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Ecology and Structure of Black Bear (Ursus americanus) Populations in the Interior Highlands of Arkansas

Thea Vandervelde Kristensen
University of Arkansas, Fayetteville

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Ecology and structure of black bear (*Ursus americanus*) populations in the Interior Highlands of Arkansas

Ecology and structure of black bear (*Ursus americanus*) populations in the Interior Highlands of Arkansas

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology

By

Thea V. Kristensen
Eckerd College
Bachelor of Arts in Environmental Studies and Psychology, 1999
Washington State University
Masters of Science in Natural Resources, 2001
Simmons College
Master of Arts in Teaching, 2004

August 2013
University of Arkansas

This dissertation is approved for recommendation to the Graduate Council.

Dr. Kimberly G. Smith
Dissertation Director

Dr. Don White, Jr.
Committee Member

Dr. David Krementz
Committee Member

Dr. Steven Beaupre
Committee Member

ABSTRACT

In the Interior Highlands of Arkansas, Missouri, and Oklahoma, overharvest, extensive logging, and reductions of habitat availability by other means contributed to the decline of black bears (*Ursus americanus*). Bears were extirpated from the majority of the region by the 1940's Oklahoma by 1915 and from Missouri by 1931. From 1958-1968, the Arkansas Game and Fish Commission undertook a reintroduction to the Ouachita and the Ozark National Forests in Arkansas. The successful growth and expansion of the released population caused these efforts to be considered one of the most successful reintroductions of carnivores. In this dissertation, I sought to examine the current population size and density of bears in the Ouachita and the Ozark National Forests in Arkansas and to explore how dispersal patterns are influenced by population expansion. Density estimates are comparable to or above previous estimates done in the late 1980's/early 1990's. The population appears to have maintained or exceeded previous density estimates. There was evidence for female philopatry in both source and expanding populations, with relatedness declining with distance until about 30 km. In recently expanding populations, male-male dyads followed a similar pattern to female-female dyads with relatedness decreasing with distance. Female-female dyads in expanding populations also had higher levels of closely related dyads than female-female dyads in source populations. Only in recent years have large predator reintroductions been actively pursued and the goals of restoring a functional ecosystem been approached. The genetics of reintroduction and dispersal received research attention even more recently. Dispersal and gene flow into and out of populations, a process called connectivity, fundamentally shape wildlife distribution and abundance across the landscape. Connectivity determines taxonomic distinctiveness, colonization of new sites, and persistence of both local populations and metapopulations of linked populations. With measures of

connectivity in hand, we can better understand the role it plays for a particular wildlife species, and predict the consequences of changes in a human-altered landscape.

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DEDICATION

This dissertation is dedicated to my husband Paul Kristensen and our two amazing children.

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List of papers:

Ch. IV Kristensen, T. V., K. M. Faries, D. White, and L. S. Eggert. 2011. Optimized methods for high-throughput analysis of hair samples for American black bears (*Ursus americanus*). Wildlife Biology in Practice 7:123-128.

INTRODUCTION

Role of carnivores in conservation

Through such means as change in land use patterns, harvest, population expansion, resource use, introduction of invasive species, and global climate change, humans have massively reduced distribution and abundance of species worldwide. As a result, conservation biology, with its goal of maintaining biodiversity, has become an important field. Conservation of carnivore populations is essential to this goal because of the role of carnivores in regulation of ecosystems (Hilderbrand et al. 1999, Terborgh et al. 1999, Clark 2009). For instance, grizzly (*Ursus arctos horribilis*) and black bear (*Ursus americanus*) consumption of salmon (*Oncorhynchus* spp.) alters local ecosystem structure (Gende et al. 2002), provides a vector for nitrogen into surrounding terrestrial systems (Hilderbrand et al. 1999, Helfield and Naiman 2006), and increases nutrient availability for aquatic macroinvertebrates (Quinn et al. 2003, Winder et al. 2005).

Additionally, carnivores often have an influence on other species through predation and interspecific competition, which can result in changes in ecosystem processes (Estes et al. 1998, Berger et al. 2001, Treves and Karanth 2003). Predation may alter abundance and distribution of other species and the remaining carrion provides a rich food resource for scavengers (Rose and Polis 1998, Wilmers et al. 2003). As such, removal or addition of a predator to a system can cause trophic cascades (Estes et al. 1998, Post et al. 2002, Ripple and Beschta 2004;2012). Killer whale (*Orcinus orca*) predation upon sea otters (*Enhydra lutris*) results in an increase in sea urchin density which subsequently causes deforestation of kelp beds (Estes et al. 1998). Restoration of wolves (*Canis lupus*) into ecosystems influences abundance and distribution of prey species which in turn can influence vegetation production (Post et al. 2002, Ripple and

Beschta 2004;2012). Some biologists go so far as to posit that herbivores are limited by predation and that therefore, vegetation dynamics are highly subject to changes in predation on the herbivores in the system, as with the "green world" hypothesis (Hairston et al. 1960, Terborgh et al. 2006).

In addition to their important roles within ecosystems, large carnivores have other characteristics which make them ideal model species for ecological studies. Due to their large home range sizes, relatively low densities, and propensity for conflict with humans, large carnivores are sensitive to the habitat destruction and fragmentation that are commonplace throughout the landscape and are increasing with human population size (Beier 1993, Noss et al. 1996, Crooks 2002, Hostetler et al. 2009). As a result, responses of large carnivores can be indicative of resultant problems for other species as well (Beier 1993, Noss et al. 1996, Crooks 2002, Hostetler et al. 2009). Black bears are a relatively abundant large carnivore and may be studied by non-invasive techniques, making them an optimal and relatively economical carnivore species to study. Thus, assessing patterns of distribution and abundance of black bears may be a feasible way to aid in management of many species and help elucidate ecosystem processes that have potential impacts on a wide range of species.

Reduction and subsequent expansion of carnivores

In the last 100 years, there have been significant declines in many carnivore populations throughout the world and corresponding range reductions of these species (Gittleman and Gompper 2001). Alteration of the landscape, along with harvest, and in some cases specific eradication efforts, effectively reduced the range and population size of many carnivore species in North America, including cougars (*Puma concolor*), wolves, grizzly bears, and black bears (*Ursus americanus*) (Young and Goldman 1944, Young and Goldman 1946, Mech 1970, Servheen 1990, Pelton and van Manen 1994, Brown 1996, Sunquist and Sunquist 2002). However, with shifting public attitudes, greater legislative protection, and organized conservation efforts, some species have increased and recolonized former parts of their respective ranges, particularly in the past 20 years. For instance, some wolf populations have been expanding and were recently removed from the endangered species list (Mech 1995, Forbes and Boyd 1996, Pletscher et al. 1997, Wydeven et al. 2009, USFW 2012), grizzly bears have recolonized the Southern Yellowstone Ecosystem and have expanded within the Grand Teton National Park (Pyare et al. 2004), and cougars are recolonizing the Midwest (LaRue et al. 2012) and have been sighted dispersing from their reduced range into previously occupied areas in the eastern United States (Network 2011).

Due to habitat destruction and fragmentation, black bear populations in North America began declining in the 1700's (Pelton 1982, Maehr 1984, Pelton and van Manen 1994). Black bears were also a source of meat, fat, and skins for pioneers, and were killed more frequently than any large mammal except deer (McKinley 1962). There was a massive reduction in range from the original extent of the species, which encompassed most forested regions throughout North America, to a more patchy distribution in remaining forested areas with low density of humans (Pelton 1982, Maehr 1984, Pelton and van Manen 1994, Servheen et al. 1999). Specific populations, like Louisiana black bears (*U. a. luteolus*), have received attention due to their threatened status, but across the country black bears have not been, nor are they currently considered, endangered. Recently, populations have expanded back into their historical range (Pelton and van Manen 1994), including localities in the Trans-Pecos region and Big Bend Ecosystem in Texas (Onorato and Hellgren 2001, Onorato et al. 2007) and in Kentucky (Frary et al. 2011). Reintroductions have also been used successfully to restore black bears to former parts of their range, including the San Bernardino Mountains in California (Brown et al. 2009) and the Interior Highlands of Arkansas (Smith and Clark 1994).

Source-sink dynamics

With expansion of populations, there is the potential for source-sink dynamics to influence the system. A source population is one in which births exceed deaths whereas a sink population has higher mortality than births; a sink population could not be maintained without dispersers from the source population (Pulliam 1988). In fragmented landscapes, a strong source population with large area is necessary to maintaining the sink populations (Pulliam 1988, Temple and Cary 1988, Howe et al. 1991, Donovan et al. 1995); despite this, the presence of sink populations can contribute to the overall size and longevity of the metapopulation (Howe et al. 1991).

In the case of recently expanding populations, the area experiencing expansion is potentially a sink. Because these new populations are often small, lack of diversity is likely due to the founder effect, which can influence establishment and persistence of the population (Thrall et al. 1998, Ingvarsson 2001, Nieminen et al. 2001). However, conservation strategies, such as improving connectivity and introducing additional individuals, may be used to alleviate such issues (Madsen et al. 2004, Hogg et al. 2006, Hedrick and Fredrickson 2010). Increasing levels of migration from source populations to sinks, even to a small extent, and augmentation of populations with individuals from the source population, can increase genetic diversity (Madsen et al. 1999, Vilà et al. 2003, Madsen et al. 2004, Hogg et al. 2006).

Reintroductions

Reintroductions are commonly used as a strategy for conservation and management of wildlife species (Griffith et al. 1989, Sarrazin and Barbault 1996, Wolf et al. 1996, Seddon et al.

2007). The goal of reintroductions is to introduce individuals from captive populations or populations in other locations into an area where the target species has been extirpated or vastly reduced in number with the hope of establishing a reproducing population (Griffith et al. 1989). However, reintroductions can be extremely costly and often are unsuccessful in establishing self-sustaining populations (Lyles and May 1987, Griffith et al. 1989, Wolf et al. 1996). Mortality rates are high due to factors including predation, stress, lack of familiarity with the area, and large movements of reintroduced individuals (Griffith et al. 1989, Wolf et al. 1996, Fischer and Lindenmayer 2000, Teixeira et al. 2007).

Additionally, because reintroductions are often composed of a small number of individuals, low genetic diversity can also be of concern (Fitzsimmons et al. 1997, Armstrong and Seddon 2008). Many reintroduced populations have reduced genetic diversity compared to the source population (Hedrick et al. 2001, Maudet et al. 2002, Mock and Rhodes 2004). Low genetic diversity can result in lowered fitness and higher potential of extinction for reintroduced populations (Saccheri et al. 1998, Madsen et al. 1999, Jamieson et al. 2007, Armstrong and Seddon 2008).

Evaluating success of reintroductions and gathering information about what factors influence success is essential for optimizing future reintroductions (Kleiman et al. 2000, Armstrong and Seddon 2008). Case studies are often used to assess reintroduction efforts for various taxonomic groups (Fischer and Lindenmayer 2000, Strum 2005, Coonan and Schwemm 2009). Due to the reduction in range of carnivore species over the last 100 years, reintroduction has been an important conservation strategy for carnivore species. This strategy has been used for the conservation of species including: cougars (Ruth et al. 1998), wolves (Sime et al. 2007), swift foxes (*Vulpes velox*) (Ausband and Foresman 2007), and black bears (Smith et al. 1991, Smith and Clark 1994, Clark et al. 2002, Brown et al. 2009). Bears in particular are of interest because five species are vulnerable and one is endangered according to IUCN listings. Black bears have been reintroduced in California (Brown et al. 2009), Louisana (Benson and Chamberlain 2007), and Arkansas (Smith and Clark 1994, Wear et al. 2005). Information about successful reintroductions of the American black bear, a species of least concern, could provide managers of more vulnerable species with a basis from which to construct their own reintroductions.

Black bear reduction, reintroduction, and expansion in the Interior Highlands

In the Interior Highlands of Arkansas, Missouri, and Oklahoma, overharvest, extensive logging, and reductions of habitat availability by other means contributed to the decline of black bears (Clark 1991, Smith and Clark 1994). Bears were extirpated from Oklahoma by 1915 and from Missouri by 1931 (Bennitt and Nagel 1937, McCarley 1961). Despite a ban on harvest in Arkansas in 1927 (Smith and Clark 1994), two of the three most important regions in Arkansas supporting good bear habitat, the Ozark and Ouachita Mountains, were virtually devoid of bears by the 1940's, while the third area, within what is now the White River National Wildlife Refuge, was reduced to roughly 25-50 individuals (Dellinger 1942, Holder 1951). In 1958, the Arkansas Game and Fish Commission initiated a reintroduction of bears into the Interior Highlands of Arkansas, with one release site in the Ouachita National Forest and two release sites in the Ozark National Forest (Rogers 1973, Smith and Clark 1994). Over the subsequent 10 years, 254 bears were translocated from sites in northern Minnesota and Manitoba, Canada to the release sites in Arkansas (Rogers 1973, Smith and Clark 1994). The successful growth and expansion of the released population caused these efforts to be considered one of the most successful reintroductions of a carnivore species (Smith and Clark 1994). By the 1980's, evidence of a population in Oklahoma was recorded, with bears expanding their range from the Ouachita Mountains of Arkansas into southeastern Oklahoma (Bales et al. 2005). A hunting season was reinstated in Arkansas in the 1980's and in Oklahoma in 2009. Missouri experienced little bear activity until the 1990's, after which bear sightings and nuisance reports increased, especially at the southern reaches of the state (Titus et al. 1993). Additionally, sightings of sows with cubs have risen in the last decade, indicating the possibility of a reproducing bear population in Missouri (Titus et al. 1993). By the early 1990's, approximately 2500 bears were present in the Interior Highlands of Arkansas, Oklahoma, and Missouri (Smith and Clark 1994).

Purpose of dissertation

The purpose of my dissertation was to determine how the reintroduction and subsequent expansion influenced the black bears in the Interior Highlands and to provide managers with empirical data on abundance and density. The sections of my dissertation focus on population abundance and density, population structure and genetics, and dispersal patterns of black bears in this region respectively. These pieces together will provide a picture of the ecology of black bears in the Interior Highlands of Arkansas.

On a broader scale, this type of investigation contributes to the understanding of factors central to the field of ecology, including distribution, abundance, and dispersal. In particular, populations studied here provide information about successful reintroduction and expansion of populations which may be of use in conservation efforts. Genetic diversity and structure in reintroduced and expanding populations can be a central concern which may influence the success of these efforts. Dispersal mediates genetic diversity and structure. Deriving an understanding of dispersal patterns is essential at a time when invasive species, climate change and habitat loss are contributing to changes in species distributions and ecosystem function and composition (Kokko and López-Sepulcre 2006). Because they are inextricably linked, abundance has and will continue to respond to these forces as well. Determining abundance and distribution help contribute to conservation and maintenance of the target species, as well as providing insights into how these factors may be influenced for similar species of concern.

Sections of dissertation

Population abundance and density

Some of the most fundamental questions in ecology focus on abundance and distribution of organisms (Andrewartha and Birch 1954). Distribution and abundance are probably the most important pieces of information in wildlife conservation and management. Distribution refers to the geographic limits in which a species is established, while abundance complements, and is necessarily tied to, distribution by describing the number of organisms within specific areas within the greater distribution (Andrewartha and Birch 1954). Among other things, distribution and abundance are important in making informed management decisions related to population status and trends, harvest management, evaluating the effects of predation or human disturbance, and determining the effects of global climate change. Thus, it is imperative that rigorous, empirical methods be used to assess abundance and density. As mentioned above, estimating abundance and distribution of bears and other large carnivores has further important because they influence ecosystem processes, abundance and distribution of other species, and are sensitive to alteration of the environment (Beier 1993, Noss et al. 1996, Hilderbrand et al. 1999, Crooks 2002, Clark 2009, Hostetler et al. 2009).

Clark and Smith (1994) completed the most recent estimate of black bear abundance and density in the Ozark and Ouachita mountains in the late 1980’s and early 1990’s. They sampled the White Rock Wildlife Management Area in the Ozark National Forest and the Dry Creek

Wildlife Management Area in the Ouachita National Forest, using spring-activated foot snares and barrel traps. Abundance of bears in the White Rock study area was estimated at 35.8-37.5 bears with a density of 7.5 bears per 100 km^2, while it was higher in the Dry Creek area with estimates of 56.0-72.0 bears and 9.0 bears per km^2.

