in southwestern North America. Calculation of population assignment followed the protocol of Paetkau et al. (1995).

	Assigned Population								
Known Population	BIBE	BGWMA	SDB	SDC	SMM	Trans-Pecos	MM	*n*	% Correctly Assigned
BIBE	29	0	3	0	0	0	0	32	90.6%
BGWMA	0	6	1	2	0	0	0	9	66.7%
SDB	6	7	36	2	3	4	0	58	62.1%
SDC	0	1	0	2	0	2	0	5	40.0%
SMM	0	0	1	2	1	0	0	4	25.0%
Trans-Pecos	1	0	1	0	0	5	1	8	62.5%
MM	0	0	0	0	0	0	29	29	100%

FIGURE LEGENDS

Figure 1.—Locations of the 7 collection sites for tissue samples of American black bears collected in southwestern North America. Collection sites include: BIBE, Big Bend National Park, Texas, U.S.A; BGWMA, Black Gap Wildlife Management Area, Texas, U.S.A; SDB, Serranias del Burro Mountains, Coahuila, Mexico; SDC, Sierra Del Carmen Mountains, Coahuila, Mexico, SMM, Sierra Madre Mountains, Nuevo Leon, Mexico; ⊡, Trans-Pecos region of western Texas, U.S.A.; MM, Mogollon Mountains, New Mexico, U.S.A. Populations BIBE, BGWMA, SDB, SDC, SMM and ⊡ were designated as the Mex-Tex populations. Guadalupe Mountains National Park (GMNP) contains black bear habitat and is mentioned in the discussion section.

Figure 2.—Assessment of genetic distinctiveness using likelihood ratio genetic distance values (D_{LR}) in an unrooted neighbor-joining tree. The scale of the branches is relative to the differences in D_{LR}. Population abbreviations as in Figure 1.


MM
New Mexico
Texas
GMNP
Trans-Pecos
BGWMA
Chihuahua
Contour intervals (m)
1500
2000
N
W
E
S
BIBE
SDB
Coahuila
SDC
Nuevo Leon
SMM
0
300
600 Kilometers


SDB
BGWMA
Trans-Pecos
BIBE
SDC
MM
SMM
2

PATERNITY AND RELATEDNESS OF AMERICAN BLACK BEARS RECOLONIZING A DESERT MONTANE ISLAND: INFERENCES VIA GENETIC AND FIELD DATA.

DAVID P. ONORATO

Department of Zoology and Oklahoma Cooperative Fish and Wildlife Research Unit, 430 LSW, Oklahoma State University, Stillwater, OK, 74078 USA

Abstract

American black bears (*Ursus americanus*) have begun to recolonize portions of western Texas via immigration from populations located in northern Mexico. A small (< 30) population of black bears now resides in Big Bend National Park (BIBE), Texas after a 40-year absence. We assessed genetic paternity and relatedness among bears within BIBE via maternally and biparentally inherited markers. Additionally, field observations recorded between 1998-2001 supplemented our analyses of relationships among black bears in BIBE. Data from 7 microsatellite loci permitted us to assign paternity for 8 of 12 cubs from 6 litters. Multiple paternity was revealed in 2 litters. Levels of relatedness in BIBE were comparable to those found in the large population in the nearby Serranias del Burro in Coahuila, Mexico. Female black bears in BIBE were more closely related to each other than males were to each other. Microsatellite data and previous analyses on mtDNA sequences indicate that bears in the Mex-Tex metapopulation exhibit male-biased dispersal. Demographic and genetic data provided a pedigree for 22 of 32 sampled bears and depicted an elevated level of relatedness between adult females.

Recolonization and maintenance of genetic variation in western Texas appear to be reliant on male dispersal from Mexico and episodic female dispersal.

Introduction

With the use of highly polymorphic genetic markers, it is now possible to assess predictions concerning relatedness (Blouin et al. 1996; Cronin et al. 1999; Lunn et al. 2000), immigration (Rannala and Mountain 1997), dispersal (Banks et al. 2002; Girman et al. 1997; Gompper et al. 1998), paternity (Clapham and Palsboll 1997; Constable et al. 2001) and genetic structure (Paetkau et al. 1995; Waits et al. 2000) for animal populations. Conclusions derived from these data can be useful in determining appropriate conservation and management measures for declining, threatened or endangered species (Blundell et al. 2002; Flagstad et al. 2000; Lucchini et al. 2002; Richardson et al. 2001; Wilson et al. 2000). Additionally, insight into behavioral characteristics of social species (Girman et al. 1997; Kays et al. 2000) and implications for natural recolonization of extirpated populations (Blundell et al. 2002; Onorato et al. 2003) can be assessed with molecular markers.

Quantification of genetic paternity and relatedness in a small population of large carnivores that have naturally recolonized former range can provide important insight into the recolonization process. Such data permit researchers to assess dispersal patterns (Burland et al. 2001; Gompper et al. 1998; Kays et al. 2000), a characteristic essential for preserving small, isolated populations. The level of relatedness within and between sexes provides insight regarding gene flow and descriptions of these demographic characteristics via a relatedness index can aid researchers in assessing inbreeding coefficients (Cronin et al. 1999) and consequently help prevent the negative impacts that inbreeding can produce (Testa and Scotton 1999).

Several mammalian families that produce >1 offspring in a litter (Canidae, Ursidae, Sciuridae) have been recorded to have occurrences of multiple paternity within litters (Haynie et al. in press; Robinson 1999; Schenk and Kovacs 1995). Assessing frequency of multiple paternity is critical for the management of the genetic health of a population due to the benefits that may ultimately result from this event (Craighead et al. 1995). Litters containing offspring sired by different males should contain higher levels of genetic variation than litters comprised of full siblings (Craighead et al. 1995). Furthermore, assessing reproductive success of individuals within a small population can help describe the potential for maintaining genetic diversity within a system. All of these factors have significant implications for recolonizing populations.

Our specific objectives were to describe paternity and relatedness for a small population of American black bears (*Ursus americanus*) located in Big Bend National Park (BIBE) in the Trans-Pecos region of western Texas. Additionally, data on relatedness of known mother-offspring dyads, a nearly complete census of the population, and the recent nature of the recolonization (Onorato and Hellgren 2001; Onorato et al. 2002) permitted the development of a pedigree for a majority of the population.

We predicted that relatedness of black bears in BIBE would be equivalent to those found in source populations in Mexico due to previously noted male-biased dispersal patterns in this ecosystem. Intrasexual relatedness levels in BIBE should be higher in females than males due to patterns of haplotype distribution noted in previously analyzed mtDNA sequence data (Onorato et al. 2003) and knowledge of female philopatry in bears (Rogers 1987b; McLellan and Hovey 2001). Additionally, we expected that paternity assignment would include adult males that are highly related to reproductive females due to the isolated nature of this population. Lastly, we predicted that, if recolonization of BIBE was initiated by the dispersal and colonization of a single matriarch female (as hypothesized by Onorato and Hellgren 2001) and the aforementioned patterns of female philopatry apply, the female segment of the population would be primarily descendents of that matriarch.

Materials and Methods

Sample collection—Fieldwork and laboratory analyses concentrated on the population of black bears located in Big Bend National Park (BIBE), Texas (Figure 1). Individuals were trapped using barrel traps typically located in the higher elevations of the Chisos Mountains (Figure 2). Bears were immobilized using Telazol (Fort Dodge Laboratories Inc., Fort Dodge, Iowa USA) at a concentration of 5.5 mg/kg. At the time of initial capture, each bear was given a unique identification number by implanting a passive integrated transponder (PIT) tag to provide a permanent and unequivocal marker. The first upper premolar of all bears > 1 year old was extracted using dental elevator and extractor tools. Age was estimated via cementum annuli analysis (Willey 1974) by a commercial laboratory (Matson's Laboratory, Milltown, Montana, USA).

Tissue samples (blood or ear tissue) were collected from 31 bears between 1998 and 2000. An additional sample from a large adult male (muscle tissue) found dead in a remote canyon within the Park in 1994 was included in this study. For some analyses, these 32 samples were compared to samples from populations of bears in western Texas and northern Mexico (Figure 1). These samples were analyzed in previous work by the authors (see Chapter III and IV, Onorato et al. 2003, Onorato et al. in prep) and were collected during several concurrent black bear studies in southwestern North America (Costello et al. 2001; Doan-Crider 2003; McKinney and Pittman 2000).

DNA isolation and microsatellite PCR—Samples were either stored frozen (-20°C) or in lysis buffer (Longmire et al. 1997) until returning to the laboratory where total genomic DNA was extracted using phenol extraction (Longmire et al. 1997). Seven $(GT)_n$ microsatellite loci were amplified using the polymerase chain reaction (PCR) and primers described in Paetkau et al. (1998). Six of these loci (G1D, G10B, G10C, G10L, G10P, G10O) were cloned from a small insert-size American black bear genomic library (Paetkau et al. 1995; Paetkau and Strobeck 1994), whereas CXX20 was derived from a domestic dog (*Canis familiaris*) genomic library (Ostrander et al. 1993). One primer of each pair was synthesized with a fluorescent dye (FAM, HEX, or TET) to permit detection and sizing of microsatellite repeats on a Perkin-Elmer ABI Prism 377 Automated Sequencer.

Amplifications were performed in 15 μl reactions using 50-200 ng DNA, 0.17 μM of each primer, 9 μl True Allele PCR premix (Perkin-Elmer Applied Biosystems, Foster City, CA) and 3.8 μl double deionized water. The following thermal profile was used during amplification: 12 min at 95°C; 10 cycles of 15 s at 94°C, 1 min at 49-55°C (annealing temperatures were specific for different loci), 30 sec at 72°C; 25 cycles of 15 s at 89°C, 1 min at 55°C, 30 s at 72°C; and 30 min at 72°C. PCR products were diluted and combined based on the size, fluorescent dye and yield. One microliter of PCR dilution was added to 3 μl of loading buffer containing 0.5 μl GS-400HD ROX size standard, 0.5 μl of loading-dye, and 2.5 μl of formamide. This mixture was denatured at 95°C for 5 min and loaded on a 6% Long-Ranger acrylamide gel with resulting data analyzed using GENESCAN™ version 2.1 and GENOTYPER™ version 2.1 software packages.