Since then, non-invasive genetic samples obtained through hair snares have largely replaced physical mark-recapture of brown and American black bears for population estimates (Taberlet et al. 1997, Woods et al. 1999, Mowat and Strobeck 2000, Kendall et al. 2008). Using genetic techniques rather than physically marking and recapturing the bears themselves reduces harm to bears, avoids problems with tag loss, increases the ability to sample a larger geographic range, and reduces costs and effort (Woods et al. 1999, Mills et al. 2000, Mowat and Strobeck 2000, Boersen et al. 2003). Additionally, there have been advances in models available to estimate population size and density. The Robust design in program MARK allows users to model data across multiple years of study and provides more precise estimates of population size (Kendall et al. 1995, Pederson et al. 2012). The secr package for program R utilizes the combination of mark-recapture data with location data to provide density estimates for the study area of interest (Borchers and Efford 2008, Efford et al. 2009, Efford 2013).

Current, reliable abundance data are now more important than ever, particularly because harvest has increased in Arkansas since 2001 when baiting became legal on privately-owned land. The objective for this section of the dissertation was to estimate abundance and density of black bears in the Muddy Creek Wildlife Management Area (WMA) in the Ouachita Mountains and the White Rock WMA in the Ozark Mountains, Arkansas, using non-invasive genetic sampling. Assessing the population this way will better inform managers as they make decisions about these populations, particularly in regards to how the harvest is managed in future years.

Dispersal

Dispersal is clearly tied to population structuring because it can mediate gene flow, impact abundance, and influence population dynamics, all of which make it central to the understanding of the ecology of a species (Hestbeck 1981, Bohonak 1999, Dieckmann et al. 1999). In mammals, males tend to exhibit dispersal while females are often philopatric (Greenwood 1980, Dobson 1982), though variation within this pattern and entirely different patterns have been found within the mammalian class (Lawson Handley and Perrin 2007). The type of mating system also influences dispersal patterns because it impacts the cost of mate competition and cost of inbreeding by sex (Dobson 1982, Waser et al. 1986, Lawson Handley and Perrin 2007). Density may also play a role in levels of dispersal for some species, though it has not been explored thoroughly in mammals and other factors, including spatial and temporal variation in density, may be confounding (Matthysen 2005).

Expanding populations may exhibit dispersal patterns that deviate from those of stable populations, with individuals dispersing long distances. In some species that must continually colonize new patches within their range, there is variation in dispersal-related characteristics and strategies, resulting in dispersive individuals travelling to new patches while there is a higher level of philopatry displayed by those in the core area (MacKay and Lamb 1979, Peroni 1994, Taylor and Merriam 1995, Hanski et al. 2004, Fjerdingstad et al. 2007, Duckworth 2008, Piquot et al. 1998). Similar patterns appear along areas of range expansion, with natural selection favoring phenotypes that contribute to long distance dispersal (Kokko and López-Sepulcre 2006, Duckworth 2008, Lowe and McPeek 2012). For instance, traits that are indicative of superior flight ability (i.e. longer wings, larger thoraxes) were more frequent at the expanding edge of the population than in the core area for butterflies (*Hesperia comma and Aricia agestis*) and crickets

(*Conocephalus discolor*, *Conocephalus dorsalis*, *Metrioptera roeselii*, and *Metrioptera brachyptera*) (Hill et al. 1999, Thomas et al. 2001, Simmons and Thomas 2004). Differential leg morphology promotes dispersal in cane toads (*Bufo marinus*) and stream salamanders (*Gyrinophilus porphyriticus*), with cane toads displaying this phenotype more frequently along the invading front of an expanding population (Phillips et al. 2006, Lowe and McPeek 2012). Dispersers to non-core areas also may display more aggressive or asocial behaviors (Duckworth 2008, Cote et al. 2010). Some species display trade-offs between fecundity and dispersal, with dispersive traits declining in frequency as the population becomes established (Baguette and Schtickzelle 2006, Burton et al. 2010). These effects would influence which individuals disperse and patterns of dispersal along expanding edges as opposed to core areas. Thus, along the expanding edge, individuals may be more dispersive (Gundersen et al. 2001, Duckworth 2008), potentially lowering levels of relatedness with surrounding individuals compared to relatedness of individuals in close proximity within core areas.

A variety of studies, using both genetic and field-based techniques, have described dispersal behaviors in American black bears. Females settle near their mothers, creating a pattern in which proximity in space indicates higher levels of relatedness for females, and males are more likely to disperse (Rogers 1987, Onorato et al. 2004, Moyer et al. 2006, Costello et al. 2008, Costello 2010). However, this is not always the case and there is variation in degrees of philopatry and dispersal in different populations (Schenk et al. 1998, Costello et al. 2008, Roy et al. 2012). Despite extensive overlap in home range for females in northern Ontario, there was no relationship between proximity and relatedness in females, possibly due to high density and food distribution (Schenk et al. 1998). While bears did exhibit the pattern of male dispersal and female philopatry in New Mexico, females in close proximity exhibited less relatedness than expected while males in close proximity were more closely related than expected (Costello et al. 2008). Here, difference in levels of resource or mate competition, mediated by levels of density, were suggested to explain reduced male dispersal, with the low density in this population potentially reducing competition (Costello et al. 2008). In southwestern Québec, in low density areas, relatedness decreased with distance in females, but there was no significant relationship between distance and relatedness of male dyads or male-female dyads (Roy et al. 2012). In contrast, Roy et al. (2012) did not detect genetic structure for females in high density areas. Males did exhibit local genetic structure at high density, which the authors explained by suggesting reduced dispersal distances and delayed dispersal in subadult males at the high density (Roy et al. 2012).

Thus, literature on black bear dispersal reveals a pattern of male dispersal and female philopatry, though female philopatry dissolves and male dispersal decreases in some populations in response to specific local conditions including variation in density. Additionally, brown bears have deviated from traditional patterns in cases of expanding populations (Swenson et al. 1998, Jerina and Adamic 2008), suggesting the possibility that additional complexity may also be present in dispersal of black bears in expanding populations, like those in the Interior Highlands of Arkansas and in Kentucky. Here, I sought to examine patterns of dispersal and philopatry of black bears in expanding populations and in their corresponding source populations. I hypothesized that source populations would follow expected patterns of male dispersal and female philopatry, while expanding populations, particularly recent expansions, would have deviations from the pattern.

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Young, S. P., and E. A. Goldman. 1946. The puma, mysterious American cat American Wildlife Institute, Washington, D.C.

Multi-year density and population estimates of an expanding black bear (Ursus americanus) population in the Interior Highlands, Arkansas

Thea Kristensen, Kaitlyn Faries, Myron Means, J. David Carr, Lori Eggert, Kimberly G. Smith and Don White, Jr.

ABSTRACT

American black bear (Ursus americanus) populations in the Interior Highlands, Arkansas, have expanded since reintroduction in the late 1950s and early 1960s requiring management of harvests and nuisance complaints. Success of bear conservation efforts cannot be evaluated without reliable information on population abundance, trends, and distribution. Moreover, concern and interest in bears from the general public, combined with a growing need to integrate land management efforts to conserve biodiversity, have intensified the need for efficient, well-coordinated management efforts for black bears in the Interior Highlands. Harvest levels have increased since baiting was permitted on private land, further increasing the need for information about population size and density of bears in the Interior Highlands. In this study we used noninvasive genetic sampling (5 7-day trapping sessions in June and July) to estimate the population size of black bear populations at two locations in the Interior Highlands: the Ouachita Mountains (2006-2008) and the Ozark Mountains (2009-2011). We also utilized spatially explicit capture-recapture (SECR) methods to estimate density for the areas sampled. Under the Robust model, capture probabilities were influenced by sex, year, and time for the Ozarks, but there was no strong top model for the Ouachitas. Year, sex, and trap-specific behavior were all important components of density models. Top models for regional density included percent forested landscape cover and density of roads as covariates of density, with percent forest having a positive association and road density having a slightly negative association. Density estimates were comparable to or above previous estimates done in the late 1980's/early 1990's. Density was ~14 bears/100km^2 in the Ouachitas and ~25/100 km^2 for the Ozarks. The population appears to have maintained or exceeded previous density estimates, but should be monitored further since the year of the highest harvest did not occur until the middle of this study.

KEY WORDS density, reintroduction, Robust model, SECR, Ursus americanus

American black bears (*Ursus americanus*) historically ranged throughout most forested regions in North America (Hall 1981). However, due to habitat destruction and fragmentation, black bear populations in North America began declining in the 1700s (Pelton 1982, Maehr 1984, Pelton and van Manen 1994). As a result, there was a substantial reduction in range from the original extent of the species (Pelton 1982, Maehr 1984, Pelton and van Manen 1994, Servheen et al. 1999). Recently, there has been expansion of populations back into their historical range (Pelton and van Manen 1994), including localities in the Trans-Pecos region and Big Bend Ecosystem in Texas (Onorato and Hellgren 2001, Onorato et al. 2007) and in the Cumberland Plateau in Kentucky (Frary et al. 2011). Reintroductions have also been used successfully to restore black bears to former parts of their range, including the San Bernardino Mountains in California (Brown et al. 2009) and the Interior Highlands of Arkansas (Smith and Clark 1994).

In the state of Arkansas, overharvest, extensive logging, and reductions of habitat availability by other means all contributed to the decline of black bears (Smith et al. 1991). Two of the three major habitat areas, the Ozark and Ouachita Mountains, were devoid of bears by the 1940's, while the third area, near White River, was reduced to roughly 25-50 individuals

(Dellinger 1942, Holder 1951). To restore the state's bear population, 254 bears from Minnesota and Manitoba were released into the Ozark and Ouachita Mountains from 1958-1968 (Rogers 1973, Smith and Clark 1994). This reintroduction has been cited as the most successful reintroduction of black bears (Smith et al. 1991, Smith and Clark 1994), with the population size in the state was thought to be roughly 2,500 by the early 1990s.

Due to success of the reintroduction, harvest was resumed in the Interior Highlands of Arkansas in 1980. The state has a fall harvest, October through early December, with specific dates based on harvest method and zone. Baiting on private lands was permitted starting in 2000. Harvest numbers have increased over time, particularly recently since baiting has been permitted (Fig 1). In 2006, harvest quotas were lifted because numbers were consistently lower than the quotas, which were set at 200 in Zone 1, roughly corresponding to the Ozark Mountains region, and 150 in Zone 2, roughly corresponding to the Ouachita Mountains region. However, in 2009 harvest was the largest on record, with 530 bears harvested in the state. As a result, a quota was reinstated in zone one for the most recent harvest season, fall 2012.

To maintain sustainable harvest levels, it is imperative that rigorous, empirical methods be used to assess the current population size. Clark and Smith (1994) completed the most recent and thorough estimate of black bear abundance and density in the Ozark and Ouachita mountains in the late 1980s and early 1990s. Abundance was estimated between 35-37 bears (7.5 bears/100km^2) in the White Rock Wildlife management area in the Ozark Mountains, and 56-72 bears (9.0/100 km^2) in the Dry Creek Wilderness Area of the Ouachita Mountains (Clark and Smith 1994).

Since then, non-invasive genetic samples obtained through hair snares have largely replaced physical mark-recapture of brown (Ursus arctos) and American black bears for population estimates (Taberlet et al. 1997, Woods et al. 1999, Mowat and Strobeck 2000, Kendall et al. 2008). Using genetic techniques rather than physically marking and recapturing the bears themselves reduces harm to the bears, avoids problems with tag loss, increases the ability to sample a larger geographic range, and reduces costs and effort (Woods et al. 1999, Mills et al. 2000, Mowat and Strobeck 2000, Boersen et al. 2003).

Additionally, there have been advances in models available to estimate population size and density. The Robust design in program MARK allows users to model data across multiple years of study and provides more precise estimates of population size (Kendall et al. 1995, Pederson et al. 2012). Spatially explicit capture-recapture (SECR) methods offer a potentially more accurate method of estimating density than the $\widehat{N}/\widehat{A}$ (estimated abundance/estimated area) approaches (Efford 2004, Borchers and Efford 2008, Obbard et al. 2010). The secrpackage for program R utilizes distance sampling principles (Burnham et al. 1980) in the combination with mark-recapture data and its corresponding location data to provide density estimates for the study area of interest (Efford 2004, Borchers and Efford 2008, Efford et al. 2009, Efford 2013). (Please note that SECR refers to this method of estimating density whereas secr refers to a specific package for program R.) In doing so, it reduces the potential to over-estimate abundance due to closure violations caused by the presence of animals with only part of their home range encompassed by the study area and removes the need to define the effective trapping area, which is often an elusive parameter to estimate (Efford 2004, Borchers and Efford 2008, Obbard et al. 2010). Consequently SECR models have been recommended for use with large carnivores, particularly where there is potential for violation of the geographic closure assumption (Obbard et al. 2010).

Our objective was to estimate abundance and density of black bears in the Muddy Creek area in the Ouachita Mountains and the White Rock Wildlife Management Area in the Ozark Mountains. We hypothesized that abundance and density estimates would be similar to those estimated by Clark and Smith (1994) in the late 1980's. Assessing the population using the Robust design and SECR techniques will better inform managers as they make decisions about these populations, particularly in regards to how the harvest is managed in future years.

STUDY AREA

The two areas sampled were located in the Ouachita and Ozark National Forests in the Interior Highlands of Arkansas, USA. The section of the Ouachita National Forest that constituted our study area is roughly bound by highways 71 and 270 along the north and Highway 88 along the south and comprises 756 km^2 (Fig 2). The area studied in the Ouachitas is primarily made up of shortleaf pine (Pinus echinata) and mixed pine-hardwood, with elevations reaching up to 747m (Clark 1991). Land in this area is primarily forest land. In contrast, the White Rock Wildlife Management Area (WMA) which was sampled in the Ozark National Forest has many inholdings (Fig 2). The area sampled is 1080 km^2 in size, with elevation reaching up to 740 m (Clark 1991).   Mountains and ridges are separated by narrow valleys throughout the White Rock WMA, which is predominantly oak- oak-hickory forest (Clark 1991).

METHODS

Sampling methods

We imposed a systematic grid across each study area, with each cell being 6 km x 6 km to approximate female home range size (Clark 1991). Thirty grid cells were imposed over the White Rock area and 21 were imposed over the Ouachita area. We selected at least two snare sites within each cell, keeping each snare >1.6 km away from any other snare on the study area.

We specifically selected sites on public land that were accessible by forest roads. Based on accessibility, 32, 50, and 60 snare sites were used in the Ouachitas in 2006, 2007, and 2008. In the Ozarks, in 2009, the mean number of bears detected for cells with 2 snares (7.34, SE=0.20) was smaller than the mean detected in cells with 4 snares (18.13, SE=0.89) (t=-3.22, p= 0.0216). Thus, in 2010 and 2011 the number of snares per cell was increased to 4 per cell where possible. In 2009 65 snares were employed, 98 in 2010, and 94 in 2011.

We utilized the barbed wire hair snares (Woods et al. 1999, Mowat and Strobeck 2000, Poole et al. 2001). Hair snares consisted of a single strand of 4-pronged perimeter barbed wire positioned 50 cm above the ground. At the center of each hair snare, a nylon mesh bag containing rancid fish entrails was suspended at least 3 m off the ground. We used carp and catfish as the primary scent and rotated secondary scents each year to prevent accustomization. Secondary scents included sardines, beef fat, dog food, pastries, molasses, peanut butter, and fish fertilizer. Our methods were approved by the Insitutional Animal Care and Use Committee at the University of Arkansas, Fayetteville (IACUC #09031).

Every barb on each hair-snare was examined for bear hair every 7 days for 5 weeks during June and July, 2006-2008 (Ouachita Mountains), and 2009-2011 (Ozarks). Hair samples were stored in coin envelopes in cool, dry conditions. We shipped the Ouachita samples to Wildlife Genetics International and transported the Ozark samples to the University of Arkansas in Fayetteville, AR weekly for DNA extraction.

Genetic methods

Individuals were identified using microsatellite loci. We sent samples from the Ouachitas to Wildlife Genetics International in Nelson, British Columbia. They used the following seven loci to identify individuals: CXX20,G10C, G10H, G10J, G10M, G10P, and

G1D (Ostrander et al. 1993, Paetkau et al. 1995, Paetkau and Strobeck 1995, Taberlet et al. 1997, Paetkau et al. 1998).