Data analyses—Assessment of observed (H_o) and expected (H_e) heterozygosity, and deviations from Hardy-Weinberg equilibrium (HWE, Guo and Thompson 1992) were calculated using ARLEQUIN 2.0 (Schneider et al. 2000). Determination of polymorphic information content (PIC) and exclusion probabilities were calculated using CERVUS (Marshall et al. 1998). Probability of individual identity (PID) was estimated using the web-based computer program Doh developed by J. Brzustowski (http://www2.biology.ualberta.ca/ jbrzusto/Doh.php).

We used genotypic data collected on all cubs with known mothers (verified via den workup or capture) to estimate paternity based on the exclusion process of Mendelian genetics. When paternity could not be determined unambiguously using genetic exclusion, likelihood-based paternity analyses were utilized. Likelihood-based paternity assessment incorporates probability of mutation events and genotyping error in assessing paternity that can be qualified statistically. Paternity using likelihood-ratios was calculated using CERVUS (Marshall et al. 1998). CERVUS calculates a ΔLOD score, which is defined as the difference of the log-likelihood ratios at each locus (LOD) among the most likely and second most likely candidate parent. The LOD for each candidate father is calculated using genotypes of the candidate father, offspring and known parent (the mother in our study). A negative LOD score indicates that the candidate parent is less likely to be the actual parent than an arbitrarily chosen individual from the population. Conversely, a positive LOD score indicates that the candidate father is more likely to be the true parent than a randomly chosen male from the population.

The ΔLOD statistic provides an assessment of reliability in assigning paternity to the most likely father as predicted by the LOD (Marshall et al. 1998). Statistical significance of ΔLOD is determined via simulation that incorporates incomplete sampling, genotyping error rates, number of candidate parents, and proportion of missing genotypes. For our analyses, we are confident that we sampled 75% of the candidate males in BIBE with 3 adult males (BIBE11, 30 and 31) categorized as breeders (> 3 years of age) when corresponding cubs were born. Marshall et al. (1998) noted that assuming genotypic data to be free of errors can lead to an overestimation of confidence levels, therefore we assumed a genotyping error rate of 5%. The percentage of missing genotypes (0.4%) was estimated by determining the proportion of loci that did not amplify for all 32 bear tissue samples collected in BIBE. Confidence levels for ΔLOD were set at 80% and 95%.

We calculated an index of relatedness R_{xy} using RELATEDNESS 5.0.8 (Queller and Goodnight 1989) to estimate relationships among individuals within BIBE and between other populations of black bears in southwestern North America (Figure 1). This index uses data on population allele frequency to assess the proportion of alleles present in a population that are identical by descent between two individuals. The index of relatedness (R_{xy}) can range from –1 to 1, with negative values indicating unrelated dyads and positive values indicating some degree of relatedness. In calculating R_{xy}, bias is corrected for small sample size in each population by recalculating population mean frequencies after omitting the population under consideration (Queller and Goodnight

1989). The index of relatedness was weighted equally among individuals and standard errors of R_{xy} were estimated by jackknifing over all 7 loci (Queller and Goodnight 1989).

Comparisons of R_{xy} between bears in BIBE with those from 6 other southwestern North American populations (see Chapter III and IV or Onorato et al. in press) were made to assess levels of relatedness within this region of the American black bear's distribution. Pairwise comparisons also were made between mean R_{xy} values of mothers and known offspring and between potential fathers (as assessed via paternity analyses) and offspring to determine if levels were comparable to expected values for parent-offspring relationships ($R_{xy} = 0.50$). Pairwise estimates of R_{xy} for male-female, female-female, and male-male dyads were made for BIBE bears. Mean relatedness of female-female and male-male dyads were compared in BIBE and SDB using a non-parametric two-group randomization test (Sokal and Rohlf 1995). This test assumed that mean pairwise relatedness values for the above groupings at each study site did not differ from randomly selected relatedness values assorted among these categories. Observed relatedness values were permutated among groupings 5000 times to compare means obtained via observed distributions and permuted distributions. To remove bias that would be introduced by verified mother/cub-of-the-year combinations, these dyads were not included in the analyses.

A neighbor-joining tree was developed using transformed relatedness values ($1-R_{xy}$) using MEGA (Kumar et al. 2001) to achieve a pictorial representation of relationships of bears in BIBE and other portions of western Texas where recolonization is suspected to be in progress. Additionally, we assessed relationships among black bears in BIBE via pedigree path analysis. We used data sources including relatedness values, previous mtDNA sequence data, demographic data, historical accounts, and microsatellite analyses (Onorato and Hellgren 2001; Onorato et al. 2003; Onorato et al. 2002) to derive information necessary to complete the pedigree. All captured males that contained an mtDNA haplotype different from adult females were automatically omitted from the pedigree because it is implausible that they descended from those females (Onorato et al. 2003).

Results

The number of alleles detected in the 7 microsatellite loci analyzed ranged from 3 to 6 for the 32 bears sampled in BIBE (Table 1). Levels of H_o were on average lower than H_e. Mean PIC was 0.611, whereas the total exclusionary powers for the first and second parents were 0.8851 and 0.9816 respectively. Only two loci (G10B and CXX20) did not violate the assumptions of Hardy-Weinberg equilibrium. The probability of identity calculated for the population of bears in BIBE using the 7 microsatellite loci was 1.5×10^{-6}, which equates to a probability of randomly sampling 2 individuals having identical genotypes at all 7 loci in BIBE once every 666,670 bears.

The exclusion process to identify potential fathers of cubs-of-the-year was successful in only 2 cases. Adult male BIBE11 could not be excluded as the father of cubs BIBE16 and BIBE20 at 6 and 7 loci, respectively. Assessment of paternity via a likelihood-based approach was effective at resolving paternity for 8 of 12 cubs-of-the-year with high levels (≥ 80%) of statistical confidence (Table 2). Multiple paternity was estimated to have occurred in 2 litters that displayed significant levels of confidence for likelihood-based paternity estimates (≥ 80%).

Mean relatedness values within 7 populations ranged from 0.0017 (SDC) to 0.1156 (MM), with an overall average among 145 bears of 0.0698 (Table 3). Bears in BIBE had an average R_{xy} of 0.0511, which was lower than values found in the 2 large populations sampled (SDB and MM). Relatedness values for known mother-offspring dyads in BIBE averaged 0.6238 ± 0.128 whereas father-offspring R_{xy} derived via likelihood-based or exclusion methods were lower (0.4445 ± 0.1520; Table 4).

Estimates of R_{xy} of female-female dyads in BIBE were higher than the relatedness of male-male dyads (Figure 3). On average, females exhibited relatedness levels indicative of half-siblings (R_{xy} $\overline{X} = 0.2675$, SD = 0.2761), suggesting that a large percentage of reproductive females in the Park are related to some degree. Two-group randomization testing indicated that relatedness of female-female dyads (R_{xy} females $\overline{X} = 0.2675$) in BIBE tended to be higher ($P = 0.065$) than male-male dyads (R_{xy} males $\overline{X} = 0.1679$). In SDB, a source population of BIBE, there was no difference ($P = 0.538$) in relatedness for male-male or female-female dyads (R_{xy} females $\overline{X} = 0.1983$, R_{xy} males $\overline{X} = 0.2082$).

The neighbor-joining (NJ) tree gave further credence to the high level of relatedness among bears in BIBE (Figure 4). Almost 70% of the bears collected in BIBE were allocated to the two upper clades of the NJ tree. Furthermore, bears that could be classified as dispersing individuals were congregated on the external node of the tree (Figure 4). Over 70% of these dispersing bears were male. Additionally, 5 of the 8 bears assigned to the Trans-Pecos population (a conglomeration of dispersing bears from northern Mexico collected throughout western Texas) were located on this node. Adult male BIBE11 was closely associated with cubs BIBE16 and 20, both whom were described as offspring of this male via paternity exclusion and likelihood-based analyses.

Demographic and genetic data were used to reconstruct the pedigree relationships for 21 (of 32) bears in the Park between 1998-2000 (Figure 5). This pedigree graphically depicts the elevated level of relatedness between adult females. Six of 7 adult females appear to be descended from a hypothesized matriarch female. We did not include 10 male bears and one subadult female (BIBE29) in this pedigree for the following reasons: low levels of relatedness, exclusion of kinship connections determined via mtDNA haplotypes, or demographic data that did not correlate with reproductive cycles of adult females.

Discussion

Our results supported our initial prediction concerning similar levels of relatedness within BIBE and a source population of bears in SDB. Similarly, our data supported the prediction of high levels of female relatedness in the Park that resulted from female philopatry and the mtDNA haplotype that was present in all female bears in the Park (Onorato et al. in press). Conversely, paternity assignments did not include adult males that were closely related to reproductive females, thereby emphasizing the importance of male migration and dispersal between Mexico and the Park. Our genetic data are consistent with the prediction that a single matriarch female recolonized the park during the mid-1980's and subsequently resulted in high levels of relatedness between her female offspring.

Black bears in BIBE exhibited levels of H_e (0.682, Chapter IV) similar to a number of the populations in the Mexico-Texas borderlands (SDB = 0.718, BGWMA =

0.714; Chapter IV) and higher than those from New Mexico (MM = 0.4795, Chapter IV). Populations of other large carnivores, such as wolverines (*Gulo gulo*) or brown bears (*Ursus arctos*), typically have levels of H_e < 0.6 when populations are isolated from the benefits of migration or dispersal from other populations due to either natural or anthropogenic barriers (Kyle and Strobeck 2001; Paetkau et al. 1998; Waits et al. 2000). Levels of H_e for black bears in habitats considered insular (0.360, Paetkau and Strobeck 1994) or impacted by low levels of gene flow (0.380, Warrillow et al. 2001) are much lower than those reported for recolonizing populations in Texas. The impermeability of the oceanic barrier impacting populations on Newfoundland may be to blame for the reduced variation, but other factors such as genetic drift and a population bottleneck also may be responsible for this low H_e (Paetkau and Strobeck 1994). The White River NWR population in Arkansas also was affected by a bottleneck when it was reduced to approximately 25 individuals in the 1940's. It has subsequently rebounded to approximately 400 bears (Oli et al. 1997; Smith and Clark 1994).

Low levels of H_e do not necessarily indicate vulnerability of these populations to the effects of inbreeding depression because bear populations in Newfoundland are reported to number between 3,000 and 10,000 and the White River NWR population is steadily increasing. Nevertheless, results for BIBE are important from a conservation perspective. High levels of genetic variation are indicative of a population recharged by intermittent levels of gene flow from conspecifics in adjacent populations (Spong et al. 2000). Movement of bears between SDC and BIBE has been corroborated with field data (Onorato et al. 2003). Undoubtedly, the small population of black bears in BIBE will be reliant on continued dispersal events from northern Mexico to maintain high genetic variation.

The utility of these loci in deciphering paternity and genetic relatedness was determined using informative statistics PIC, PID and probability of exclusion. Values obtained for these indices denote sufficient variation within these loci to provide accurate conclusions concerning paternity, especially when one parent is known. Probability of identity values between 0.01 and 0.0001 are considered low and should be sufficient at identifying bears to the individual level (Waits et al. 2001).

Instances of multiple paternity in mammals that produce more than 1 offspring in a litter is not unusual and has been noted in common shrews *Sorex araneus* (Tegelstrom et al. 1991), brown and black bears (Craighead et al. 1995; Schenk and Kovacs 1995), and white-tailed deer *Odocoileus virginianus* (DeYoung et al. 2002). On the other hand, quantification of the prevalence of this behavior in the family Ursidae has rarely been reported in the literature. Craighead et al. (1995) described 4 cases of multiple paternity in Alaskan brown bears out of 30 sampled litters (13.3%). Two of 5 litters (40%) that were completely censused in BIBE (BIBE 15-17 and BIBE 20-21) were putatively determined to contain half-sibs.

A high occurrence of multiple paternity in the small population of bears in BIBE could be justified by ecological and demographic characteristics of the population. Data collected during field work between 1998-2000 demonstrated a large degree of overlap in home ranges of both male and female bears in the Chisos Mountains (Onorato et al. 2002). With only 6 known reproductive females active in the Park between 1998-2001 and approximately 3-4 adult male bears, the chances of promiscuity appear high. Roemer et al. (2001) unexpectedly found high levels of promiscuity among a population of island foxes (*Urocyon littoralis*) on Santa Cruz Island, California. They attributed this behavior to the high density of the species on the island and the increased opportunities for extra-pair fertilizations that density and home range overlap provided. We estimated the density of black bears in BIBE at 23/100 km^2 between 1998-2000 (Onorato et al. 2002), which is in the mid-range of black bear densities described across the United States (Garshelis 1994). However, the insular nature of bear habitat in the Chisos Mountains of BIBE may increase the likelihood for intraspecific encounters and multiple fertilization of females.

Paternity assignment via exclusion was not effective in most cases for this study. Reliability of exclusion probabilities can be affected by the presence of numerous close relatives in a system and high levels of philopatry (Double et al. 1997). As our relatedness analyses demonstrated, a large portion of the population in BIBE is related, especially the adult females and cubs. It is also commonly accepted that female philopatry is prevalent among black bears (Rogers 1987b; Schwartz and Franzmann 1992; Smith and Clark 1994). Additionally, we know at least one adult male eluded capture during our trapping sessions (a potential sire of some of these cubs). We believe that these were the primary reasons why the exclusion process was ineffective.

The population of bears in BIBE maintained a slightly lower level of relatedness than the large population in SDB. We suspect that this is a result of the compounding effects of the young age of the recolonizing population and the impact of periodic dispersal of males and females from Mexico into BIBE. The overall low levels of relatedness observed in the Trans-Pecos, BGWMA, and SDC populations may be a result of small sample size, but program RELATEDNESS uses a correction factor to minimizes this bias (Queller and Goodnight 1989). Low levels of R_{xy} in BGWMA and the Trans-Pecos also could be a result of the numerous dispersing individuals present in those populations (especially dispersing male bears from Mexico). Because SDC is believed to sustain a large population of bears, it is likely that the R_{xy} within this population would change if additional samples could be obtained.

Relatedness comparisons within groups of mammals have infrequently been reported in the literature. Burland et al. (2001) reported relatedness values within 23 colonies of brown long-eared bats (*Plecotus auritus*) in Scotland that ranged from –0.09 to 0.17 ($\overline{X} = 0.033$). Yu et al. (2001) compared R_{xy} among 5 geographically separated populations of mole shrews (*Anourosorex squamipes*) in Taiwan. Values ranged between 0.2601 and 0.4667, demonstrating a high level of relatedness within colonies. Lucchini et al. (2002) also reported high levels of relatedness ($R_{xy} = 0.252$ and 0.498) in 2 recolonizing wolfpacks in the western Italian Alps. This level of relatedness would be expected in a highly social mammal such as wolves, which typically roam in packs with a large proportion of related individuals. Cronin et al. (1999) described R_{xy} levels for brown bears in 3 populations located in northern Alaska (R_{xy} range –0.0002 to -0.0019). Negative R_{xy} values indicate low levels of relatedness within these Alaska populations, but standard deviations reported were high and suggested the presence of related and unrelated bears in this region. Black bears in the Mex-Tex metapopulation appeared to maintain overall levels of R_{xy} not indicative of highly intra-related populations. Additionally, the variances that we report were lower than those reported by Cronin et al. (1999). The lower level of relatedness in northern Alaska brown bears was probably caused by a variety of factors, including larger populations, greater dispersal distances, and more contiguous habitat.

The trend towards higher levels of relatedness in female-female pairs compared to male-male dyads in BIBE is indicative of a species that exhibits male-biased dispersal patterns. Subadult (1-3 yr old) male black bears typically disperse from their mother's natal range in search of a new home range (LeCount et al. 1984, Rogers 1987a, Rogers 1987b, Schwartz and Franzmann 1992, Smith and Clark 1994). The Park provides only a limited amount of suitable habitat (ca. 100 km^2), resulting in dispersal of male bears from BIBE to mountain ranges north (Glass, Davis, or Del Norte Mountains) or east into Mexico. We verified the movement of subadult and yearling males from BIBE into northern Mexico via field observations (Onorato et al. 2002). Similarly, male dispersal probably occurs somewhat regularly from SDC to western Texas and supplements genetic variation to the semi-isolated population in BIBE.

Mean level of R_{xy} for mother-offspring dyads (0.6238) in BIBE was approximately the expected value (0.5) for this relationship. Cronin et al. (1999) assessed mother-offspring relationships for brown bears in the Prudhoe Bay Region of Alaska and found that levels of R_{xy} for this relationship averaged 0.4948 for 11 different litters. Similar levels of relatedness were also noted for mother-offspring dyads in polar bears (*Ursus maritimus*, $\overline{X} = 0.5417$ $n = 6$, Lunn et al. 2000). The higher level of R_{xy} observed in BIBE is likely the result of the recent recolonization and small size of the Park population.

The neighbor-joining tree based on transformed relatedness values clusters all adult female and 69% of all bears captured in BIBE into 2 distinct clades. These two clades note a difference between the oldest adult female (BIBE7) and remaining adult females in the Park (see discussion below). Using a similar technique, Luchhini et al. (2002) demonstrated the presence of two separate groups of wolves recolonizing portions of the western Alps in Italy.

The NJ tree for black bears from western Texas portrays several other groups besides BIBE bears, including a clade composed of a disproportionate number of dispersers. Five of 9 bears in this clade can be verified as dispersers as they were captured in regions of western Texas where no viable bear populations are presently known to survive. A case could be made for including some of the other bears into this disperser category as well. Ten of the 15 bears remaining bears in the tree contained an mtDNA haplotype that is dominant in northern Mexican populations but is only found in adult and subadult male bears in BIBE (Onorato et al. 2003). Additionally, almost 50% of these bears were collected in BGWMA, where a large percentage of the population is male and recolonization is still in the preliminary stages compared to BIBE (McKinney and Pittman 2000).

We hypothesized that a majority of reproductive females in BIBE were probably descendents of a single matriarch female. Our data within the pedigree (Figure 5) support our prediction that a matriarch female recolonized the Chisos Mountains of BIBE during the mid-1980's by dispersing from the mountains of northern Coahuila. This female probably crossed the expanse of Chihuahuan Desert between SDC and BIBE, ultimately choosing to den in the Park (Onorato and Hellgren 2001). Verification of ensuing reproduction in BIBE occurred in 1988, when a Park visitor photographed a female with cubs-of-the-year (Skiles 1995). This female and her offspring probably contained the A mtDNA haplotype that presently dominates the Park population (Onorato et al. 2003). Although this haplotype occurs in northern Mexico, it is far less common than in BIBE (Onorato et al. 2003).