For Ozark samples, we used previously published protocols for DNA extraction and multiplex microsatellite genotyping (Kristensen et al. 2011). The microsatellite loci used were G1A, G1D, G10B, G10C, G10J, G10L, G10M, G10P (Paetkau et al. 1995, Paetkau and Strobeck 1995, Paetkau et al. 1998). We used Micro-Checker (van Oosterhout et al. 2004) to check for null alleles. We used the microsatellite toolkit for Excel (Park 2001) to identify matching samples and check for genotyping error on individuals that differed at 4 loci or less. We used program DROPOUT (McKelvey and Schwartz 2005) to detect and remove any individuals that may have been misidentified due to problems with dropout.

We used program Identity (Wagner and Sefc 1999) to determine the probability that full siblings would have the same genotype (PSIBs) and the probability that two randomly selected individuals would share the same genotype (PID). We used the Microsatellite Toolkit for Excel (Park 2001) to determine average heterozygosity and Genepop (Raymond and Rousset 1995, Rousset 2008) to determine deviations from Hardy-Weinberg and linkage disequilibrium. Bears appeared to be more closely related than expected by chance; many loci were linked and one was out of Hardy-Weinberg Equilibrium (HWE). Therefore, we then used program ML-Relate (Kalinowski et al. 2006) to determine unrelated pairs of individuals. We randomly selected a subset of unrelated pairs and removed any parent-offspring pairs from the list. We had a remaining list of 50 unrelated individuals from the Ozarks and 27 individuals from the Ouachitas. We ran these lists through Genepop to reassess deviations from Hardy-Weinberg and linkage disequilibrium. Because G10P was still linked with G10L in the Ozark population, we removed G10P from further analyses.

Data analysis

We used the Robust design (Pollock 1982, Kendall et al. 1995) with the Huggins estimator (Huggins 1991) in Program MARK to estimate population size (White and Burnham 1999). We presume the assumption of demographic closure was met because births do not occur during the trapping period, survival is high, and yearly study sessions were short in duration, but that geographic closure may have been violated because movement was not restricted to the study areas. We considered the influence of trapping session/year, time, behavior, sex, and combinations thereof on capture probability (p). A behavioral response indicates a change in capture probability, based on whether the organism was captured previously or not. We looked the following patterns in time: time independent model (i.e. all sampling intervals have their own estimate) (t), linear model through time (T), quadratic model over time (TT). Because γ was not the primary parameter of interest, a null model was used for this parameter. A null model is a model with no specified predictor variables. Models containing a year effect on survival did not converge and thus were not used for either population. For the Ouachita data set, models containing a sex effect on survival also did not converge and were not included. This was likely because we did not have enough data to accommodate such complex models. We evaluated models based on the Akaike Information Criterion for small sample sizes (AIC_c), ΔAIC_c, and model weight (Burnham and Anderson 2002). Models with a ΔAIC_c below ten were included here and population estimates and capture probability (p) were determined through use of model averages based on AIC_c weight (Burnham and Anderson 2002).

We used the Pradel Robust Model with Survival and Lambda, with the Huggins closed capture estimator, in program MARK to estimate λ (Pollock 1982, Huggins 1991, Kendall et al. 1995, Pradel 1996, White and Burnham 1999). In this model, λ is the realized growth, estimated by dividing ϕ_i by (γ_i + 1) . The parameter ϕ_i is defined as the probability of surviving and remaining present in the population from time i to time i+1 while γ_i is defined as the probability being present at time i-1, given that the organism was present in time I (Cooch and White 2010). We used the top models from the Robust model with Huggins estimator from above, defined as having ΔAIC_c below ten to set up predictors for capture probability (p) for the Ozark population. For the Ouachita population, we used the top five models from the Robust model with Huggins estimator from above. We then used models with null, sex, or year as predictors of λ and ϕ. Models containing more than one predictor variable for ϕ or λ did not converge, so we only used a single predictor for each parameter. For the Ozark population, the model containing behavior as a predictor of p, would not converge and hence was not included in this analysis. As above, we evaluated models using ΔAIC_c, and model weight, selecting models below ΔAIC_c of ten and model averaging for λ (Burnham and Anderson 2002). We conducted chi-square goodness of fit test to determine if the populations deviated from 1:1 sex ratio.

We used the secr package in program R to calculate multi-year density estimates for each study area for each sex. We separated sexes because there were differences in capture probability sex. We set the buffer at 10 km. Subsequently, we used all three years of data to calculate density for each sex at each location. The base model included session as a predictor of detection probability (g_0) and spatial extent (σ). Spatial extent refers to the area in which an organism may be detected. Session refers to the trapping session in the secr package and for this study it is the equivalent to the year of sampling. We ran models with time (T), behavior (b), and a trap-specific behavior (bk) as predictors of g_0 and with session as a predictor of density. T refers to a linear trend in time, b refers to a response to previous capture, and bk refers to a response to previous capture at a specific trap location. We ranked models using AIC and used a model average for those with a ΔAIC under ten.

Finally, we modeled regional density for each sex by including data from both locations and incorporated habitat covariates. We constructed a mask from a spatial grid covering each study area with locations spaced at 250m and a buffer of 10km beyond the perimeter of each detection array. As per Drewrey et al. (2013), we used two search radii, one based on hourly movement rates (Clark 1991) and the other on the shortest mean recapture distance ($\bar{d}$) calculated in secr, which were 360 m and 1100 m respectively.

Because food availability and cover are important determinants of bear distribution (Pelton 2003), we used percent forest cover as one spatial covariate. Using the 2006 National Land Cover Database land cover layer, we combined deciduous, coniferous, and mixed forest into one forest class through using the reclassify tool in ArcMap™ v. 10.1 (ESRI 2011). We then extracted percent of land cover coded as forest for each mask location at two search radii, 360 m and 1100 m, using focal neighborhood functions in ArcMap™ v. 10.1 (ESRI 2011). We also used roads as a spatial covariate. We extracted road density in km/km^2, for each mask location from August 15, 2012 Arkansas Highway and Transportation Department roads vector data at two search radii, 1100 m and 5000 m, using line density functions in ArcMap™ v. 10.1 (ESRI 2011). Both locations included the model with session as a predictor for g_0 and σ and behavior as a predictor of g_0 so this was used as a base model onto which we added the habitat covariates as a predictor for density. We included models with forest at the 360 and 1100 m scales as a predictor of density. Roads may also influence black bear distribution (Beringer et al. 1990), but potentially at a broader scale, so we also used models with density of roads at the 1100 and 5000 m scales as a predictor of bear density.

RESULTS

Trap success and genotyping

Percent of traps visited averaged 87% in the Ozark National Forest and 62% in the Ouachita National Forest, with trap success averaging 56% in the Ozark National Forest and 31% in the Ouachita National Forest (Table 1). There was considerable variation among years, with the middle year having the lowest success for each location. The Ouachitas had lower trap success than the Ozarks (F=8.09, p=0.047). The percent of samples identified at all loci averaged 83% for the Ozarks and 79% for the Ouachitas (Table 1).

An average of 165 bears was detected in the White Rock WMA of the Ozark National Forest each year whereas an average of 43 was detected in the area sampled in the Ouachita National Forest (Table 2). Over the course of the study, a total of 351 individuals were identified at White Rock, with 165 males, and 186 females, and 99 at the area in the Ouachita National Forest, with 45 males and 54 females (Table 2). Over the three years of sampling, the samples collected from the Ozark population did not differ from an apparent 1:1 sex ratio (χ^2=0.6559,p=0.4180). However, the samples collected from the Ouachita population did differ from an apparent 1:1 sex ratio (χ^2=4.10,p=0.043), though the poor capture probability of males in 2007 may be driving this difference (Fig 2).

Mean observed heterozygosity across all loci was 0.765 for the population sampled in the Ozark National Forest and 0.779 for the population sampled in the Ouachita Mountains. None of the loci differed from Hardy-Weinberg equilibrium (HWE) in the Ouachita National Forest, however G10P was out of HWE in the Ozark population (p= 0.0009). We found linkage disequilibrium for many pairings of loci in the Ozark National Forest population and some in the Ouachita National Forest population. However, after taking a random subsample, excluding close relationships, no loci deviated from HWE and only G10P was linked with G10L in the Ozark National Forest population. We dropped G10P from further analyses on the Ozark population and found that no individuals were lost in doing so. For the Ozark National Forest, PID, or the probability that two randomly selected individuals would share the same genotype, was 3.49×10^{-10}, and the PSIB, or the probability that full siblings would have the same genotype was 6.91×10^{-4}. For the Ouachita National Forest population, PID was 1.02×10^{-9}, and the PSIB was 9.83×10^{-4}.

Population estimation and realized λ calculation

For the Ozark population, two models had a ΔAIC_c of less than ten and 98.8% of the weight (Table 3). The top two models, contained sex as a predictor of survival and capture probability. Capture probability was also influenced by an interaction of year and T or TT for the top two models. Capture probability was variable over the course of the study (Fig 3). Estimates for the number of males ranged from 95-101 and number of females ranged from 88-119 over the course of the study (Table 4). Survival (S) was estimated at 0.56 (CI: 0.43-0.69) for males and 0.82 (CI: 0.62-0.93) for females over the course of the study, with γ at 0.29 (CI: 0.15-0.50). The Pradel Robust model allows for an estimate of ϕ, which indicates how likely it is that an individual will be present in the study area during the next time step. The top models included sex as a predictor of ϕ. For λ the predictor sometimes included sex or year, or was null. For males, ϕ was 0.46 (CI: 0.38-0.54) and 0.66 (CI: 0.56-0.75) for females. Realized λ was 1.06 (CI: 0.85-1.27) for the first time step, between 2009 and 2010 and 1.02 (CI: 0.87-1.17) for the second time step, between 2010 and 2011 for males. For females, realized λ was 1.14 (CI: 0.97-1.32) and 1.10 (CI: 0.92-1.2) respectively.

The Ouachita population did not have a definitive list of top models. Many models would not converge and no model ranked higher than 16% in weight (Table 5). Capture probability also varied over the course of the study, with wider confidence intervals than the Ozark population, likely due to the smaller sample size (Fig 3). Abundance averaged 27.8 and 46.1 for males and females respectively over the course of the study (Table 4). Confidence interval was so large that the survival estimate (S) of 0.95 (CI: 0.00-1.00) and γ estimate of 0.45 (CI: 0.06-0.92) are not useful. There were similar challenges with the Pradel Robust model for the Ouachita population, with no model having a weight higher than 12%. Confidence intervals were extremely large, so estimates of realized λ and ϕ should be interpreted very carefully. ϕ was 0.77 (CI: 0.30-0.96) for males and 0.85 (CI: 0.23-0.99) for females. Realized λ was 1.23 (CI: 0.62-1.85) for males in the first time step, 2006-2007, and 1.09 (CI: 0.63-1.55) for the second time step, 2007-2008. For females, realized λ was 1.13 (CI: 0.47-1.79) and 0.98 (0.00-1.00) respectively. The second estimate has such large confidence intervals that it should not be used.

Density

Multiple year--In both study areas, when we ran multiple year models, the site-specific behavior response model (bk), which also included session as a predictor of g_0 and σ was the top model for both sexes. The second most highly ranked model also incorporated a density by year response. Ouachita male density was 4.2-4.5/100km^2 and female density was 10.0-11.4/100km^2 over the course of the study (Fig 4, Table 6), which is comparable to the estimates from 1989. Male density in the region we sampled in the Ozark National Forest was estimated at 7.1-10.0 bears per 100 km^2 (Fig 4, Table 6), which is comparable to the individual year models. However, for females, density was estimated at 13.3-18.3 per 100 km^2 (Fig 4, Table 6).

Regional Density-- For both males and females, the models that included forest cover at the 1.1 km scale had much higher weight than both the null and other habitat covariate models (Table 7). The top model also contained road density as a predictor of bear density. There was a positive association with forest cover (males: β=6.5, CI: 1.2-11.7, females β=5.8, CI: 1.8-9.8). There was a negative association with road density (males: β=-0.5, CI: -1.3-0.3, females: β=-0.5, CI: -1.2-0.2), but the confidence interval crosses zero so this is not significant.

DISCUSSION

The reintroduction of black bears into the Interior Highlands of Arkansas has been one of the most successful reintroductions of carnivores on record, with over 2500 bears estimated to live in the region (Smith and Clark 1994). However, there has been concern that the increase in harvest since baiting on private land was permitted in 2000 would not be sustainable. Here we sought to provide estimates of population size and density that would better inform managers as they make decisions about bear harvest in the region of study.

In the Ouachitas, density of ~14 bears/100 km^2 was comparable to estimates done in 1989. For the Ozarks, the density of ~25 bears/100 km^2 exceeded that of the Ouachitas and the previous 1989 estimates for the Ozarks. Caution must be taken in interpreting these comparisons because Smith and Clark (1994) used a different method of density estimation than we did and while they did not include cubs-of-the-year in their density estimates, we may have had cubs-of-the-year included in our estimates. The Ouachita estimates were lower than the White River region of Arkansas (25/100 km^2), but estimates from the Ozarks were comparable (Clark et al. 2010). Both estimates fall within the range (10-46/100 km^2) reported from a series of wildlife management units in Ontario and two sites within South Carolina (4.6 and 33.9/100 km^2), where authors also employed the SECR method of estimation (Obbard et al. 2010, Drewry et al. 2013).

Use of the secr package provides a more clearly defined density estimate, without the concern for closure violations or estimation of area sampled (Efford 2004, Borchers and Efford 2008, Obbard et al. 2010). Spatial information is incorporated into the density estimate, which is based on capture probability and spatial extent (Efford 2004, Borchers and Efford 2008, Obbard et al. 2010).

Growth rate or realized λ was inestimable for the Ouachitas. Confidence intervals were large for realized λ, but estimates were above 1 in the Ozarks suggesting that this population may be continuing to grow in size. However, the confidence interval included values below one, so definitive conclusions population growth cannot be made. Additionally, mark-recapture data for the Ouachitas were gathered prior to the largest harvest and Ozark data overlapped the largest year of harvest. Future monitoring will be necessary to assess impacts of the increased harvest.

While there was not enough power to detect differences in survival by sex in the Ouachitas, survival of females, 0.82, was higher than that of males, 0.56, in the Ozarks. Hair snare work does not allow for differentiation by age, so some of the disparity in survival by sex may be due to age since dispersing juvenile males in particular have a lower survival than both juvenile females and adult bears (Schwartz and Franzmann 1992, Beringer et al. 1998, Obbard and Howe 2010). Adult females typically have higher survival rates than males, which also could contribute to the difference (Hellgren and Vaughan 1989, Schwartz and Franzmann 1992, Beringer et al. 1998, Koehler and Pierce 2005). Sex had an impact on all model types and influenced estimates of capture probability (p), detection probability (g_0), spatial extent (σ), density, realized growth (λ), presence at the following time step (ϕ) and survival (S). This disparity was particularly apparent in the estimates of density from the secr models.

A difference in sex ratio was detected in the number of samples collected in the Ouachitas. Additionally, a significant difference in density by sex was also detected by Clark and Smith (1994) and in this study for the Ouachita population. However, they did not detect a difference in density by sex in the Ozarks nor did our individual year models, aside from that of 2011. We detected a discrepancy in density by sex for the Ozarks, though confidence intervals overlap for two of the three years of sampling. Our findings could represent a true difference in density by sex. However, detectability differs by sex in grizzly bears (Boulanger et al. 2008) and could potentially play a role here as well if males were not detected as often as females. Because males are polygynous (Rogers 1987, Schenk and Kovas 1995), population growth in black bears is limited by the number of females and their ability to produce cubs successfully, so the discrepancy is not cause for concern in this case.

Our data provide strong evidence that gathering data over multiple years for mark-recapture estimates of black bears would be advantageous whenever possible. Year or session was an important predictor in both the Robust and secr models. The middle year of in each study area had poor capture probability and a great reduction in number of samples collected. Because food availability and abundance can alter movements and distribution of black bears (Garshelis and Pelton 1981, Rogers 1987, Hellgren et al. 1991), this was likely due to differences in food availability during those years of study. In 2007 in particular there was a frost after plants had started budding, which reduced available forage and increased nuisance complaints, suggesting that bears were moving out of the study area to find food. The reduction in samples and capture probability greatly impacts the ability to model population size and density. There was not enough data for a 2007 individual year model for male density in the Ouachitas and confidence intervals are much larger for population and density estimates for both sexes that year, even within the three year models. There was variation in estimates of density and population size by year and vital rates such as survival and lambda are difficult to estimate without sufficient data. Previous studies have indicated that such yearly variation results in the need for data across multiple years to accurately estimate vital rates (Brongo et al. 2005, Harris et al. 2011). Our findings also indicate the need for multi-year studies to adequately assess population size, density, and vital rates.