We postulate 3 females (BIBE 6, 3, 2) to be direct offspring of this matriarch. Ages and reproductive histories (based on cementum annuli analyses, Coy and Garshelis 1992) of these females follow a plausible reproductive history for the structure of the female cohort in BIBE (Onorato et al., unpublished data). We speculate that the matriarch successfully reproduced in 1989, 1992, and 1994. Levels of relatedness between BIBE 6, 3, and 2 are typical of full- or half-siblings. The pedigree of their offspring is mainly supported by observations made during field data collection and the majority of the relationships it describes are irrefutable (i.e., known mother-offspring connections). This pedigree accounts for 66% of the 32 bears collected in BIBE and portrays an extensive view of kinship that has rarely been documented for a large carnivore.

The oldest female bear captured in the Park (BIBE7) was not highly related (R_{xy} $\overline{X} = 0.1175$, 5 pairwise comparisons) to the other adult females (BIBE1-3, 5-6), which were related to each other at the sibling or mother-offspring level (R_{xy} $\overline{X} = 0.4661$, 10 pairwise comparisons). We initially predicted that a large portion of the population in BIBE would be related to BIBE7 because of her age and reproductive history. This prediction was not verified by our data and we believe that the original matriarch female was either not captured, died, or returned to Mexico. However, we have behavioral and genetic evidence that female BIBE7 gave birth to BIBE14. Additionally, BIBE11, 30, and 31 were estimated to be fathers of 8 cubs represented in the pedigree via paternity analyses. The majority, if not all, of adult males in the Park are likely migrants from Mexico and ultimately serve as a source of gene flow to the small population in the Park. In total, these bears account for 75% of the population censused in BIBE.

The population of black bears in BIBE will be reliant on periodic gene flow via male bears dispersing from ranges in northern Coahuila to persist, sustain genetic diversity, and remain devoid of problems associated with inbreeding. Additionally, the infrequent, yet verified movement of females between populations in the Mex-Tex ecosystem will further help maintain a healthy population in the Park (Onorato et al. 2002). These two factors highlight the importance of corridors between Coahuila and western Texas for continued dispersal of bears along the international border.

Acknowledgments

We thank B. R. McKinney (TPWD & CEMEX), D. L. Doan-Crider and C. Costello (Hornocker Wildlife Institute) for contributing samples for genetic analyses. Additional thanks go F. S. Mitchell, S. Ginger, P. Luce, M. Kasparian, M. Criffield, C. Tredick, G. Vose, N. Herring, numerous BIBE employees and field volunteers, and the RAVDB lab crew for their assistance in making the collection of these data feasible. This study was supported by funding from the Natural Resource Preservation Program (through the U.S. Geological Survey and USDI National Park Service, and Big Bend National Park). We thank D. M. Leslie, Jr. and the Oklahoma Cooperative Fish and Wildlife Research Unit (U.S. Geological Survey-Biological Resources Division, Oklahoma State University, Oklahoma Department of Wildlife Conservation, and Wildlife Management Institute, cooperating) for administrative and logistic support. We acknowledge additional funding granted by the Wyoming Chapter of the Wildlife Society

(Memorial Bear Grant), the American Museum of Natural History (Theodore Roosevelt Memorial Fund), and the Robert L. Lochmiller II Endowed Scholarship.

Literature Cited

BANKS, S. C., L. F. SKERRATT, and A. C. TAYLOR. 2002. Female dispersal and relatedness structure in common wombats (*Vombatus ursinus*). Journal of Zoology 256:389-399.

BLOUIN, M. S., M. PARSONS, V. LACAILLE, and S. LOTZ. 1996. Use of microsatellite loci to classify individuals by relatedness. Molecular Ecology 5:393-401.

BLUNDELL, G. M., M. BEN-DAVID, P. GROVES, R. T. BOWYER, and E. GEFFEN. 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.

BURLAND, T. M., E. M. BARRATT, R. A. NICHOLS, and P. A. RACEY. 2001. Mating patterns, relatedness and the basis of natal philopatry in the brown long-eared bat, *Plecotus auritus*. Molecular Ecology 10:1309-1321.

CLAPHAM, P. J., and P. J. PALSBOLL. 1997. Molecular analysis of paternity shows promiscuous mating in female humpback whales (*Megaptera novaengliae*, Borowski). Proceedings of the Royal Society of London Series B-Biological Sciences 264:95-98.

CONSTABLE, J. L., M. V. ASHLEY, J. GOODALL, and A. E. PUSEY. 2001. Noninvasive paternity assignment in Gombe chimpanzees. Molecular Ecology 10:1279-1300.

COSTELLO, C. M., ET AL. 2001. A study of black bear ecology in New Mexico with models for population dynamics and habitat suitability. New Mexico Department of Game and Fish, W-131-R, Federal Aid in Wildlife Restoration Project.

COY, P. L., and D. L. GARSHELIS. 1992. Reconstructing Reproductive Histories of Black Bears from the Incremental Layering in Dental Cementum. Canadian Journal of Zoology 70:2150-2160.

CRAIGHEAD, L., D. PAETKAU, H. V. REYNOLDS, E. R. VYSE, and C. STROBECK. 1995. Microsatellite analysis of paternity and reproduction in Arctic grizzly bears. Journal of Heredity 86:255-261.

CRONIN, M., R. SHIDELER, J. HECHTEL, C. STROBECK, and D. PAETKAU. 1999. Genetic relationships of grizzly bears (*Ursus arctos*) in the Prudhoe Bay region of Alaska: Inference from microsatellite DNA, mitochondrial DNA, and field observations. Journal of Heredity 90:622-628.

DEYOUNG, R. W., S. DEMARAIS, R. A. GONZALES, R. L. HONEYCUTT, and K. L. GEE. 2002. Multiple paternity in white-tailed deer (*Odocoileus virginianus*) revealed by DNA microsatellites. Journal of Mammalogy 83:884-892.

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. Dissertation, Texas A&M University-Kingsville, Kingsville, Texas USA.

DOUBLE, M., A. COCKBURN, S. BARRY, and P. SMOUSE. 1997. Exclusion probabilities for single-locus paternity analysis when related males compete for matings. Molecular Ecology 6:1155-1166.

FLAGSTAD, O., ET AL. 2000. Genetic variability in Swayne's hartebeest, an endangered antelope of Ethiopia. Conservation Biology 14:254-264.

GARSHELIS, D. L. 1994. Density-dependent population regulation of black bears, Pp. 3-14 in Density-dependent population regulation of black, brown and polar bears (M. Taylor, ed.). International Association for Bear Research and Management, Monograph Series No. 3, Missoula, Montana, USA.

GIRMAN, D. J., M. G. L. MILLS, E. GEFFEN, and R. K. WAYNE. 1997. A molecular genetic analysis of social structure, dispersal, and interpack relationships of the African wild dog (*Lycaon pictus*). Behavioral Ecology and Sociobiology 40:187-198.

GOMPPER, M. E., J. L. GITTLEMAN, and R. K. WAYNE. 1998. Dispersal, philopatry, and genetic relatedness in a social carnivore: comparing males and females. Molecular Ecology 7:157-163.

GUO, S. W., and E. A. THOMPSON. 1992. Performing the exact test of Hardy-Weinberg proportion for multiple alleles. Biometrics 48:361-372.

KAYS, R. W., J. L. GITTLEMAN, and R. K. WAYNE. 2000. Microsatellite analysis of kinkajou social organization. Molecular Ecology 9:743-751.

KUMAR, S., K. TAMURA, I. B. JAKOBSEN, and M. NEI. 2001. MEGA2: molecular evolutionary genetics analysis software. Bioinformatics 17:1244-1245.

KYLE, C. J., and C. STROBECK. 2001. Genetic structure of North American wolverine (*Gulo gulo*) populations. Molecular Ecology 10:337-347.

LECOUNT, A. L., R. H. SMITH, and J. R. WEGGE. 1984. Black bear habitat requirements in Central Arizona. Arizona Game and Fish Department, Report No.14.

LONGMIRE, J. L., M. MALTBIE, and R. J. BAKER. 1997. Use of "lysis buffer" in DNA isolation and its implication for museum collections. Occasional Papers, The Museum, Texas Tech University 163:1-3.

LUCCHINI, V., E. FABBRI, F. MARUCCO, S. RICCI, L. BOITANI, and E. RANDI. 2002. Noninvasive molecular tracking of colonizing wolf (*Canis lupus*) packs in the western Italian Alps. Molecular Ecology 11:857-868.

LUNN, N. J., D. PAETKAU, W. CALVERT, S. ATKINSON, M. TAYLOR, and C. STROBECK. 2000. Cub adoption by polar bears (*Ursus maritimus*): determining relatedness with microsatellite markers. Journal of Zoology 251:23-30.

MARSHALL, T. C., J. SLATE, L. E. B. KRUUK, and J. M. PEMBERTON. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology 7:639-655.

MCKINNEY, B. R., and M. T. PITTMAN. 2000. Habitat, diet, home range, and seasonal movement of resident and relocated black bears in west Texas. Texas Parks and Wildlife Department, Project WER57-STATE.

MCLELLAN, B. N., AND F. W. HOVEY. 2001. Natal dispersal of grizzly bears. Canadian Journal of Zoology 79:838-844.

OLI, M. K., H. A. JACOBSON, and B. D. LEOPOLD. 1997. Denning ecology of black bears in the White River National Wildlife Refuge, Arkansas. Journal of Wildlife Management 61:700-706.

ONORATO, D. P., and E. C. HELLGREN. 2001. Black bear at the border: the recolonization of the Trans-Pecos, Pp. 245-259 in Large mammal restoration:

ecological and sociological challenges in the 21st Century (D. S. Maehr, R. F. Noss and J. L. Larkin, eds.). Island Press, Washington D.C., USA.

ONORATO, D. P., E. C. HELLGREN, R. A. VAN DEN BUSSCHE, and D. L. DOAN-CRIDER. 2003. Phylogeographic patterns within a metapopulation of black bears (*Ursus americanus*) in the American Southwest. Journal of Mammalogy 84:000-000.

ONORATO, D. P., E. C. HELLGREN, R. A. VAN DEN BUSSCHE, and D. M. LESLIE, JR. 2002. Conservation ecology of an isolated population of black bears in the Big Bend Ecosystem. National Park Service, Final Report, Project 97-08: 1-54.

OSTRANDER, E. A., G. F. SPRAGUE, and J. RINE. 1993. Identification and characterization of dinucleotide repeat $(CA)_n$ markers for genetic mapping in dog. Genomics 16:207-213.

PAETKAU, D., W. CALVERT, I. STIRLING, and C. STROBECK. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4:347-354.

PAETKAU, D., G. F. SHIELDS, and C. STROBECK. 1998. Gene flow between insular, coastal and interior populations of brown bears in Alaska. Molecular Ecology 7:1283-1292.

PAETKAU, D., and C. STROBECK. 1994. Microsatellite analysis of genetic variation in black bear populations. Molecular Ecology 3:489-495.

QUELLER, D. C., and K. F. GOODNIGHT. 1989. Estimating relatedness using genetic markers. Evolution 43:258-275.

RANNALA, B., and J. L. MOUNTAIN. 1997. Detecting immigration by using multilocus genotypes. Proceedings of the National Academy of Sciences of the United States of America 94:9197-9201.

RICHARDSON, D. S., F. L. JURY, K. BLAAKMEER, J. KOMDEUR, and T. BURKE. 2001. Parentage assignment and extra-group paternity in a cooperative breeder: the Seychelles warbler (Acrocephalus sechellensis). Molecular Ecology 10:2263-2273.

ROBINSON, R. 1999. Genetics for dog breeders. 2nd ed. Butterworth-Heinemann, Oxford, England ; Woburn, MA.

ROEMER, G. W., D. A. SMITH, D. K. GARCELON, and R. K. WAYNE. 2001. The behavioural ecology of the island fox (Urocyon littoralis). Journal of Zoology 255:1-14.

ROGERS, L. L. 1987a. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monographs 97:1-72.

ROGERS, L. L. 1987b. Factors influencing dispersal in the black bear, Pp. 75-84 in Mammalian dispersal patterns (B. D. Chepko-Sade and Z. T. Halpin, eds.). University of Chicago Press, Chicago.

SCHENK, A., and K. M. KOVACS. 1995. Multiple mating between black bears revealed by DNA fingerprinting. Animal Behaviour 50:1483-1490.

SCHNEIDER, S., D. ROESSLI, and L. EXCOFFIER. 2000. A software for population genetics data analysis. Genetics and Biometry Lab, Dept. of Anthropology, University of Geneva, Geneva, Switzerland.

SCHWARTZ, C. C., and A. W. FRANZMANN. 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. Proceedings of the Western Black Bear Workshop 5:67-73.

SMITH, K. G., and J. D. CLARK. 1994. Black bears in Arkansas - characteristics of a successful translocation. Journal of Mammalogy 75:309-320.

SOKAL, R. R., and F. J. ROHLF. 1995. Biometry. 3rd ed. W. H. Freeman and Company, New York.

SPONG, G., M. JOHANSSON, and M. BJORKLUND. 2000. High genetic variation in leopards indicates large and long-term stable effective population size. Molecular Ecology 9:1773-1782.

TEGELSTROM, H., J. SEARLE, J. BROOKFIELD, and S. MERCER. 1991. Multiple paternity in wild common shrews (Sorex-Araneus) is confirmed by DNA-fingerprinting. Heredity 66:373-379.

TESTA, J. W., and B. D. SCOTTON. 1999. Dynamics of an isolated population of Weddell seals (*Leptonychotes weddellii*) at White Island, Antarctica. Journal of Mammalogy 80:82-90.

WAITS, L., P. TABERLET, J. E. SWENSON, F. SANDEGREN, and R. FRANZEN. 2000. Nuclear DNA microsatellite analysis of genetic diversity and gene flow in the Scandinavian brown bear (*Ursus arctos*). Molecular Ecology 9:421-431.

WAITS, L. P., G. LUIKART, and P. TABERLET. 2001. Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. Molecular Ecology 10:249-256.

WARRILLOW, J., M. CULVER, E. HALLERMAN, and M. VAUGHAN. 2001. Subspecific affinity of black bears in the White River National Wildlife Refuge. Journal of Heredity 92:226-233.

WILLEY, C. H. 1974. Aging black bears from first premolar tooth sections. Journal of Wildlife Management 38:97-100.

WILSON, G. M., R. A. VAN DEN BUSSCHE, P. K. KENNEDY, A. GUNN, and K. POOLE. 2000. Genetic variability of wolverines (*Gulo gulo*) from the Northwest Territories, Canada: conservation implications. Journal of Mammalogy 81:186-196.

YU, H. T., Y. Y. LIAO, and C. H. KAO. 2001. Relatedness structure and individual identification in a semi-fossorial shrew (Soricidae : *Anourosorex squamipes*) - an application of microsatellite DNA. Zoological Studies 40:226-232.

Table 1.—Diversity characteristics of 7 microsatellite loci amplified for black bears collected in Big Bend National Park, Texas between 1994 and 2000. Abbreviations are defined in the text with the exception of k, Excl1 and Excl2. These are the number of alleles per locus, and the exclusionary power of each locus for parentage analyses when no parents are known (Excl1) or when 1 parent is known (Excl2).

Locus	k	*n* genotyped	H_o	H_e	PIC	Excl1	Excl2	HWE (SE)
G1D	5	32	0.406	0.693	0.617	0.250	0.425	<0.001 (0.000)
G10B	5	32	0.719	0.713	0.643	0.277	0.452	0.429 (0.001)
G10C	4	32	0.563	0.751	0.679	0.305	0.477	0.023 (0.000)
G10L	3	31	0.313	0.586	0.459	0.141	0.267	<0.001 (0.000)
G10P	6	32	0.688	0.783	0.736	0.378	0.557	0.043 (0.001)
G10O	4	32	0.313	0.481	0.431	0.114	0.261	0.002 (0.000)
CXX20	6	32	0.625	0.765	0.715	0.356	0.534	0.105 (0.001)
Mean	4.7		0.518	0.682	0.611	0.885	0.982	

Table 2.—Assessment of paternity in American black bear cubs-of-the-year from Big Bend National Park, Texas using likelihood ratios calculated in program CERVUS with genotypic data from 7 microsatellite loci.

Offspring	Mother	Father	Number of loci	Δ LOD	Confidence
BIBE14	BIBE7	BIBE31	7	0.111	≥ 80%
BIBE15	BIBE1	BIBE30	7	0.227	≥ 80%
BIBE16	BIBE1	BIBE11	7	3.010	≥ 95%
BIBE17	BIBE1	BIBE31	7	0.000	< 80%
BIBE18	BIBE5	BIBE31	7	0.316	≥ 80%
BIBE19	BIBE5	BIBE31	7	1.400	≥ 95%
BIBE20	BIBE2	BIBE11	7	3.940	≥ 95%
BIBE21	BIBE2	BIBE31	7	0.219	≥ 80%
BIBE22	BIBE3	BIBE30	7	0.007	< 80%
BIBE23	BIBE3	BIBE31	7	0.000	< 80%
BIBE24	BIBE6	BIBE30	7	1.100	≥ 80%
BIBE25	BIBE6	BIBE31	7	0.000	< 80%

Table 3.—Average coefficients of relatedness (R_{xy}) values for 7 populations of black bears in the American southwest calculated using genotypic data from 7 microsatellite loci. See Figure 1 for locations of populations.

Population	*n*	R_{xy}	Jackknifed SE
Big Bend National Park	32	0.0511	0.0157
Black Gap Wildlife Management Area	9	0.0090	0.0020
Serranias del Burro Mountains	58	0.0745	0.0161
Sierra del Carmen Mountains	5	0.0017	0.0014
Trans-Pecos	8	0.0053	0.0025
Sierra Madre Mountains	4	0.0023	0.0007
Mogollon Mountains	29	0.1156	0.0212
Total	145	0.0698	0.0102

Table 4.—Relatedness values for parent-offspring dyads in BIBE black bears derived via field observations or paternal likelihood calculations.

Adult ID	Sex	Birth Year	Reproductive History	mtDNA haplotype	Offspring ID	Birth Year	Relationship	R_{xy}
BIBE1	F	1993	?, '99	A	BIBE15	1999	Known	0.7803
BIBE1	F	1993	?, '99	A	BIBE16	1999	Known	0.4360
BIBE1	F	1993	?, '99	A	BIBE17	1999	Known	0.6714
BIBE2	F	1994	'98, '00	A	BIBE20	2000	Known	0.4333
BIBE2	F	1994	'98, '00	A	BIBE21	2000	Known	0.7219
BIBE3	F	1992	'96, '98, '00	A	BIBE22	2000	Known	0.6348
BIBE3	F	1992	'96, '98, '00	A	BIBE23	2000	Known	0.4942
BIBE5	F	1995	?, '00	A	BIBE18	2000	Known	0.8490
BIBE5	F	1995	?, '00	A	BIBE19	2000	Known	0.5586
BIBE6	F	1989	'93, '95, '97, '00	A	BIBE24	2000	Known	0.6371
BIBE6	F	1989	'93, '95, '97, '00	A	BIBE25	2000	Known	0.6468
BIBE7	F	1984	'90, '92, ?, '99	A	BIBE14	1999	Known	0.6225
BIBE31	M	~1990	NA	B	BIBE14	1999	Likelihood	0.3962
BIBE31	M	~1990	NA	B	BIBE18	2000	Likelihood	0.3676
BIBE31	M	~1990	NA	B	BIBE19	2000	Likelihood	0.6570
BIBE31	M	~1990	NA	B	BIBE21	2000	Likelihood	0.5198
BIBE30	M	1992	NA	B	BIBE15	2000	Likelihood	0.2227
BIBE30	M	1992	NA	B	BIBE24	2000	Likelihood	0.3698
BIBE11	M	1992	NA	B	BIBE16	1999	Exclusion	0.3719
BIBE11	M	1992	NA	B	BIBE20	2000	Exclusion	0.6508

FIGURE LEGENDS

Figure 1.—Locations of 7 collection sites for tissue samples of American black bears collected in southwestern North America. Collection sites include: BIBE, Big Bend National Park, Texas, U.S.A; BGWMA, Black Gap Wildlife Management Area, Texas, U.S.A; SDB, Serranias del Burro Mountains, Coahuila, Mexico; SDC, Sierra Del Carmen Mountains, Coahuila, Mexico, SMM, Sierra Madre Mountains, Nuevo Leon, Mexico; ⊡, Trans-Pecos region of western Texas, U.S.A.; MM, Mogollon Mountains, New Mexico, U.S.A. Populations BIBE, BGWMA, SDB, SDC, SMM and ⊡ were designated as the Mex-Tex populations.