Regionally, the top density model included percent forest cover as a predictor. Black bears are associated with forested regions (Pelton 1982), so it is not surprising that percent forest cover was positively associated with bear density. Roads also can influence black bear distribution (Beringer et al. 1990) and top regional models for bear density in South Carolina included roads (Drewry et al. 2013). Our models support this finding, with the model containing a combination of percent forest and road density having the highest weight.

MANAGEMENT IMPLICATIONS

Both black bear populations in the Interior Highlands of Arkansas have densities comparable to or above the estimates from the late 1980’s. However, sampling here was done during a period of high harvest levels and a subsequent quota was instituted. To assess the impact of these harvest levels, population size should be reassessed in ~5 years to determine whether maintaining harvest at the level of the new quotas is impacting the population. This study will provide a strong basis for comparison for such future estimates. If possible, a multiple-year study should be undertaken to estimate the density of bears present to account for natural variation by year.

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Table 1. Success of hair snares and identification of individual black bears for trapping done at Ozark and Ouachita National Forests from 2006-2011.

Location	Year	Trap(s)			Samples		
		visited (%)	success[a] (%)	freq.[b] (%)	collected	extracted	identified (%)
Ouachitas	2006	75.0	37.5	34.8	138	123	73
	2007	46.0	17.6	26.4	80	74	85
	2008	66.7	37	35.6	440	321	80
Ozarks	2009	93.8	58.8	35.9	730	694	94
	2010	76.0	44.3	33.9	669	628	76
	2011	91.5	63.4	39.6	1491	1133	78

[a] Trap success was calculated as number of traps hit/number of traps available (Tredick and Vaughan 2009).

[b] Trap frequency indicates the average frequency with which bears visited traps within the year (i.e. number of times detected/5 detection opportunities).

Table 2. Number of bears detected at each site per year and overall. Samples were collected in the Interior Highlands of Arkansas from 2006-2011.

Site	Year	Male	Female	Total
Ouachitas	2006	20	22	42
	2007	6	22	28
	2008	27	32	59
	Overall[a]	45	54	99
Ozarks	2009	82	68	150
	2010	84	71	153
	2011	90	99	189
	Overall	165	186	351

[a] The number detected across the three years of study. Is not the same as the sum of all years because bears may have been detected in multiple years.

Table 3. Top ranking models for estimating the population of black bears in the White Rock WMA of Ozark National Forest in Arkansas using the Robust model with Huggins estimator. Models with ΔAIC over 10 are not listed. Data were collected from 2009-2011.

Model	K[a]	$\text{AIC}_c^{\,b}$	$\Delta\ \text{AIC}_c^{\,c}$	$w_i^{\,d}$	Deviance[e]
$S^f(\text{sex}^g)\ \gamma^h(.)\ p^i(\text{sex, year*}T^j)$	10	3592.9	0.00	0.667	3970.7
$S(\text{sex})\ \gamma\ (.)\ p(\text{sex, year*}TT^k)$	13	3594.4	1.43	0.326	3966.0
$S(\text{sex})\ \gamma\ (.)\ p(\text{year*}T)$	9	36.02.0	9.11	0.007	3981.9

[a] Number of parameters.
[b] Akaike Information Criterion adjusted for small sample sizes.
[c] Difference in AIC_c compared with the AIC_c smallest model.
[d] AIC_c model weight.
[e] Model deviance.
[f] survival.
[g] impact of sex (male vs. female) on survival or capture probability .
[h] temporary emigration .
[i] capture probability.
[j] linear model of influence of time.
[k] quadratic model of influence of time.

Table 4. Population estimation of black bear abundance in the White Rock WMA in the Ozark National Forest and in the Muddy Creek in the Ouachita National Forest. Data were collected from 2006-2008 in the Ouachita National Forest and from 2009-2011 in the Ozark National Forest.

Location	Year	Male			Female		
		N	SE	95% CI	N	SE	95% CI
Ouachitas	2006	28.2	7.0	9.4-47.1	33.2	8.7	8.5-57.9
	2007	17.6	9.7	0-45.0	60.0	24.8	0-124.7
	2008	37.5	8.6	12.8-62.2	45.2	9.9	16.9-73.5
Ozark	2009	95.3	4.5	86.5-104.2	88.3	6.2	76.100.5
	2010	101.2	5.6	90.1-112.0	96.9	7.7	81.8-112.0
	2011	97.4	3.5	90.6-104.2	118.8	5.8	107.3-130.3

Table 5. Top ten models, comprising 73% of the weight, for estimating the population of black bears in the Muddy Creek are of the Ouachita National Forest in Arkansas using the Robust model with Huggins estimator. Data was gathered from 2006-2008.

Model	K[a]	AIC_c[b]	Δ AIC_c[c]	w_i[d]	Deviance[e]
S[f](.) γ[g] (.) p[h](year) c[i](.)	6	891.9	0.00	0.16	784.0
S(.) γ (.) p(T[j]*year)	8	893.1	1.19	0.09	780.9
S(.) γ (.) p(T, year)	6	893.1	1.20	0.09	785.2
S(.) γ (.) p(sex[k]*year)	9	893.2	1.25	0.08	778.8
S(.) γ (.) p(sex, year)	7	893.9	2.00	0.06	783.8
S(.) γ (.) p(T*year, sex)	9	894.0	2.11	0.06	779.6
S(.) γ (.) p(sex, T, year)	7	894.0	2.11	0.06	784.0
S(.) γ (.) p(T, year)	7	894.0	2.13	0.05	784.0
S(.) γ (.) p(TT[l],year)	7	894.6	2.68	0.04	784.5
S(.) γ (.) p(year) c(year)	8	894.8	2.87	0.04	782.6

[a] Number of parameters.
[b] Akaike Information Criterion adjusted for small sample sizes.
[c] Difference in AIC_c compared with the AIC_c smallest model.
[d] AIC_c model weight.
[e] Model deviance.
[f] survival.
[g] temporary emigration.
[h] capture probability.
[i] recapture probability.
[j] linear model of influence of time.
[k] impact of sex (male vs. female) on capture or recapture probability.
[l] quadratic model of influence of time.

Table 6. Density estimation of black bear abundance in the White Rock WMA in the Ozark National Forest and in the Muddy Creek in the Ouachita National Forest. Data were collected from 2006-2008 in the Ouachita National Forest and from 2009-2011 in the Ozark National Forest. Numbers are in bears per 100km^2.

Location	Year	Male			Female		
		Density	SE	95% CI	Density	SE	CI
Ouachitas	2006	4.2	1.1	2.5-7.0	11.4	3.8	6.0-21.7
	2007	4.5	3.5	1.2-17.3	10.0	5.2	3.8-26.2
	2008	4.1	1.1	2.5-6.9	10.2	2.4	6.4-16.2
Ozarks	2009	9.7	1.5	7.1-13.1	18.3	5.1	10.7-31.4
	2010	10.0	1.6	7.3-13.7	13.3	2.5	9.3-19.1
	2011	7.1	1.1	5.3-9.6	17.8	2.7	13.2-24.0

Table 7. Model selection results for regional density estimation of black bear abundance in the Interior Highlands of Arkansas. Data were gathered from 2006-2011. The base model contained behavior as a predictor of probability of detection (g_0) and session as a predictor of g_0 and spatial extent (σ). K is the number of parameters.

Model and parameters	K^a	$AIC_c{}^b$	$\Delta AIC_c{}^c$	$w_i{}^d$
Males				
$\hat{D}$ (forest 1.1 km, road 5 km)	15	3961.4	0.000	0.580
$\hat{D}$ (forest 1.1 km)	16	3962.0	0.649	0.420
Females				
$\hat{D}$ (forest 1.1 km, road 5 km)	15	3127.4	0.000	0.504
$\hat{D}$ (forest 1.1 km)	16	3127.9	0.035	0.496

[a] Number of parameters.
[b] Akaike Information Criterion adjusted for small sample sizes.
[c] Difference in AIC_c compared with the AIC_c smallest model.
[d] AIC_c model weight.
[e] Model deviance.

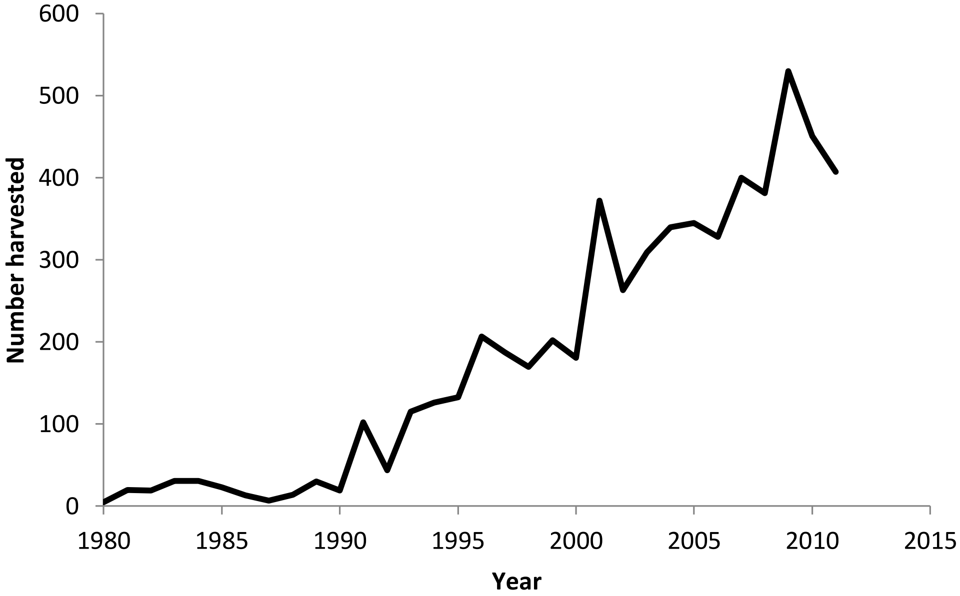

Figure 1. Number of black bears harvested in Arkansas since 1980. Harvest of black bears in the Delta region began in 2001.

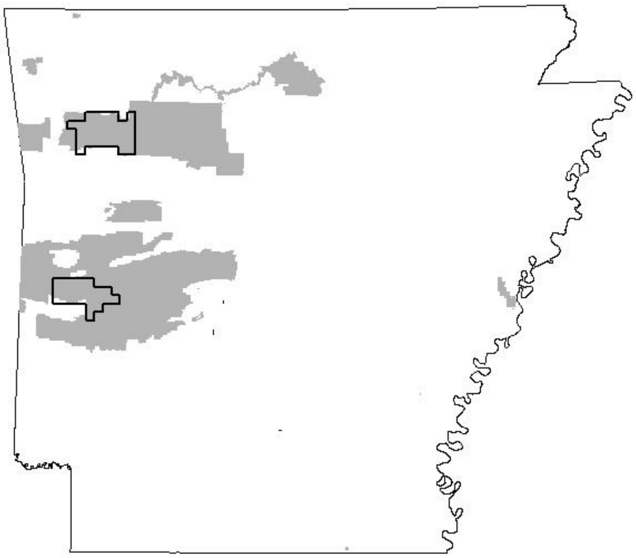

Figure 2. Locations of study sites for bear hair snares in Arkansas. The northern site is in the Ozark National Forest and the southern site is in the Ouachita National Forest. Gray areas denote public lands, including forests and national parks.

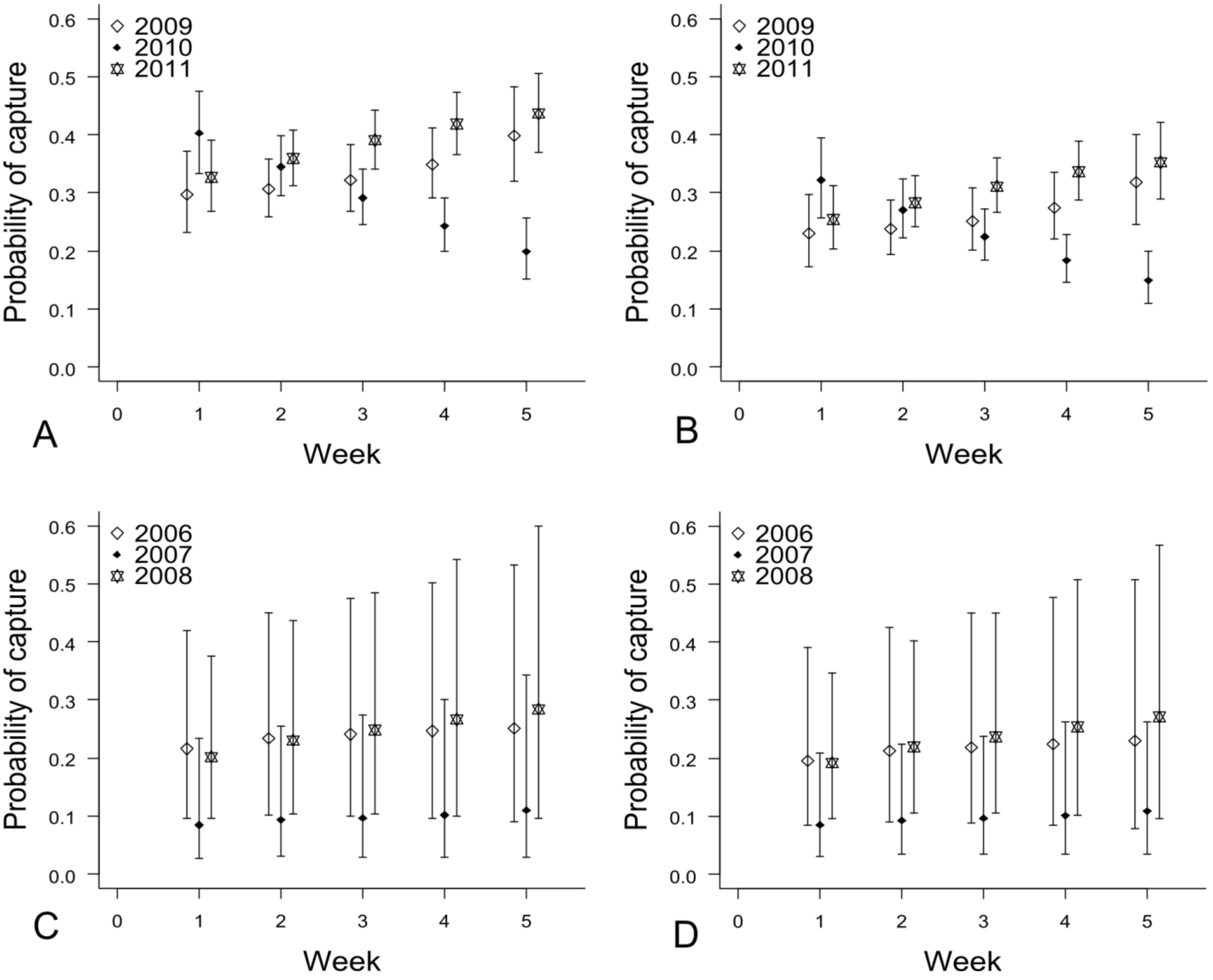

Figure 3. Capture probabilities over the three years of study of black bears in the Ozark (A and B) and Ouachita (C and D) National Forests of Arkansas, estimated through the Robust Model in program MARK with error bars representing CI. Data was gathered from 2006-2011. Males (A and C) were separate from females (B and D) for estimates.

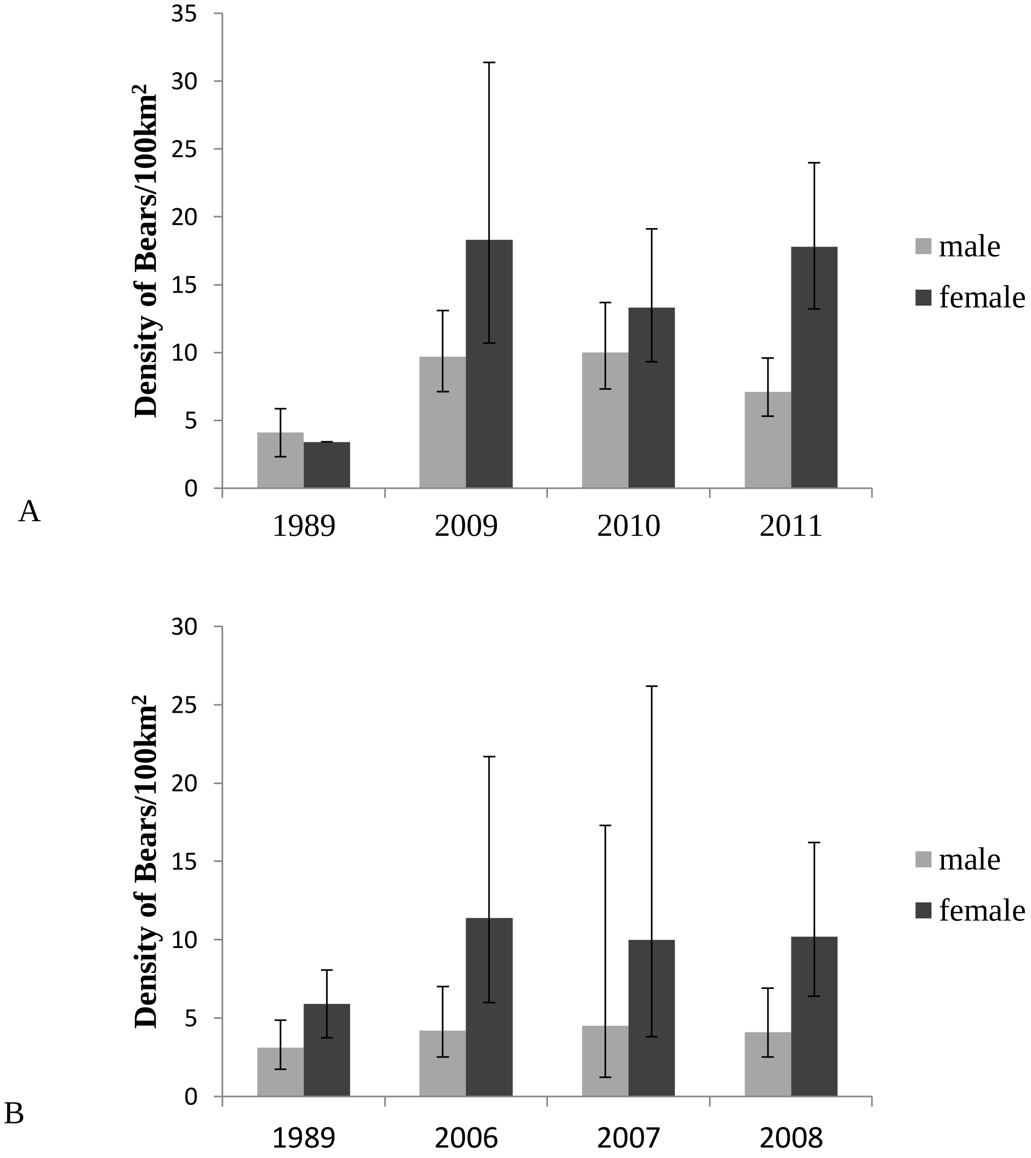

Figure 4. Comparative densities of black bears in the Ozark (A) and Ouachita (B) National Forests. Current estimates from 2006-2011 are compared to those from Clark and Smith (1994). Density is in bears per 100 km^2 with error bars representing the 95% confidence interval.

Explanation of collaboration on structure component of dissertation

The component of this dissertation that covers black bear population structure and multiplex techniques is the result of a close collaboration with Kaitlyn Faries and Lori Eggert at the University of Missouri. In 2007, Kaitlyn and Lori began collecting baseline data on the presence of black bears in Missouri using hair snares, with the intent to determine how genetics of Missouri bears may have been influenced by reintroduction and expansion of other black bear populations in the region. I began my PhD work in 2008 and asked for their guidance in learning the genetic techniques required to genotype bears for mark-recapture study. Kaitlyn trained me on DNA extraction, using the polymerase chain reaction (PCR) to amplify microsatellite loci, and interpretation of microsatellite analysis. We then proceeded to work together to optimize one locus (G10P), establish and optimize a multilocus amplification protocol (multiplex), and construct a sexing primer that could be incorporated into the multiplex. Kaitlyn and Lori had already obtained data from Joe Clark, Don White Jr., and Minnesota and Manitoba samples from Jeff Beringer of the Missouri Department of Conservation. We randomly selected 40 bears from my first field season to add to the data set looking at structure of bears in the region. Kaitlyn and I ran analyses on genetic diversity, genetic distance, and linkage disequilibrium. Lori worked with us to run analyses in program Structure and to assist us in the interpretation of the analyses. Kaitlyn and I both contributed to writing for each paper, with Lori making revisions and other authors offering edits prior to submission. Because the analysis of population structure in the region was originally Kaitlyn and Lori's idea, Kaitlyn is listed as first author on that paper. Because we designed, tested and optimized the multiplex to handle the large amount of samples gathered in my work, I was listed as first author on that paper. As such, the methods paper follows and the population structure paper may be found in the Journal of Mammalogy (Faries et al. 2013).

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Faries, K. M., T. V. Kristensen, J. J. Beringer, J. D. Clark, D. White, and L. S. Eggert. 2013. Origins and genetic structure of black bears in the Interior Highlands of North America. Journal of Mammalogy 94:369-377.

Optimized methods for multiplex genotyping analysis of hair samples for American black bears (*Ursus americanus*)

Abstract

Noninvasive sampling has revolutionized the study of species that are difficult or dangerous to study using traditional methods. Early studies were often confined to small populations as genotyping large numbers of samples was prohibitively costly and labor intensive. Here we describe optimized protocols designed to reduce the costs and effort required for microsatellite genotyping and sex determination for American black bears (*Ursus americanus*). We redesigned primers for six microsatellite loci, designed novel primers for the amelogenin gene for genetic determination of sex, and optimized conditions for a nine-locus multiplex PCR. Our methods will enable researchers to include larger sample sizes in studies of black bears, providing data in a timely fashion that can be used to inform population management.

Keywords

non-invasive, microsatellites, multiplex PCR, genetic sexing, hair extractions

Introduction

Noninvasive genetic sampling has revolutionized the study of species that are difficult or dangerous to study using traditional methods [1]. For species such as mountain lions (*Puma concolor*) [2], wolves [3], forest elephants (*Loxodonta cyclotis*)[4] and brown bears (*Ursus arctos*) [5], genotypes derived from noninvasively collected samples have been used for estimating population sizes and demography, data essential for effective management plans.

Such studies have become commonplace as a means of assessing black (*Ursus americanus*) and brown bear (*U. arctos*) population sizes [5, 6-9]. However, sampling high density bear populations or sampling over a large area may result in the collection of hundreds to thousands of samples in a single season [5,8-11]. Analysis of such large sample sizes can be prohibitively costly and labor intensive. For example, Tredick et al. [11] found that each bear sample cost on average $50 USD to send out for analysis, while Stenglein et al. [3] found that labor and supply costs for genotyping wolf samples in their lab varied from $76 USD/genotype in 2007 to $31 USD/genotype in 2008.

Noninvasive genetic surveys can provide rigorous estimates of bear population sizes across broad areas, which can be essential in determination of management policies [5]. Having sufficient numbers of reliable loci available for identification is crucial to such estimates [12], but most studies, particularly those for black bears, have limited financial resources available and subsampling is often employed to stay within budget [11, 13]. However, subsampling may result in a negative bias in estimates [11]. An alternative to subsampling would be further development of genetic techniques that reduce the effort and cost of genotyping large numbers of samples [12].

During 2009, the first of a multi-year study of American black bears (*Ursus americanus*) in the Ozark National Forest, Arkansas, we collected >700 hair samples from hair snags. Here we describe the multiplex genotyping methods we developed to reduce the effort and costs of our study. We used low-cost DNA extraction methods, redesigned and optimized primers in order to amplify eight microsatellite loci, developed new species-specific sexing primers to coamplify along with the microsatellites, and optimized methods for amplifying all loci in a single reaction.

Methods

Following the methods of Woods et al. [14], we used baited barbed wire hair snares and a systematic grid design to sample across the study area. Hair samples were stored in brown envelopes and kept dry prior to DNA extraction.

To minimize contamination, all extractions were conducted using dedicated equipment and supplies in a separate laboratory from the one in which DNA was amplified using the polymerase chain reaction (PCR). To extract DNA, we selected 5-10 hairs collected from a single barb and used flame-sterilized scissors to cut the hair shafts near the follicle. Using sterile forceps, we placed the follicles for each sample in 1.5 ml microcentrifuge tubes, added 250 µl InstaGene Matrix (a Chelex–based resin developed for DNA purification; BioRad, Hercules, CA), vortexed 10-15 sec, incubated overnight at 56°C, vortexed again, boiled for 15 min, and centrifuged at 10,000 rpm for 3 min. We then assembled the extracts into 96 well plates, using 50 µl aliquots of supernatant from each extract as amplification template.

We selected eight microsatellite loci that have been used in bear studies: G1A, G1D, G10B, G10C, G10J, G10L, G10M, G10P [15-17]. For six loci (Table 1), we redesigned one or both primers to amplify less of the flanking region to reduce the size of the amplified fragment, as smaller fragments amplify more readily from the degraded DNA found in hair extracts [18], and to facilitate multiplex PCR. All primers were optimized at 56°C for multiplexing, although individually they have higher annealing temperatures (Table 1).

Although genetic sexing methods have been described for ursids [14, 18-22], none consistently provided correct results when tested on our samples of known sex American black bears. Using published sequences of black bears (Accession # AY171040, AY171041, AY171047, Carmichael et al. *unpublished*), we designed primers to amplify the X- and Ychromosome copies of the amelogenin gene, which differ in size by 54 bp. Although amplification products were detectable in an agarose gel, we included this locus in the multiplexed PCR to reduce effort.

Multiplexed reactions were performed in 12.5 µl volumes using Qiagen Multiplex PCR kits (Qiagen Inc., Valencia, CA). Each reaction included 6.25 µl master mix, 0.1 µM labeled and unlabeled microsatellite primers, 0.05 µM labeled and unlabeled sexing primers,1.0 µl 10X BSA, and 1.5 µl extracted DNA. The PCR profile was 95°C for 15 min followed by 45 cycles of 94°C for 30 sec, 56°C for 90 sec and 72°C for 60 sec. A final cycle of 60°C for 30 min was added. Amplification products were diluted 1:20 for genotyping on the Applied Biosystems 3730 DNA Analyzer at the University of Missouri DNA Core Facility. Genotypes were scored using internal lane standards (Genescan LIZ 600) in GENE MARKER® (Soft Genetics).

Genotyping was attempted up to five times for each sample in order to confirm heterozygous genotypes twice and homozygous genotypes (including samples in which the sexing marker was called as female) three times. We analyzed 25 randomly chosen unique genotypes from our study in GENEPOP [23] to test for linkage disequilibrium and deviations from expectations under Hardy-Weinberg equilibrium (HWE), and to calculate error rates, allelic diversity, and heterozygosity values.

To facilitate comparisons with previous estimates, we calculated costs for genotyping on a per sample basis, including supplies and labor, for both single locus PCR and our multiplex PCR. Costs for fragment analysis of the single locus PCRs were estimated assuming that all loci for each sample would be combined for analysis in a single lane.

Results

We found no evidence for linkage disequilibrium or for significant deviations from expectations under HWE. The average number of alleles for eight loci was 7.0 (± 1.8 SD, range 5-10) and the mean observed heterozygosity was 0.795 (± 0.062 SD, range 0.720-0.880, Table 1). Our sample included 14 males and 11 females.

Each sample was genotyped on average 3.52 times to meet our genotyping criteria. The observed rate of allelic dropout was 0.037 (± 0.010 SD, range 0.023-0.046); the observed rate of false alleles was 0.058 (± 0.032 SD, range 0.011-0.114); and the rate of PCR failure was 0.017 (± 0.009 SD, range 0.000-0.023, Table 2).

We estimate that extraction times for our method and one of the most commonly used methods (DNeasy Blood and Tissue extraction kit, Qiagen) are approximately equal, while the cost of the extraction for our method is ¼ that of the kit. Costs are also approximately equal for each round of single-locus or multiplex PCR, but at four repetitions for each locus we estimate the total cost of PCR and labor for each sample using single-locus PCR to be approximately 8.5 times that of multiplex PCR. We estimate that the costs for single-locus genotyping would have been approximately $89.00 USD per sample. Our actual costs were approximately $34.00 USD per sample, or 38% of the estimated cost of the single-locus method.

Discussion

The multiplex methods we have developed provided genotypes with low levels of genotyping error and high rates of amplification success. Our PCR failure rate was low (1.7% ± 0.9% SD) for our sample of 25 individuals, likely due to the fact that we were able to extract DNA from 5-10 hairs per barb. Our rate of allelic dropout (3.7% ± 1.0%SD) is lower than the rate observed by Stenglein et al. [3] for wolves (13%) and by Skrbinšek [12] for brown bears, but does not approach the extremely low levels observed by Luikart et al. [24] in their study of bighorn sheep (0.11%). Our false allele rate (5.8% ± 3.2%) is higher than that the 3% observed by Stenglein et al. [3], and is mainly driven by a relatively high rate at locus G1A. Other studies that have used this locus on black bears with the originally designed primers did not include locus specific false allele rates, thus we were not able to compare our results. We caution that results at this locus should be confirmed before inclusion in a population study.

Others have estimated that multiplexing microsatellites saves up to a third of costs of sending samples out for analysis [12]. By genotyping samples in our own lab, we realized an even higher magnitude of savings. In addition, we were able to genotype samples within a few days of their arrival in the lab, saving both shipping costs and time. We estimated that our cost per sample was $34.00 USD, similar to the costs cited by Stenglein et al. [3] for genotyping wolf samples using a multiplex microsatellite protocol. At 38% of our estimated cost for genotyping using a single-locus protocol, this represents a substantial savings. It also allows us to repeat genotypes for confirmation as needed without depleting the small amount of extracted DNA and to archive the remaining extract for future studies.

Our optimized methods will reduce the time and costs of analysis for the larger number of samples that will become commonplace in studies of wild populations of elusive species. For American black bears, they will provide important data that will assist population managers as they attempt to anticipate and reduce levels of human-wildlife conflict.

Acknowledgements

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Table 1. Microsatellite and sexing loci optimized for American black bears.

Locus	Sequence (5’ – 3’)	T_A(°C)	Label	Product Size	A	H_O	H_E	P_{HWE}
G1A[a]	F:GAGGGAGACCCTGCATACTC*	60	Pet	109-131	6	0.720	0.768	0.345
	R:GAAGCAGGACTTCAATCACTCA*							
G1D[a]	F: TTTTCCTTTAGGGGACTCCAA*	57	Vic	120-138	8	0.840	0.795	0.772
	R: ACCTAGCACCCAGCAAGGTA*							
G10B[a]	F: GCCTTTTAATGTTCTGTTGAATTTG	60	Pet	157-167	5	0.720	0.680	0.995
	R: GACAAATCACAGAAACCTCCATCC							
G10C[a]	F: AAAGCAGAAGGCCTTGATTTCCTG	60	Ned	103-119	5	0.760	0.716	0.394
	R:GGTGGACATAAACACCGAGACAGC*							
G10J[b]	F: GATCAGATATTTTCAGCTTT	57	Vic	82-106	8	0.840	0.842	0.496
	R: AACCCCTCACACTCCACTTC							
G10L[a]	F: TGATTTAATTCACATTTCCCTAGTT*	57	6-Fam	121-155	10	0.760	0.776	0.638
	R: AGAAACCTACCCATGCGATAA*							
G10M[a,b]	F: TTCCCCTCATCGTAGGTTGTA	57	Ned	191-205	6	0.880	0.795	0.472
	R: AATAATTTAAGTGCATCCCAGG*							
G10P[a,b]	F: AGTTTTACATAGGAGGAAGAAA*	57	6-Fam	162-178	8	0.840	0.775	0612
	R: TCATGAGGGGAAATACTCTGAA							
AmelFrag	F: AACCTCCCTCTGCCTGCCCA	65	Vic	X band – 231				
	R: CCGCTTGGTCTTGTCTGTTG			Y band - 177				

[a] from Paetkau et al. 1995; [b]from Paetkau and Strobeck 1995; *designates primers redesigned for this study; T_A = locus specific annealing temperature if amplified alone; A= number of alleles detected; H_O = observed heterozygosity; H_E = heterozygosity expected under Hardy-Weinberg equilibrium (HWE); P_{HWE} = probability that locus conforms to heterozygosity expectations under HWE. Values of A, H_O, H_E and P_{HWE} based on 25 samples from the Ozark National Forest.