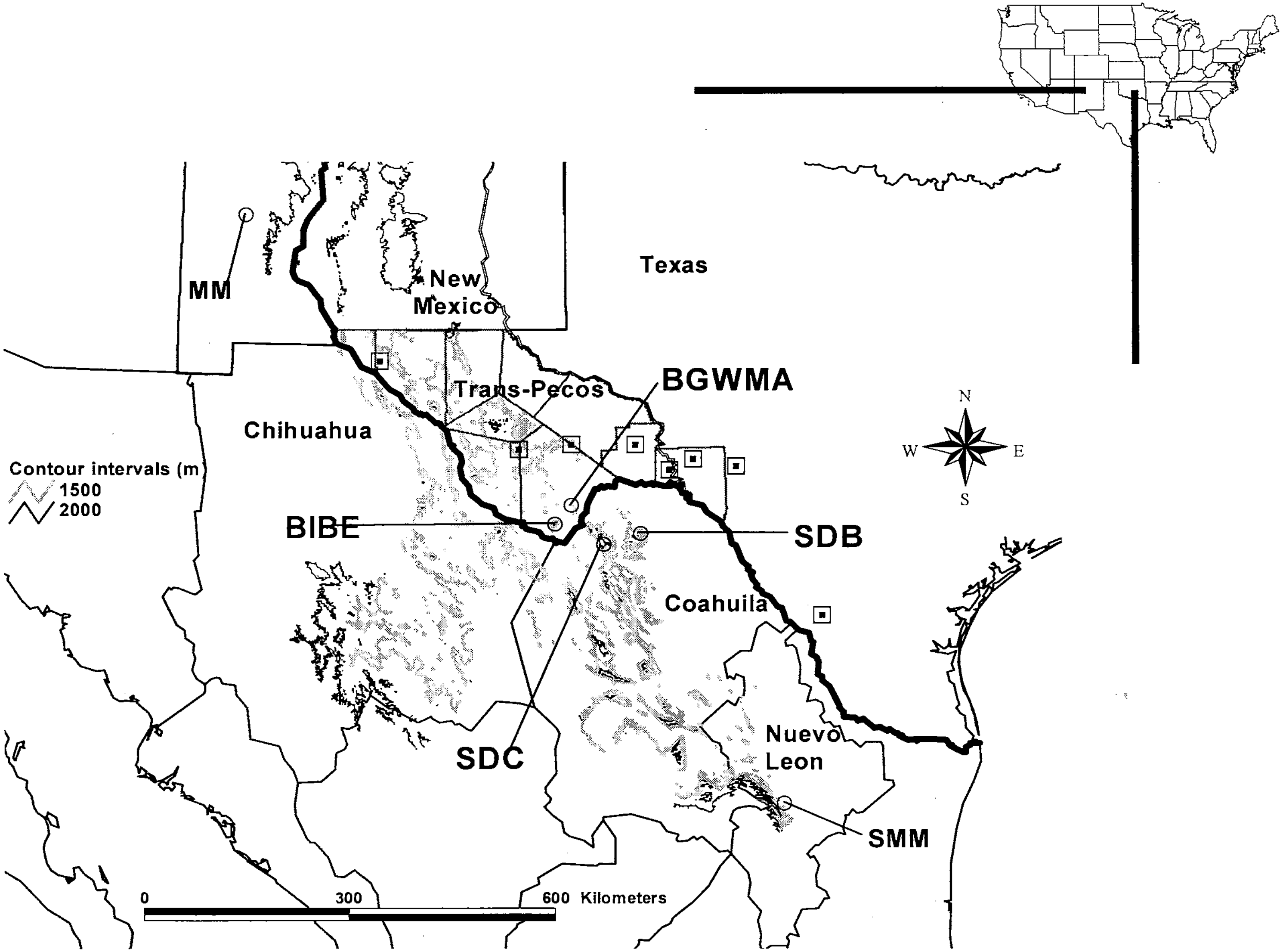
Figure 2.—Location of sampling areas within the Mex-Tex borderlands ecoregion. The primary habitat for black bears in Big Bend National Park, the Chisos Mountains, is indicated by a ☆. Former range once inhabited by reproductively viable populations of black bears in western Texas include the Glass, Del Norte and Davis Mountains.

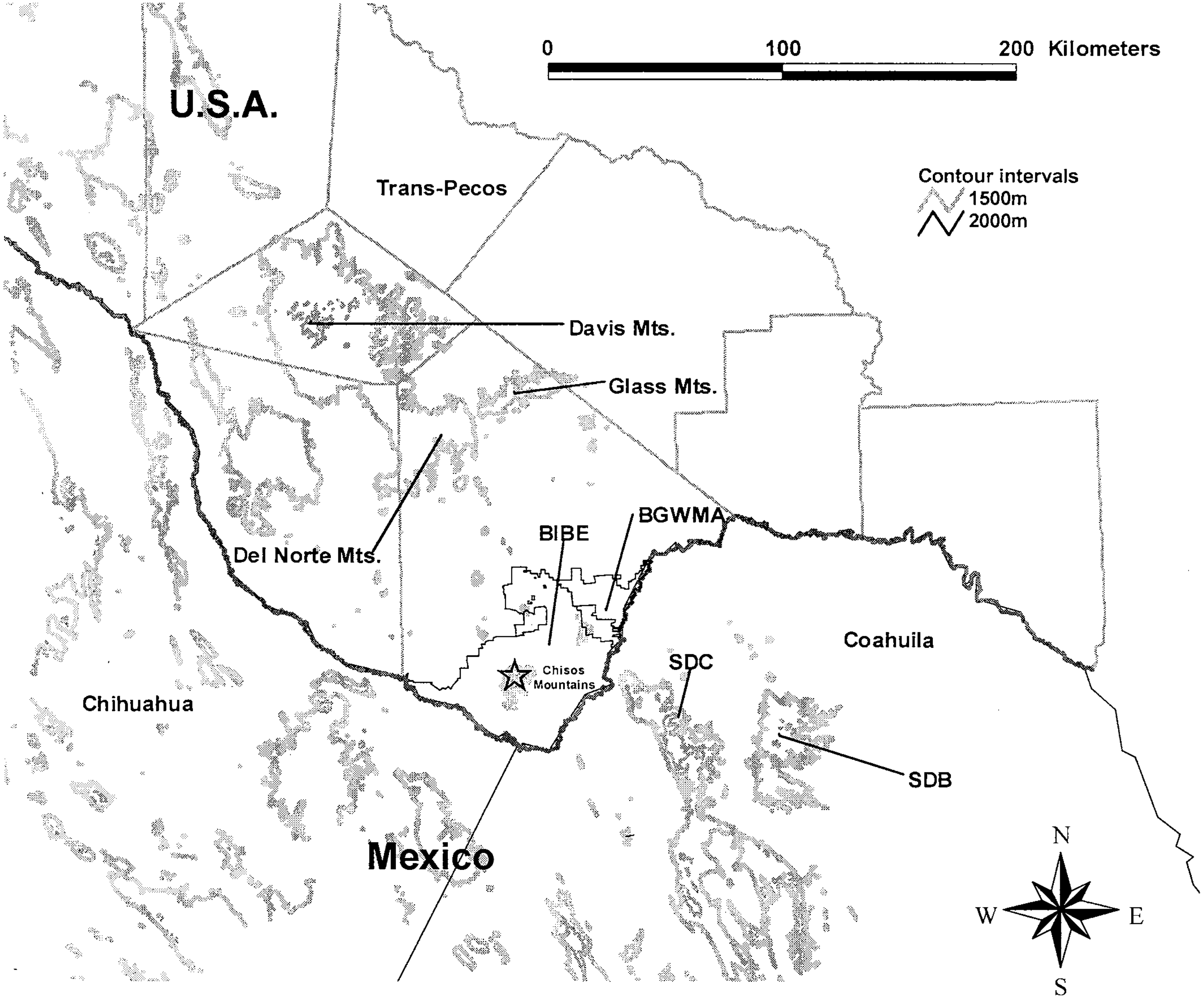
Figure 3.—Distribution of the proportion of pairwise relatedness estimates for black bears in Big Bend National Park, Texas. Pairwise comparisons were calculated for female-female (*n* = 36), male-male (*n* = 55), and male-female dyads (*n* = 190).