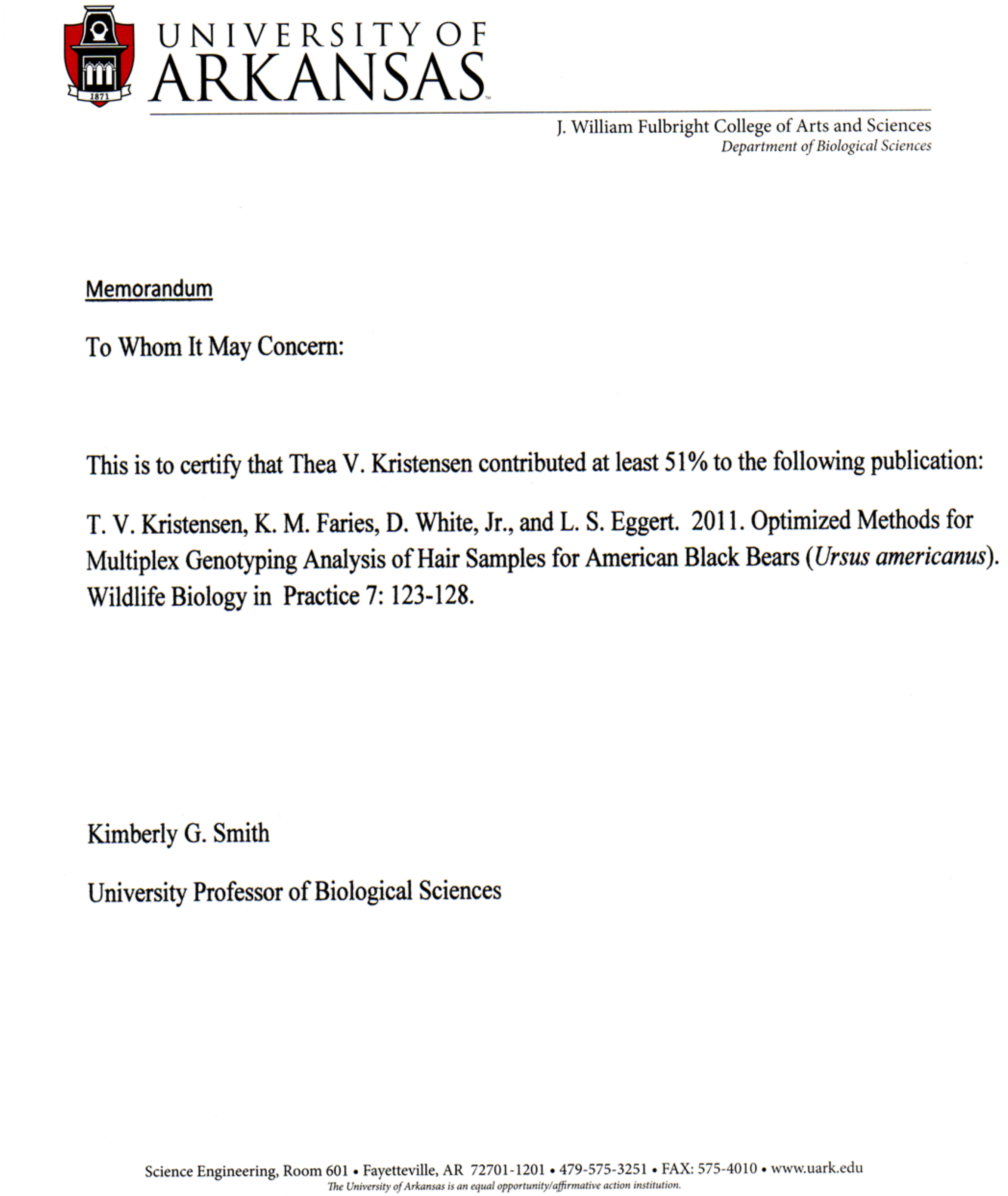
Table 2. Genotyping error rates for 25 black bears from the 2009 sampling period.

Locus	Allelic dropout	False allele	PCR failure
G1A	0.045	0.114	0.011
G1D	0.034	0.079	0.000
G10B	0.023	0.023	0.011
G10C	0.034	0.057	0.023
G10J	0.023	0.045	0.023
G10L	0.045	0.067	0.022
G10M	0.045	0.011	0.023
G10P	0.046	0.069	0.023
Average	0.037	0.058	0.017
St dev	0.010	0.032	0.009

Appendix A

Kristensen, T. V., K. M. Faries, D. White, and L. S. Eggert. 2011. Optimized methods for high-throughput analysis of hair samples for American black bears (*Ursus americanus*). Wildlife Biology in Practice 7:123-128.

Appendix B



UNIVERSITY OF ARKANSAS
J. William Fulbright College of Arts and Sciences
Department of Biological Sciences

Memorandum

To Whom It May Concern:

This is to certify that Thea V. Kristensen contributed at least 51% to the following publication:

T. V. Kristensen, K. M. Faries, D. White, Jr., and L. S. Eggert. 2011. Optimized Methods for Multiplex Genotyping Analysis of Hair Samples for American Black Bears (*Ursus americanus*). Wildlife Biology in Practice 7: 123-128.

Kimberly G. Smith

University Professor of Biological Sciences

Science Engineering, Room 601 • Fayetteville, AR 72701-1201 • 479-575-3251 • FAX: 575-4010 • www.uark.edu

Black bear (*Ursus americanus*) dispersal in expanding populations

Thea V. Kristensen, Emily E. Puckett, John Hast, Colin Carpenter, Jaime L. Sajecki, Jerrold L. Belant, Jeffery Berringer, Myron Means, John Cox, Ronald A. Van Den Bussche, Lori S. Eggert, Don White Jr., Kimberly G. Smith

ABSTRACT

Dispersal influences gene flow, population size, and population dynamics, making consideration of dispersal essential to understanding the ecology of a species. Both brown bears (*Ursus arctos*) and American black bears (*Ursus americanus*) exhibit female philopatry and male dispersal. However, recent studies have found deviations from this pattern including reduced male dispersal, and/or low or no spatial structuring of relatedness in female-female pairs, with deviations from the expected pattern potentially due to density, mate competition, and resource availability. Expanding populations may also diverge from the more typical pattern of high relatedness of females in close proximity because females disperse over long distances. Some American black bear populations have expanded their ranges over the past 3 decades in response to decreased persecution, forest regrowth, and direct species protection. In this study, expanding populations in the Interior Highlands and Cumberland Plateau regions and their respective source populations were explored. For the Interior Highlands, we included samples from expanding populations in Missouri and Oklahoma and the potential source populations from two locations in Arkansas; the samples from the Cumberland Plateau included two localities in Kentucky and the potential source populations included those from Virginia, West Virginia and the Smoky Mountains in Tennessee. Bears from Arkansas, Oklahoma, and Missouri were genotyped at 15 microsatellite loci, while those from Virginia, Kentucky, West Virginia and Tennessee were genotyped at 20 loci. Relatedness (r) for all pairs was determined using MLRelate. We then determined how relatedness varied in space for each locality for female-female, female-male, male-male, and all dyads. We expected source populations to more closely follow the pattern of female philopatry and male dispersal, but that the expanding populations would potentially show lower levels of relatedness among females in close proximity and that male-male pairs would have higher levels of relatedness than source populations. Average relatedness of female-female dyads declined significantly up through about 30 km between pairs. All pairs and female-male dyads displayed a similar pattern, though with a less-pronounced decline. Males in source populations did not differ in relatedness across space. However, this was not the case in some expanding populations where male-male dyads displayed a decline in relatedness with distance. Female-female dyads in expanding populations also had higher levels of closely related dyads than those in source populations. With many American black bear populations expanding in many regions, exploration of such deviations from strict male dispersal and female philopatry in expanding populations may have important management implications.

KEY WORDS dispersal, relatedness, population expansion, *Ursus americanus*

Dispersal is clearly tied to population structuring because it can mediate gene flow, impact abundance, and influence population dynamics, all of which make it central to understanding of ecology of a species (Hestbeck 1981, Bohonak 1999, Dieckmann et al. 1999). Mate and resource competition (Clark 1978, Moore and Ali 1984), inbreeding avoidance, and kin cooperation are hypothesized to explain patterns of sex-biased dispersal (Greenwood 1980, Dobson 1982, Clobert et al. 2001, Lawson Handley and Perrin 2007). In mammals, males tend to exhibit dispersal while females are often philopatric (Greenwood 1980, Dobson 1982), though different patterns and greater levels of complexity within those patterns may occur (Lawson Handley and Perrin 2007). Type of mating system also influences dispersal patterns because it impacts costs of mate competition and inbreeding, with effects varying by sex (Dobson 1982, Waser et al. 1986, Lawson Handley and Perrin 2007).

A variety of studies, using both genetic and field-based techniques have elucidated dispersal behaviors in American black bears (*Ursus americanus*). Radio-collared individuals in Minnesota displayed the expected pattern of male dispersal and female philopatry (Rogers 1987). Yearlings stayed within the mother's home range and males dispersed before sexual maturity at roughly two years of age, while females expanded their yearling range, either overlapping or adjacent to their mother's range (Rogers 1987). Furthermore genetically-based studies found that female black bears settle near their mothers, creating a pattern in which proximity in space indicates higher levels of relatedness for females (Onorato et al. 2004, Moyer et al. 2006, Costello et al. 2008, Costello 2010). However, this pattern is not the rule and there is variation in degrees of philopatry and dispersal in different populations (Schenk et al. 1998, Costello et al. 2008, Roy et al. 2012).

Despite extensive overlap of home ranges of females in northern Ontario, there was no relationship between proximity and relatedness in females, possibly due to high population density or patterns of food distribution (Schenk et al. 1998). While bears did exhibit the pattern of male dispersal and female philopatry in New Mexico, females in close proximity exhibited less relatedness than expected while males in close proximity were more closely related than expected in areas of low density (Costello et al. 2008). The low density potentially reduced competition for males, allowing them to settle near more closely related individuals (Costello et al. 2008).

In contrast, in low density areas of southwestern Québec, relatedness decreased with distance in females but was not structured for males (Roy et al. 2012). Females at high density did not display genetic structure, potentially due to a reduction of kin association with increased competition at high density (West et al. 2001, Roy et al. 2012). Males exhibited local genetic structure at high density, which the authors explained by suggesting reduced dispersal distances and delayed dispersal in subadult males at the high density (Roy et al. 2012).

Thus, literature on black bear dispersal reveals a pattern of male dispersal and female philopatry, but variations in this pattern occur in multiple systems without a clear causal mechanism. Additionally, brown bears have deviated from expected dispersal patterns in cases of expanding populations (Jerina and Adamic 2008), suggesting the possibility that additional complexity may also be present in dispersal of black bears in expanding populations, like those in the Interior Highlands and in Kentucky. A variety of factors could influence dispersal of bears in these expanding populations including differences in density, levels of competition, and food availability. Because dispersal has implications for population characteristics like sex ratio and age structure, patterns of dispersal may influence the success and rapidity with which populations are able to expand.

Historically, black bears were presumed to have been extirpated from the majority of the Interior Highlands by the early 1900s (Smith et al. 1991, Smith and Clark 1994). Black bears from Minnesota and Manitoba were reintroduced to the Ozark and Ouachita National Forests in Arkansas from 1958-1968 (Smith et al. 1991, Smith and Clark 1994). The population has grown to over 2500 bears (Smith and Clark 1994) and expanded into Oklahoma and Missouri (Titus et al. 1993, Bales et al. 2005, Gardner-Santana 2007, Brown 2008, MDC 2008, Faries et al. 2013). The Kentucky population of black bears was also extirpated by the early 1900’s (Barbour and

W.H. 1974, Unger 2007, Frary 2008). In the late 1980's black bears were again detected in the eastern part of the state and have continued to expand their range since (Unger 2007, Frary 2008, Hast 2010). Fourteen individuals were also translocated to the Big South Fork region from the Great Smoky Mountains in Tennessee (Eastridge and Clark 2001, Clark et al. 2002). Virginia and West Virginia are likely the source of the bears in the Pine Mountain region of Kentucky and the reintroduced bears from the Great Smoky Mountain National Park are the likely source of the majority of the bears in the Big South Fork region (Hast 2010).

Here, we sought to examine patterns of dispersal and philopatry of black bears in expanding populations and in their corresponding source populations in the Interior Highlands and Southern Appalachians. We did this by looking at patterns of relatedness among different dyad types (all, female-female, male-male, and female-male) in space. We hypothesized that source populations would follow expected patterns of male dispersal and female philopatry, while expanding populations, particularly recent expansions, would have deviations from this pattern. This type of knowledge could complement population estimators, allowing managers to make more informed decisions about allowing and setting limits for a harvest in newly-established populations.

STUDY SITES

Interior Highlands

Samples came from Ouachita and Ozark National Forests in the Interior Highlands, USA (Fig. 1). The Ouachita National Forest is primarily made up of shortleaf pine (*Pinus echinata*) and mixed pine-hardwood, with low to high mountain ridges running east to west and wide valleys (USDA 1999). Elevations range from 90- 792 m (USDA 1999). Land in this area is primarily forest, with few inholdings. In contrast, the Ozark National Forest has many inholdings (Clark 1991). The elevation ranges from 90-850 m (USDA 1999). Mountains and ridges are separated by narrow valleys throughout the Ozark National Forest, which is predominantly oak-hickory forest (USDA 1999). Both areas have been and continue to be exposed to logging efforts (USDA 1999).

Southern Appalachian Mountains

The areas sampled in Kentucky are primarily composed of horizontal ridge tops with steep slopes and deep, narrow valleys with rivers and streams (Kleber 1992, Leopold et al. 1998). Sandstone, siltstone, and shale with interspersed beds of coal are the predominant sediment types (Wharton and Barbour 1973, Leopold et al. 1998, Ulack et al. 1998). Forests are hardwood and were heavily logged between 1880 and 1920 (Braun 1950, Overstreet 1989).

Samples from Tennessee came from the Great Smoky National Park (GSMNP). In GSMNP, steep ridges extend outward from main ridges that are separated by narrow valleys (King and Stupka 1950, Laufenberg 2010). Land bordering the GSMNP is privately owned and developed (Laufenberg 2010). Elevations range from 270 to 2,024 m (Laufenberg 2010). Forest composition varies by elevation, with low elevations predominated by hardwood and high elevations predominated by spruce and fir species (King and Stupka 1950).

Virginia samples were from the southwest corner of the state (Hast 2010). This area is highly fragmented by private land (Olfenbuttel 2005). Ridges in the area are primarily National Forest land and the valleys in between are primarily used for agricultural purposes (Bridges 2005, Olfenbuttel 2005). Elevation ranges from 480-1360 m (Bridges 2005, Olfenbuttel 2005, Kozak 1970). Oaks are the dominant tree species (Higgins 1997, Olfenbuttel 2005).

The area in West Virginia is characterized by hardwood forests (Strausbaugh and Core 1978). Northeast-southwest ridges are nearly parallel and are separated by gorges formed by erosion (Adams et al. 2010). Elevation ranges from 73 to 1524 m (Strausbaugh and Core 1978).

METHODS

Sample acquisition and genotyping

Interior Highlands--Samples from the Arkansas Ozark Mountains (OZ), Arkansas Ouachita Mountains (OU) and Missouri (MO) were from hair snare studies conducted in 2008-2011 (Kristensen et al. In Preparation), 2006-2008 (Kristensen et al. In Preparation), and 2011-2012 respectively (Wilton et al. In Preparation). Oklahoma (OK) samples were from ear punches taken during live capture in 2005. Number of samples ranged from 20 to 113 (Table 1).

Southern Appalachian Mountains--Samples from the Big South Fork (BSF) population in Kentucky were collected using hair snares in 2009; the rest of the Kentucky samples were collected from the Pine Mountain (PM) region through road kill, nuisance bears, poaching cases and through live-trapping of individuals (Hast 2010). West Virginia (WV) samples were collected as part of routine population monitoring during 2009 (Hast 2010). Virginia (VA) samples were from harvested animals, road kill, hair snares, and live-captures during 2009 (Hast 2010). Tennessee (TN) samples were a subset of samples from hair snare population monitoring in the Great Smoky Mountains National Park in 2004 (Hast 2010). Eight to twenty-nine samples were gathered per location in this region (Table 1).

Microsatellite genotyping

Interior Highlands--The following 15 microsatellite loci were optimized in two multiplex panels; the first panel contained markers G1A, G10B, G10C, G1D, G10L, G10M, and G10P (Paetkau et al. 1998) with alternative primer sets detailed in Kristensen et al. (2011). The second panel contained markers G10J, G10O, G10U (Paetkau et al. 1998, Kristensen et al. 2011); UarMU05, UarMU10, UarMU23, UarMU59 (Taberlet et al. 1997); and P2H03 (Sanderlin et al. 2009). Similarly to Kristensen et al. (2011), we redesigned primer pairs to shorten the microsatellite in an effort to increase genotyping efficiency from potentially fragmented DNA obtained from hair samples (Table S1).

Multiplex PCR reactions were performed in 8µL volumes with final concentrations of 1X Multiplex PCR Master Mix (Qiagen, Valencia, CA), 0.1µM of each primer, and 15ng DNA. The thermocycler settings were: 95°C for 15 min; 40 cycles of 94°C for 30 sec, 57°C for 90 sec, 72°C for 60 sec; and 60°C for 30 min. Forward primers were fluorescently labeled with either 6FAM, VIC, NED, or PET (Table S1). Three independent PCR reactions were performed for each sample. Products were processed by an ABI 3730 DNA Analyzer at the University of Missouri DNA Core Facility (Columbia, MO) and scored using internal lane standards (Genescan LIZ 600) in GeneMarker v1.97 (SoftGenetics, State College, PA).

Samples from OU were genotyped at Wildlife Genetics International (WGI, Nelson, British Columbia, CA) at loci G1A, G10B, G10C, G1D, G10J, G10L, G10M, and G10P. A subset of 4 samples was genotyped at the same loci to calibrate datasets for comparison.

Southern Appalachian Mountains--Wildlife Genetics International determined the sex and identified bears at 20 microsatellite loci (G10B, G10H, G10J, G10P, G10M, G10L, MU59, MU23, G1D, G1A, G10X, G10U, MU50, Cxx20, Cxx110, G10C, 145P07, MU51, 144A06, and CPH9) (Ostrander et al. 1993, Fredholm and Winterø 1995, Taberlet et al. 1997, Paetkau et al. 1998c).

Dispersal analysis

We ran Coancestry (Wang 2011) to determine the best relatedness estimator; the DyadML estimator implemented in MLRelate was the least biased based on a simulation using allele frequencies observed in this study. We used MLRelate (Kalinowski et al. 2006) to determine the maximum likelihood estimate coefficient of relatedness (r), and most likely relationship (parent-offspring, full sibling, half sibling, and unrelated) for each pair within each population. Each pair of bears forms a dyad and will be referred to as such hereafter.

For the Kentucky and corresponding source populations, we used the locations where the samples were collected. For the Arkansas populations (OZ and OU) and the Missouri bears (MO) that were only detected in hair snares, we calculated home range centers using the fxi function in the secr package (Efford 2013) in program R. For the collared Missouri bears, kernel density estimates in Geospatial Modeling Environment with PLUGIN smoothing parameter were used to calculate home range centers. We calculated distances between locations of detection or home range centers for each population using the point distance analysis with a 100,000 m radius in ArcGIS 10.1(ESRI 2011) .

To examine how relatedness differed in space, we considered all bears, female-female (FF) dyads, male-male (MM) dyads, and where possible female-male (FM) dyads. For each type of dyad, we determined average and 95% confidence intervals of relatedness at the following distance categories: 1 km, 3 km, 6 km, 9 km, 15 km, 30 km, and 45 km. We also employed a Kruskal-Wallis test in program R, followed by the kruskalmc test in the pgirmess library to determine if there was a significant difference by population and, if so, where the differences lay. We ran these tests for all dyad types at the following distance categories; 3 km, 6 km, 9 km, 15 km, 30 km, and 45 km. Tennessee (TN) did not have bears over 21 km apart and hence was not used for the 30 and 45 km distance categories; Big South Fork (BSF) and the Ouachita (OU) samples did not have bears above ~30km distant and hence they were not included for the 45 km analyses. VA could not be used for comparison of female-female dyads because only two females were present in the sample.

We collapsed relationship type from MLRelate into closely related (parent-offspring, full sibling, and half sibling) and unrelated. We compared frequencies of relationship by population within a specific dyad type using the Cochran-Mantel-Haenszel χ^2 test in program R, which allowed us to account for differences by distance category. To serve as a post-hoc analysis, for any dyad type where a difference was detected by population, we compared each population to each other population again using the Cochran-Mantel-Haenszel χ^2 test. However, it should be noted that any comparisons made using these subsequent χ^2 tests should be interpreted carefully because power is reduced when so many comparisons are made. TN was not included for this analysis because it did not have all distance categories and this test will not accept missing data. VA was also not included because its sample size was so small. We also calculated relative frequencies of all relationship types from MLRelate for comparative purposes.

We ran a correlation between relatedness values and the natural log of distance from the point distance calculations for all, FF, and MM dyads using program SAS 9.2 (SAS 2008). We subsequently calculated an adjusted p-value by running a Mantel-type test (Mantel 1967), using random permutations, which accounts for the lack of independence in dyadic data, where many dyads share at one bear in common. Pairs with <1 km distance between them were excluded from this analysis to prevent usage of pre-dispersal mother-cub pairs.

RESULTS

All Kruskal-Wallis comparisons of differences in average relatedness by population, within specific distance categories (3 km, 6 km, 9 km, 15 km, 30 km, 45 km) were significant for all dyad types. Population comparisons showed that this was primarily driven by the difference of MO and VA from other populations. Missouri (MO) bears generally had higher levels of relatedness than other populations. Virginia (VA) generally had lower relatedness, but inferences are limited by the small sample size and presence of only two females in this sample.

χ^2 tests comparing frequencies of relationship types (unrelated vs. closely related) by population were significant at the 0.001 level for all dyad types. Again, the most distinctive pattern was that MO consistently had a significantly lower percentage of pairs that were unrelated than did other populations across dyad types. For instance, for all dyads, other populations had 70-91% of the pairs assigned unrelated, depending on the distance category whereas 46-64% of MO pairs were unrelated (Table 2). Patterns of differentiation in relationship frequencies did not strictly follow a dichotomy by type of population (i.e. source vs. expanding). OK, an expanding population, generally had higher relative frequency of dyads in the unrelated category than other populations, except WV, across dyad types.

Female-female dyads

Average relatedness of female-female dyads, in both source and expanding populations, declined significantly up through about 30 km between pairs (Fig. 2, 3). Relatedness was negatively correlated with ln-distance for all populations; only the BSF relationship was not significant (Table 3). For Kruskal-Wallis comparisons, for the 15 km distance and above for female-female dyads, MO had higher relatedness than source populations. Pine Mountain (PM), one of the expanding populations, and OU, one of the source populations, differed for female-

female dyads at the 6 and 30 km distances, with OU having lower relatedness than PM. Additionally, for BSF and PM, χ^2 comparisons detected a lower relative frequency of female-female dyads in the unrelated category than source populations and OK, primarily driven by higher percentages of parent-offspring pairs in BSF and both parent-offspring and full-sibling pairs in PM. As mentioned above, MO had a lower relative frequency of unrelated female-female dyads than did all other populations.

Male-male dyads

Males in source populations did not differ in relatedness across space (Fig 4). However, in some expanding populations (OK, BSF, and MO), this was not the case (Fig. 5). In the OK population, relatedness appeared to increase and then level off. In the BSF population, relatedness seemed to drop off similarly to the female-female dyads and then slightly increase. Male-male relatedness values were much higher in MO than all other populations and thus were not included in the figure; however, relatedness values followed a similar pattern to that of female-female pairs, with high relatedness in close proximity, followed by a dramatic drop and then leveling off.

Two expanding populations, MO and PM, had a significant negative correlation between relatedness and ln-distance for male-male dyads (Table 3). In contrast to the graphical representation (Fig. 4, 5), BSF had a non-significant positive correlation between these two variables (Table 3). This was due to the removal of the bears in close proximity; when they were included, there was an insignificant negative correlation. For male-male dyads, post-hoc tests following the Kruskal-Wallis tests only revealed differences between VA and all other populations, which is attributable to the small sample size.

Female-male dyads and all dyads

All dyads and female-male dyads (Fig. 6, 7, 8, 9), in both source and expanding populations, displayed a pattern of decline in relatedness with distance, though with a less-pronounced decline than female-female dyads. Relatedness declined with ln-distance for all dyads in all populations except BSF, but the decline was only significant for OU, MO, PM, and WV (Table 3). For female-male dyads in post-hoc tests following the Kruskal-Wallis, the only difference besides those between MO or VA and other populations was between OZ and TN at the 15 km distance, with TN having lower relatedness than OZ. For all dyads, TN also had lower average relatedness than OZ and OU within the 9 km and 15 km distance for all bear dyads. χ^2 comparisons again followed aforementioned patterns, with the addition that WV showed higher relative frequency of dyads in the unrelated category than other populations, aside from OK, for all dyad types.

DISCUSSION

Patterns of dispersal help elucidate the ecology of a species. Many mammalian species display the pattern of male dispersal and female philopatry (Greenwood 1980, Dobson 1982); however even within the Ursidae family there is considerable deviation from this pattern (Schenk et al. 1998, Taylor et al. 2001, Støen et al. 2006, Zhan et al. 2007, Costello et al. 2008, Jerina and Adamic 2008, Zeyl et al. 2009, Hu et al. 2010). Black bears specifically have been shown to have variation in the extent to which they display this pattern, with density and competition suggested to explain these deviations (Schenk et al. 1998, Costello et al. 2008, Roy et al. 2012). Expanding populations might also be expected to have deviations from this pattern as animals move from areas of high density to low density, change levels of competition, and need to learn how to find food in a new environment. Here, we explored how patterns of relatedness varied in space in source and expanding populations in both the Interior Highlands and in the Southern Appalachian Mountains.

When interpreting our results, there was some variation that should be considered. It is not known exactly when each of the expanding populations began the process of expansion and this may influence differences we see in dispersal patterns. Additionally, samples for some areas were collected through different means and in varying sample sizes, potentially influencing the results. For VA in particular, only 8 samples were collected and only two of these were females. In TN, none of the dyads were more than ~20 km apart, and so analyses above these distances could not be considered. Despite these caveats however, there were a number of interesting patterns that emerged from the data.

Female-female dyads had a significant decline in relatedness with ln-distance for all populations except BSF and OK, matching the expected pattern of females settling near closely related females. This matches the typical pattern of females establishing their own home range overlapping or within close proximity to their mother's home range (Rogers 1987). All dyads and female-male dyads also displayed a similar pattern for both source and expanding populations, though it was less pronounced. If pre-dispersing males were detected in our populations, this could explain such a pattern. However, we do not have reason to believe an inordinate number of pre-dispersing males were detected in these populations and populations where a significant decline was detected differ in the means by which samples were collected. If we do not attribute this pattern to pre-dispersing males, then males may be settling near closely related females, which would not have been expected from previous work.

For male-male dyads, source populations did show the expected pattern of no difference in relatedness in space. However, for expanding populations, this was not always the case. The expanding populations did not consistently differ or differ in the same manner from the source populations. OK displayed patterns similar to those of source populations. For instance, male-male dyads did not show a significant relationship between relatedness and space. Additionally, Kruskal-Wallis and subsequent post-hoc tests did not reveal any significant differences between OK and source populations. The lack of difference between OK and source populations may be attributable to two factors. There is indication that a remnant population may have existed in the Ouachita Mountains prior to the reintroduction and subsequent dispersal of bears from Arkansas (Van Den Bussche et al. 2009, Faries et al. 2013). Additionally, expansion and increase of population in this area may have started prior to expansion into the other areas sampled for this study. By the late 1980's there was an increase in nuisance bear complaints in the state (J. Hemphill in Bales et al. 2005) and visitation to bait stations had generally increased after they were instituted in 1989 (Skeen 1997;2002).

PM, one of the expanding populations from Kentucky, had more differences from source populations than OK, but not as many as BSF and MO. Though not significant at all levels or compared to all source populations, PM, BSF, and MO female-female dyads generally had higher relatedness and higher relative frequencies of closely related dyads than source populations (Fig. 2). Female-female dyads in expanding populations also had higher levels of closely related dyads than female-female dyads in source populations. This pattern may simply be due to the founder effect, particularly if gene flow is not high from source populations (Mayr 1942). With few founders, the individuals present would be expected to be closely related (Mayr 1942). However, with the founder effect, all dyads would be expected to be more closely related than in the source populations. For PM, one of the expanding populations in Kentucky, this was not the case. Black bears were extirpated from Kentucky, but have been recolonizing over the past 20 years (Hast 2010); the first documented instance of reproduction following the extirpation was in 2003 (Unger 2007). PM has greater gene flow from source populations than BSF, because there is ample connectivity between it and its source populations in VA and WV (Hast 2010). Allelic diversity and heterozygosity are also higher in PM than its source populations and BSF (Hast 2010). Hence there may be additional factors contributing to this pattern of higher numbers of close relationships and overall relatedness of female-female dyads.

Long dispersal distances have been detected for female brown bears in expanding populations (Swenson et al. 1998, Jerina and Adamic 2008). While the possibility exists for long dispersal distances in these populations, the detection of the pattern of relatedness declining with distance for female-female dyads, regardless of whether they belonged to source or expanding populations, indicates this is not exclusively the case nor is it the predominant pattern for these populations. Remaining near the maternal home range provides an advantage in food acquisition (Rogers 1987), that likely overrides the advantages of dispersing here. Bears learn through experience and would have had the opportunity to acquire knowledge about local food availability from their mothers (Rogers 1987). This could be particularly important in expanding populations, as they are encountering novel environments.

MO and BSF graphically show a decline in relatedness with distance for male-male dyads. This decline was significant for MO. Subadult males brown bears dispersed shorter distances in expanding populations because competition with adult males was potentially lower on the expanding edge (Swenson et al. 1998), suggesting one possible cause of this pattern. Similarly, Costello et al. (2008) also found that male black bears in low density areas settled near closely related males, again likely due to lower competition at such densities. However, Roy et al. (2012) found the opposite effect, with lower dispersal for males in higher density populations than lower density populations, suggesting that the density and subsequent levels of competition may not entirely explain the male dispersal patterns in the expanding populations. Previous work has suggested that bears may have means of detecting related individuals (Rogers 1976, Støen et al. 2005) and if this is the case, perhaps settling near related males would offer a competitive advantage in expanding populations.

As with female-female dyads, the pattern of high relatedness of male-male dyads in expanding populations could also be related to the founder effect in both locations, with a potential for a bottleneck effect in MO as well. BSF is relatively isolated, with a low immigration rate and is primarily believed to be derived from the reintroduction of 14 bears in 1997 (Hast 2010). For this population, the relative isolation and presence of a road between this population and others (Hast 2010) may also make dispersal costs higher than those associated with staying near closely related males. Bear sightings increased in MO in the late 1980’s (Titus et al. 1993) and the presence of females with cubs indicates that the population is reproducing (MDC 2008), which suggests this population was present earlier than the BSF population. However there is evidence of at least one genetically different population with low diversity in MO, which possibly represents an isolated remnant population in the state (Faries et al. 2013). Missouri bears in general were not considered a separate population from those in the Arkansas Ozark Mountains and allelic diversity was similar suggesting high gene flow (Faries et al. 2013). It is possible that there are multiple isolated pockets that are driving this pattern of high relatedness of male-male dyads in space. Alternatively, this population may have different patterns of resource availability and/or competition that are driving the pattern of declining relatedness with distance in male-male dyads.