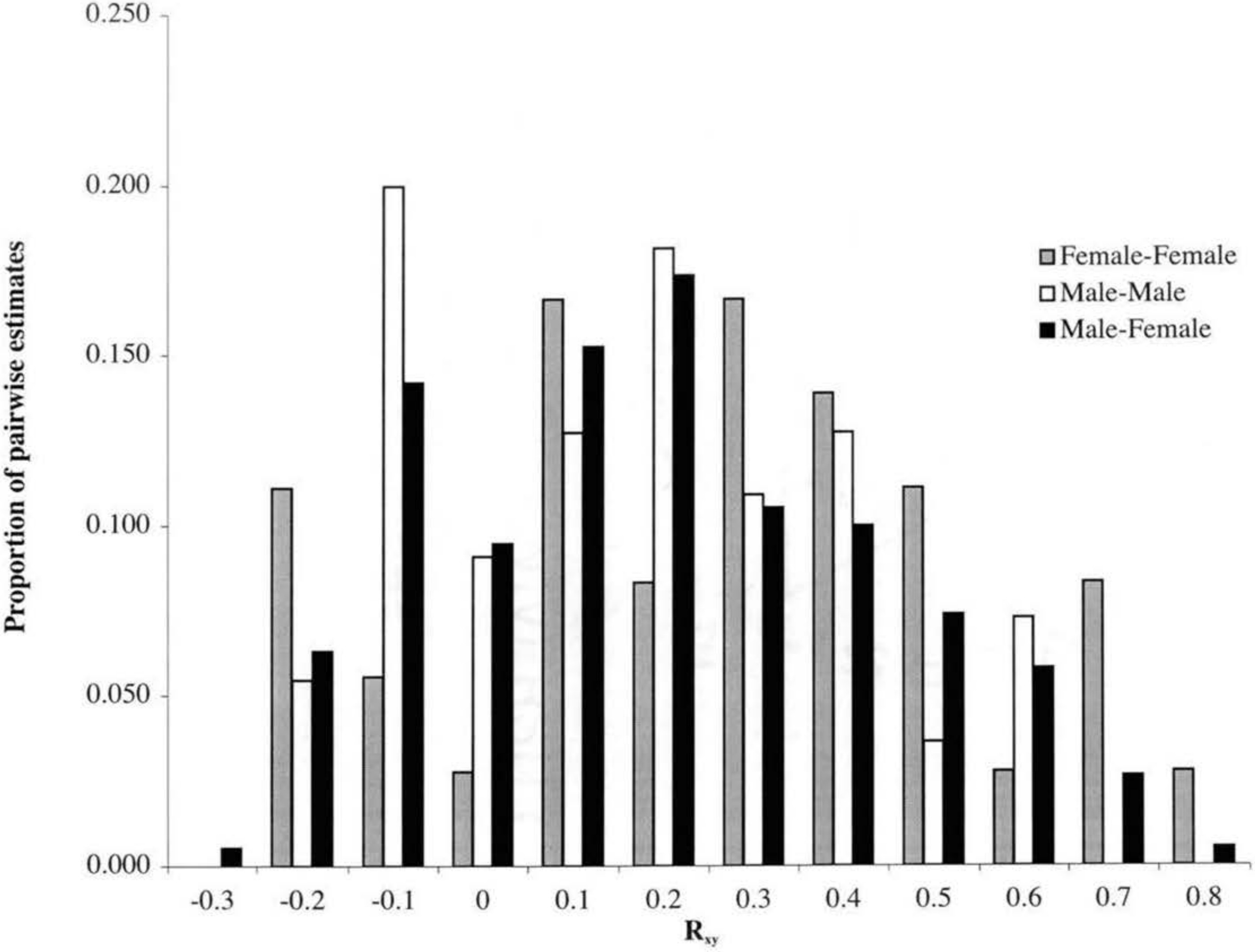
Figure 4.—Neighbor-joining tree computed using an adjusted relatedness (1-R_{xy}) index matrix for black bears collected in the Trans-Pecos region of western Texas. Groupings described in the text are represented by the solid, vertical lines. Prefixes represent: BIBE = Big Bend National Park, Texas, USA; BGWMA = Black

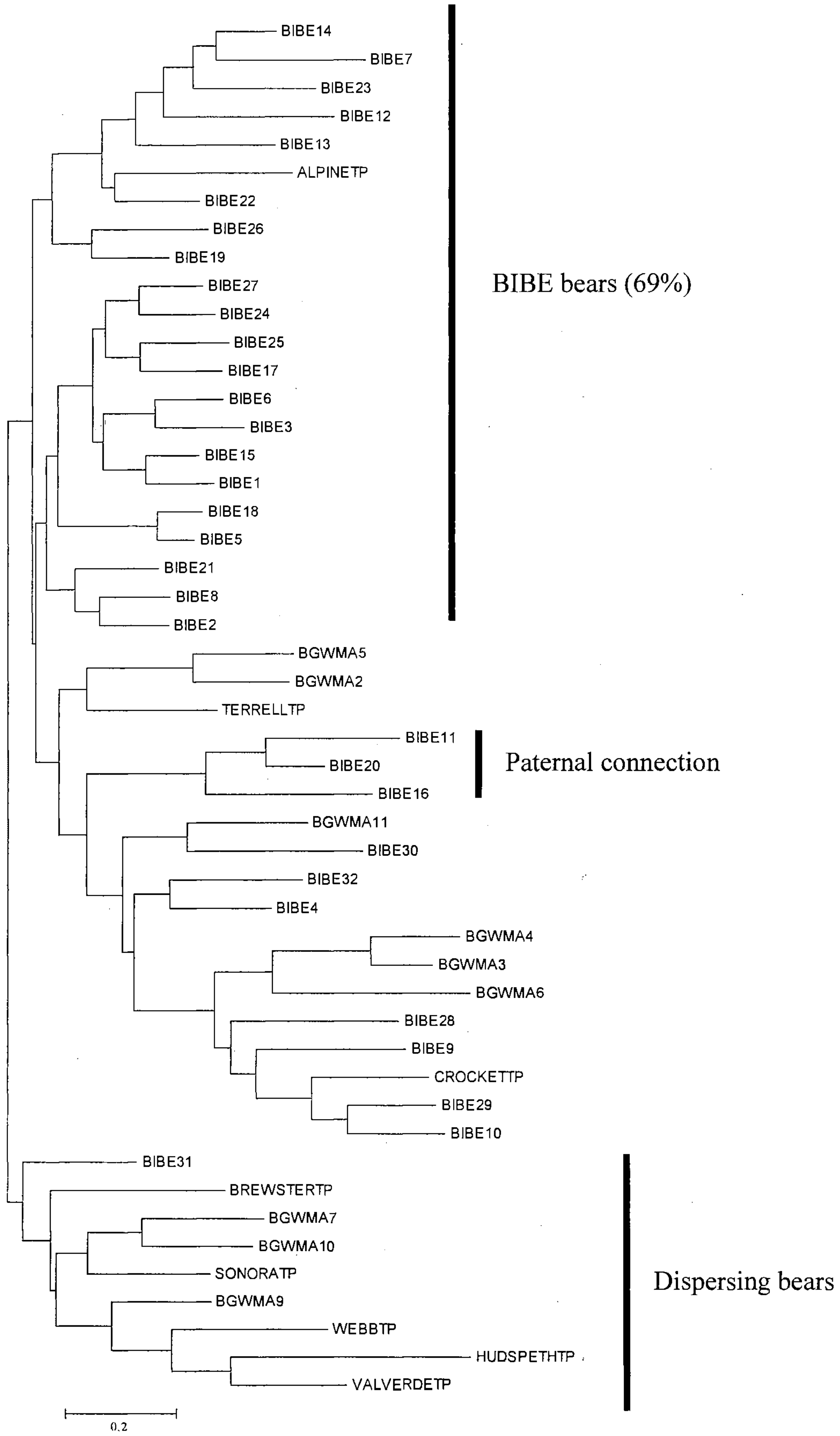
Gap Wildlife Management Area, Texas, USA. All other prefixes represent individuals collected in portions of the Trans-Pecos.

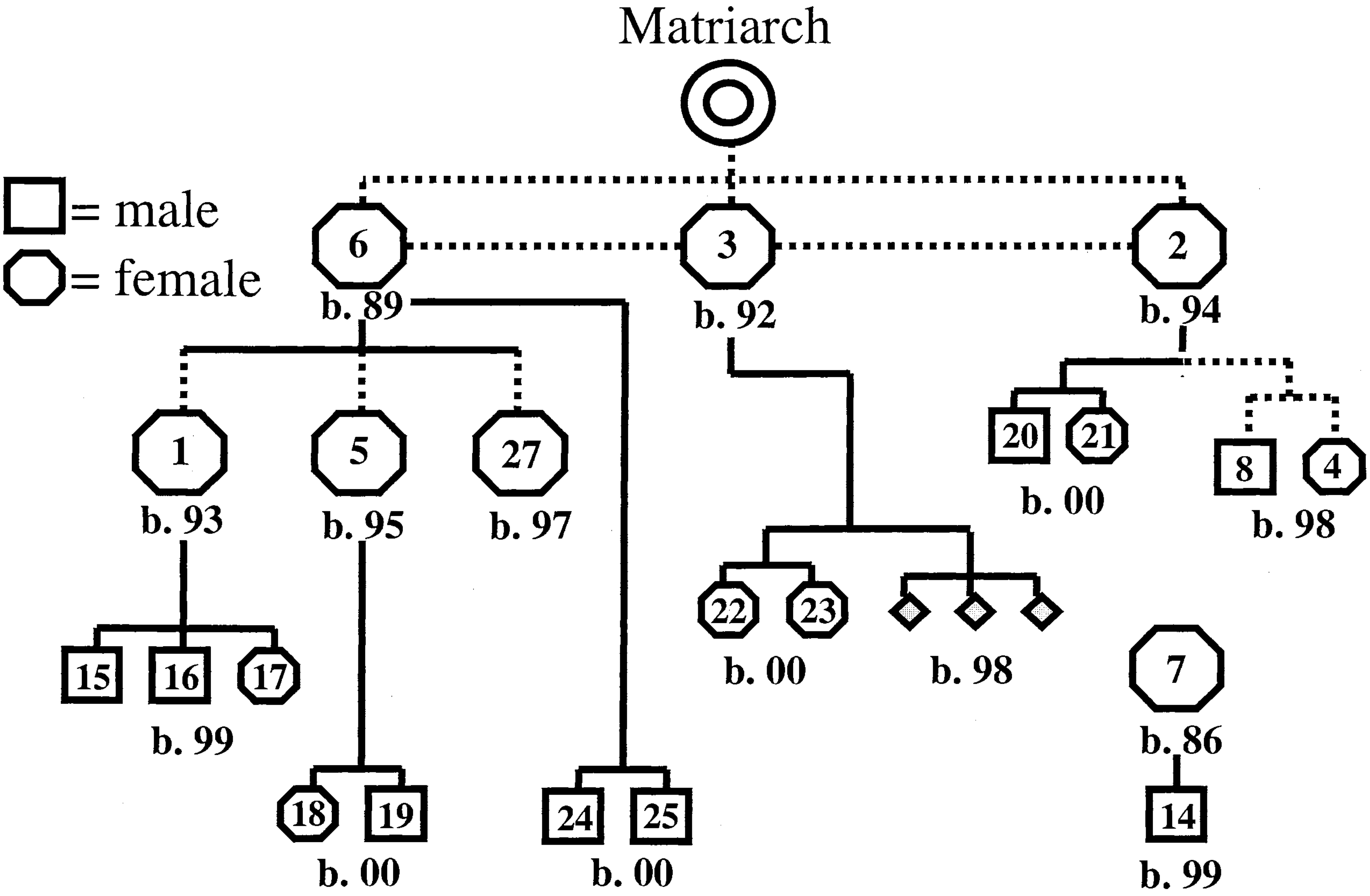
Figure 5.—Representation of the hypothesized pedigree for a majority of the population of black bears residing in Big Bend National Park, Texas between 1998-2000. Dashed lines represent relationships inferred via relatedness among descendents of the hypothetical matriarch female. Females are represented by octagons, males by squares. Values for R_{xy} are given for relationships that were described using relatedness values. All other kinship connections (solid lines) were made via field observations. Numbers represent BIBE animal ID's described in tables and the text. The year-of-birth for each animal is also noted. Diamonds represent cubs-of-the-year verified via field observations, but not sampled.


MM
New Mexico
Texas
Trans-Pecos
BGWMA
Chihuahua
Contour intervals (m)
1500
2000
BIBE
SDB
Coahuila
SDC
Nuevo Leon
SMM
N
W
E
S
0
300
600 Kilometers


0
100
200 Kilometers
U.S.A.
Trans-Pecos
Contour intervals
1500m
2000m
Davis Mts.
Glass Mts.
Del Norte Mts.
BIBE
BGWMA
Chisos Mountains
SDC
Coahuila
SDB
Chihuahua
Mexico
N
W
E
S


Proportion of pairwise estimates
0.250
0.200
0.150
0.100
0.050
0.000
▨ Female-Female
☐ Male-Male
■ Male-Female
-0.3
-0.2
-0.1
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
R_{xy}


BIBE14
BIBE7
BIBE23
BIBE12
BIBE13
ALPINETP
BIBE22
BIBE26
BIBE19
BIBE27
BIBE24
BIBE25
BIBE17
BIBE6
BIBE3
BIBE15
BIBE1
BIBE18
BIBE5
BIBE21
BIBE8
BIBE2
BIBE bears (69%)
BGWMA5
BGWMA2
TERRELLTP
BIBE11
BIBE20
BIBE16
Paternal connection
BGWMA11
BIBE30
BIBE32
BIBE4
BGWMA4
BGWMA3
BGWMA6
BIBE28
BIBE9
CROCKETTP
BIBE29
BIBE10
BIBE31
BREWSTERTP
BGWMA7
BGWMA10
SONORATP
BGWMA9
WEBBTP
HUDSPETHTP
VALVERDETP
Dispersing bears
0.2


Matriarch
= male
= female
6
b. 89
3
b. 92
2
b. 94
1
b. 93
5
b. 95
27
b. 97
20
21
b. 00
8
4
b. 98
22
23
b. 00
b. 98
7
b. 86
15
16
17
b. 99
18
19
b. 00
24
25
b. 00
14
b. 99

SUMMARY AND CONCLUSIONS

The preceding chapters have laid the groundwork to assess the status of recolonization by American black bears in western Texas. Data presented herein have noted the connection of black bears in northern Coahuila to populations presently attempting to recolonize the Trans-Pecos. At this writing (2003), recolonization continues, albeit slowly, in BIBE and BGWMA. A variety of events and circumstances demonstrated the delicate nature of this process and the ease with which it can be halted. Periods of drought, mast failures, and insect infestations ultimately resulted in a large-scale migration-dispersal event (MDE) that had a significant impact on the BIBE population and the progress of the recolonization process. The resulting population crash possibly left only 4-5 bears in the Park in the winter of 2000-2001.

Nevertheless, documentation of this MDE provided interesting data permitting reasoned speculation on black bear biology and recolonization in the desert southwest. Bears are capable of traversing vast expanses of Chihuahuan Desert in search of more prevalent food sources when supplies in natal habitats are poor. Most importantly, female black bears may embark on these movements more frequently than initially anticipated (see Onorato and Hellgren 2001). Movements of males, females, adults and subadults between Coahuila and western Texas (and vice-versa) denote that the process of recolonization in the Trans-Pecos should continue.

Park officials have noticed a slow, but steady increase in the number of visitor sightings of black bears since the MDE of 2000. Additionally, in 2002, several sightings of a female with cubs-of-the-year were noted, alluding to renewed reproduction in the Park. One collared female remains in BIBE and denned in 2003 with two apparently healthy yearlings. Invariably, the population of bears in the Park should continue to slowly increase and ultimately attain the pre-MDE levels. Alternatively, this process could be negatively impacted at any time by a variety of biotic or abiotic factors.

Continued persistence of black bears in BIBE and BGWMA bodes well for recolonization prospects in ranges to the north of these protected areas. As black bears move to ranges in the Glass, Del Norte and Davis Mountains, they will invariably face new challenges. Over 95% of the land in Texas is privately owned and ultimately large carnivores such as black bears may produce some human-related conflict. Small numbers of bears have already moved into these more northerly ranges (B. R. McKinney, Texas Parks and Wildlife Department, personal communication), and negative interactions between landowners and bears have remained infrequent. The status of black bears north of BIBE remains unknown and the presence of reproductive populations inhabiting these mountains is unlikely. Reports of sightings by the general public have increased and several researchers conducting studies on Nature Conservancy land in the Davis Mountains have noted the presence of bears in that range (B. R. McKinney, Texas Parks and Wildlife Dept, personal communication). Ultimately, a reproducing population in the Davis Mountains would prove to be important for conserving the species in western Texas. Additional research in the Trans-Pecos should focus on qualifying and quantifying the presence of bears in other ranges such as the Davis, Del Norte, Glass, Guadalupe, Chinati, and Sierra Diablo. It also would be beneficial to assess the possibility of black bears residing in borderland mountain ranges in northern Chihuahua (Sierra Grande, Sierra del Puerto Frio). Unverified reports along the borderlands west of BIBE have noted the presence of rogue bears moving within the Rio Grande River plain.

Whether these are Texas or Coahuila bears is unknown, but there is the possibility that some of these animals are moving from Chihuahua into Texas.

As long as pathways of xeric habitat between northern Coahuila and the Trans-Pecos remain undisturbed by excessive anthropogenic activity, the recolonization process should continue. After enduring a variety of obstacles during the last 100 years, this large carnivore is regaining a foothold in habitat it once shared with grizzly bears. This natural recolonization of former range will hopefully prove to be educational and beneficial to populations of this species throughout the southwestern portion of its range and to populations of carnivores globally.

VITA 2

David Paul Onorato

Candidate for the Degree of

Doctor of Philosophy

Thesis: CONSERVATION ECOLOGY OF THE METAPOPULATION OF BLACK BEARS IN THE BIG BEND ECOSYSTEM

Major Field: Zoology

Personal Data: Born in Philadelphia, Pennsylvania, on 14 February 1969, the son of Frederick Charles Onorato and Louise Cecil Showe.

Education: Graduated from Conestoga Senior High School, Berwyn, Pennsylvania in June 1987; received Bachelor of Science degree in biology from Eckerd College, St. Petersburg, Florida in May 1991; received Master of Science degree in biology from the University of Alabama at Birmingham, Birmingham, Alabama in July 1997. Completed the requirements for the Doctorate of Philosophy degree with a major in zoology at Oklahoma State University in May 2003.

Experience: Research and Teaching Assistant, Oklahoma State University; Research Technician, Department of Nutrition Sciences, University of Alabama at Birmingham, Teaching Assistant, University of Alabama at Birmingham; Field Technician, Vogelkop bowerbird research project, Iryan Jaya, Indonesia; Biological Scientist, Florida Marine Research Institute, Department of Environmental Protection, St. Petersburg, Florida.

Awards: Eckerd College Grant (1988-91); Outstanding Graduate Student Award, Department of Biology, UAB (1997); Texas Society of Mammalogists Award (2001), Elmer C. Birney Honoraria Award, American Society of Mammalogists (2002), Robert L. Lochmiller II Endowed Scholarship (2002), Graduate Research Excellence Award, Biological Sciences (2003), Wilks Award, Southwestern Association of Naturalists (2003).

Professional Memberships: American Society of Mammalogists, Society for Conservation Biology, The Wildlife Society, Texas Society of Mammalogists.