Patterns of dispersal in black bears do not exclusively ascribe to the generally expected pattern of male dispersal and female philopatry found in mammals (Schenk et al. 1998, Costello et al. 2008, Roy et al. 2012). Density, resource availability, competition, costs of dispersal, and benefits of not dispersing may all play a role in influencing dispersal patterns (Schenk et al. 1998, Costello et al. 2008, Roy et al. 2012). Expanding populations, like those studied here are likely exposed to variations in all of these factors. Female-female dyads did adhere to philopatry, but were more closely related in most expanding populations than those in the source populations. Additionally for some populations, male-male dyads had higher levels of relatedness in close proximity than would be expected in the case of male-biased dispersal. Patterns of dispersal for black bears have greater levels of complexity than basic male dispersal and female philopatry.

MANAGEMENT IMPLICATIONS

Managing the harvest is an important part of black bear management. As black bears expand into new areas and establish populations, the public often expresses interest in a harvest. In addition to use of population estimators, knowledge of the age structure, sex-ratio, levels of genetic diversity, and connectivity with other populations would help managers better assess whether harvest is feasible and, if so, help to determine limits. Differences in dispersal patterns could influence all of these population characteristics. Therefore, if concerns with any of these factors should arise, knowledge of dispersal patterns would aid managers in making decisions that would allow for further recolonization and eventual maintenance of a healthy population. For instance in populations where the sex ratio is male-biased and females are highly philopatric, translocation of females may aid in a swifter establishment of the population along expanding edges. Alternatively, if males are also not dispersing far from the natal range, strategies like establishing corridors to allow for genetic diversity and continued expansion may be important.

The findings in the MO population warrant further exploration because causality of the patterns detected here were unclear. While the population as a whole has high levels of genetic diversity and likely maintains reasonable levels of gene flow with its source population in Arkansas (Faries et al. 2013), levels of relatedness were higher than in other populations. If there are barriers to gene flow, managers will need to be aware of them as they make management decisions related to movements of bears. Additionally, if there are isolated, genetically unique groups, managers will need to decide what and if measures should be taken to maintain those genotypes.

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Table 1. Number of samples taken from populations of black bears in the Interior Highlands and Southern Appalachians. Overall number of samples and number of samples by sex are listed.

Population	N	Females	Males
Interior Highlands			
OU[a]	77	43	34
OZ[b]	96	48	48
OK[c]	20	11	9
MO[d]	113	66	47
Southern Appalachians			
BSF[e]	19	7	12
PM[f]	84	26	58
TN[g]	22	11	11
VA[h]	8	2	6
WV[i]	29	16	13

[a] Arkansas Ouachita Mountains
[b] Arkansas Ozark Mountains
[c] Oklahoma
[d] Missouri
[e] Big South Fork KY
[f] Pine Mountain KY
[g] Tennessee
[h] Virginia
[i] West Virginia

Table 2. Relative frequency of unrelated black bear dyads within specified distances by population from the Interior Highlands and Southern Appalachian Mountains. Data was gathered from 2005-2012.

Distance	OU[a]	OZ[b]	TN[c]	WV[d]	BSF[e]	PM[f]	OK[g]	MO[h]
1	60	70	100	80	75	80	83	41
3	76	78	97	84	89	80	85	46
6	83	82	96	85	80	81	82	53
9	83	84	94	86	83	82	80	55
15	84	85	95	97	83	85	87	54
30	85	86		89	83	85	91	58
45		86		89		86	91	64

[a] Arkansas Ouachita Mountains
[b] Arkansas Ozark Mountains
[c] Tennessee
[d] West Virginia
[e] Big South Fork KY
[f] Pine Mountain KY
[g] Oklahoma
[h] Missouri

Table 3. Correlation and corresponding p-values, adjusted using the Mantel test, for the relationship between relatedness values and distance in black bears in the Interior Highlands and Southern Appalachian Mountains. Values reported for all dyads, female-female dyads, and male-male dyads. Data was gathered from 2005-2012.

Population	All		Female-female		Male-male	
	r	p-value	r	p-value	r	p-value
Source populations						
OU[a]	-0.101	>0.001	-0.259	>0.001	0.012	0.400
OZ[b]	-0.017	0.133	-0.104	0.003	-0.010	0.359
TN[c]	-0.056	0.26	-0.272	0.032	-0.202	0.141
VA[d]	-0.243	0.110			0.335	0.833
WV[e]	-0.103	0.017	-0.298	0.010	0.020	0.538
Expanding populations						
BSF[f]	0.017	0.559	-0.177	0.239	0.220	0.958
PM[g]	-0.080	>0.001	-0.373	>0.001	-0.046	0.037
OK[h]	-0.095	0.097	-0.262	0.051	0.079	0.334
MO[i]	-0.330	>0.001	-0.047	>0.001	-0.166	>0.001

[a] Arkansas Ouachita Mountains
[b] Arkansas Ozark Mountains
[c] Tennessee
[d] Virginia
[e] West Virginia
[f] Big South Fork KY
[g] Pine Mountain KY
[h] Oklahoma
[i] Missouri

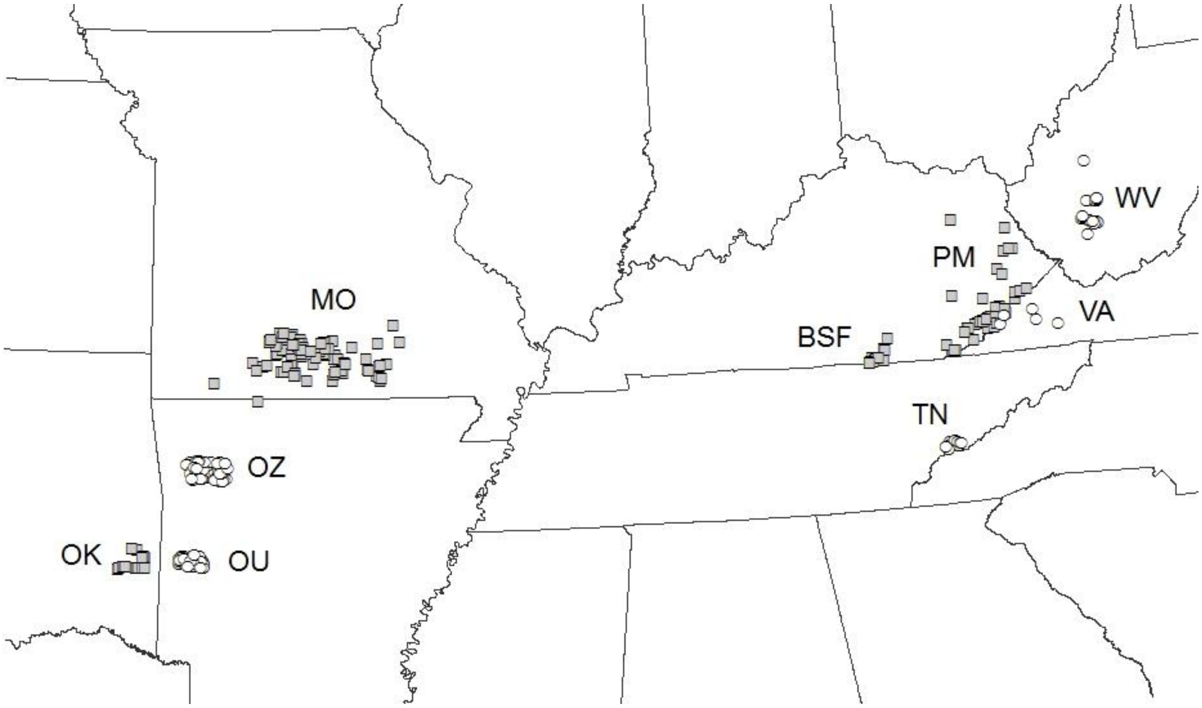

Figure 1. Samples for this study were collected from 2005-2012 in the Interior Highlands and in the Southern Appalachians. Samples from the Interior Highlands were: Arkansas Ouachita Mountains (OU) Arkansas Ozark Mountains (OZ), Oklahoma (OK), Missouri (MO). Samples from the Southern Appalachians: were Big South Fork KY (BSF), Pine Mountain KY (PM), Tennessee (TN), Virginia (VA), and West Virginia (WV).

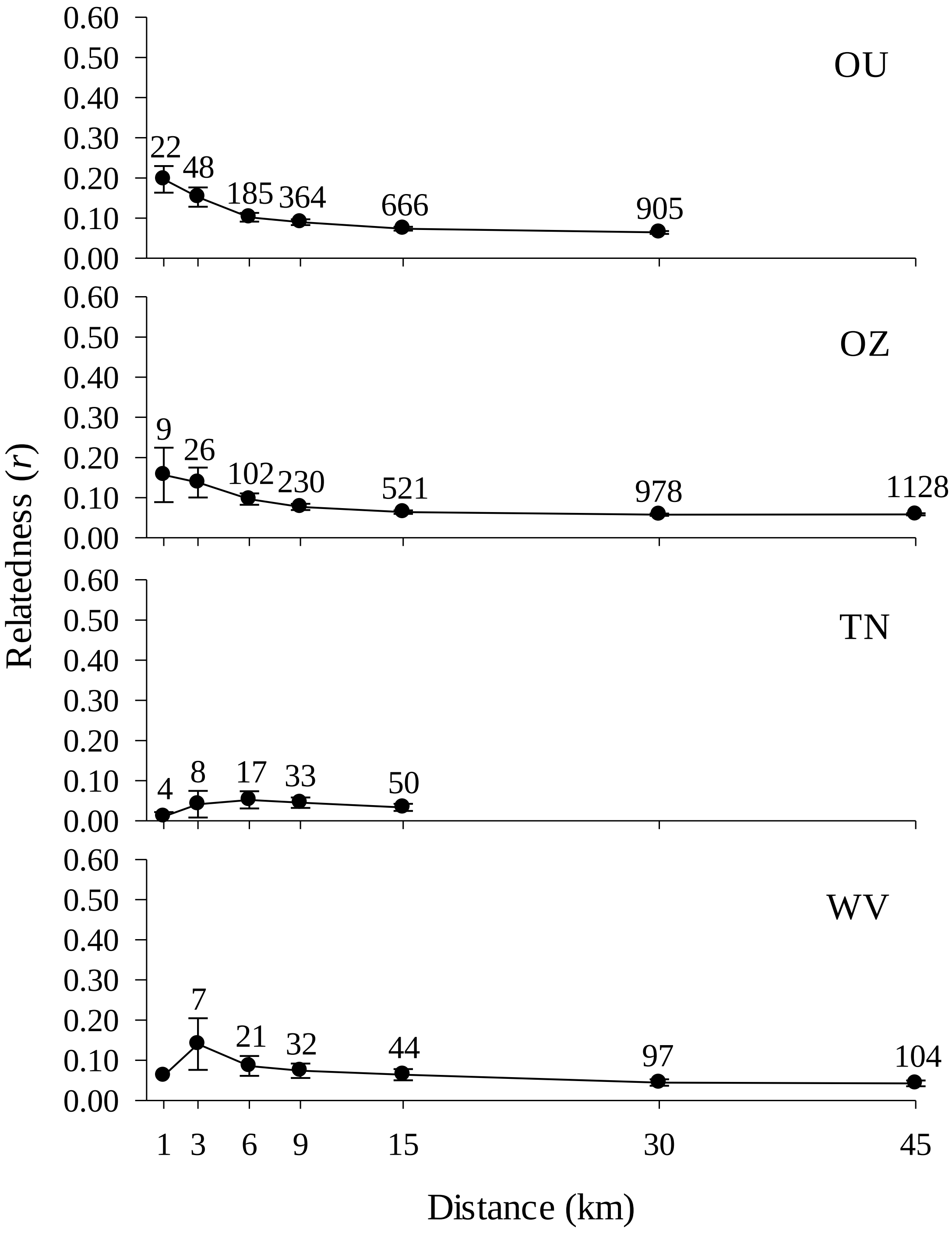

Figure 2. Relationship between distance and average relatedness (r) for female-female dyads, within specific distance categories (1, 3, 6, 9, 15, 30, 45 km) in source black bear populations. Sample size in number of dyads (pairs) is above each average and error bars represent standard error. Samples were collected from 2005-2012 in the Interior Highlands and in the Southern Appalachians. Samples were from: Arkansas Ouachita Mountains (OU) Arkansas Ozark Mountains (OZ), Tennessee (TN), Virginia (VA), and West Virginia (WV).

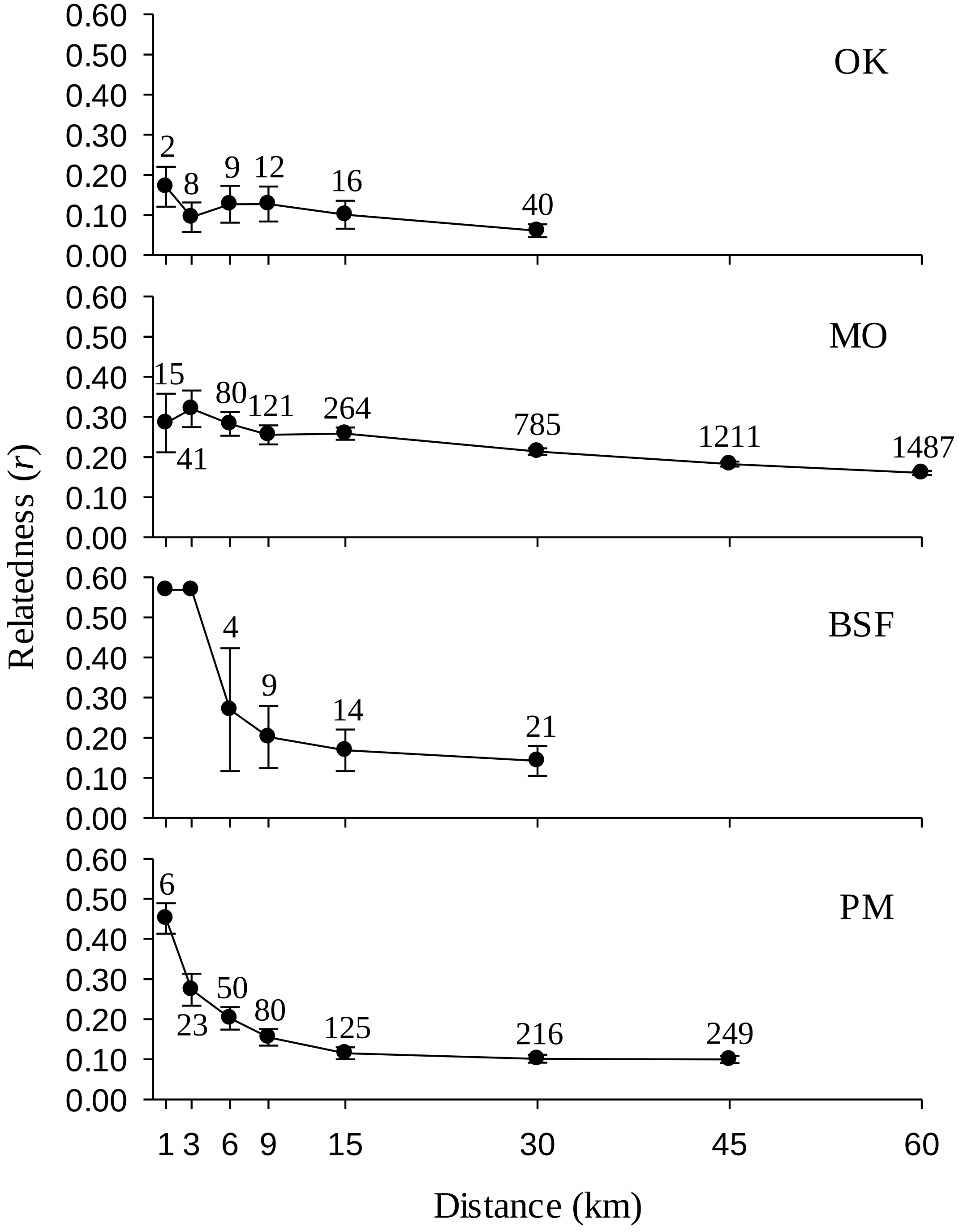

Figure 3. Relationship between distance and average relatedness (r) for female-female dyads, within specific distance categories (1, 3, 6, 9, 15, 30, 45 km) in expanding black bear populations. Sample size in number of dyads (pairs) is above each average and error bars represent standard error. Samples were collected from 2005-2012 in the Interior Highlands and in the Southern Appalachians. Samples were from: Oklahoma (OK), Missouri (MO), Big South Fork KY (BSF), and Pine Mountain KY (PM).

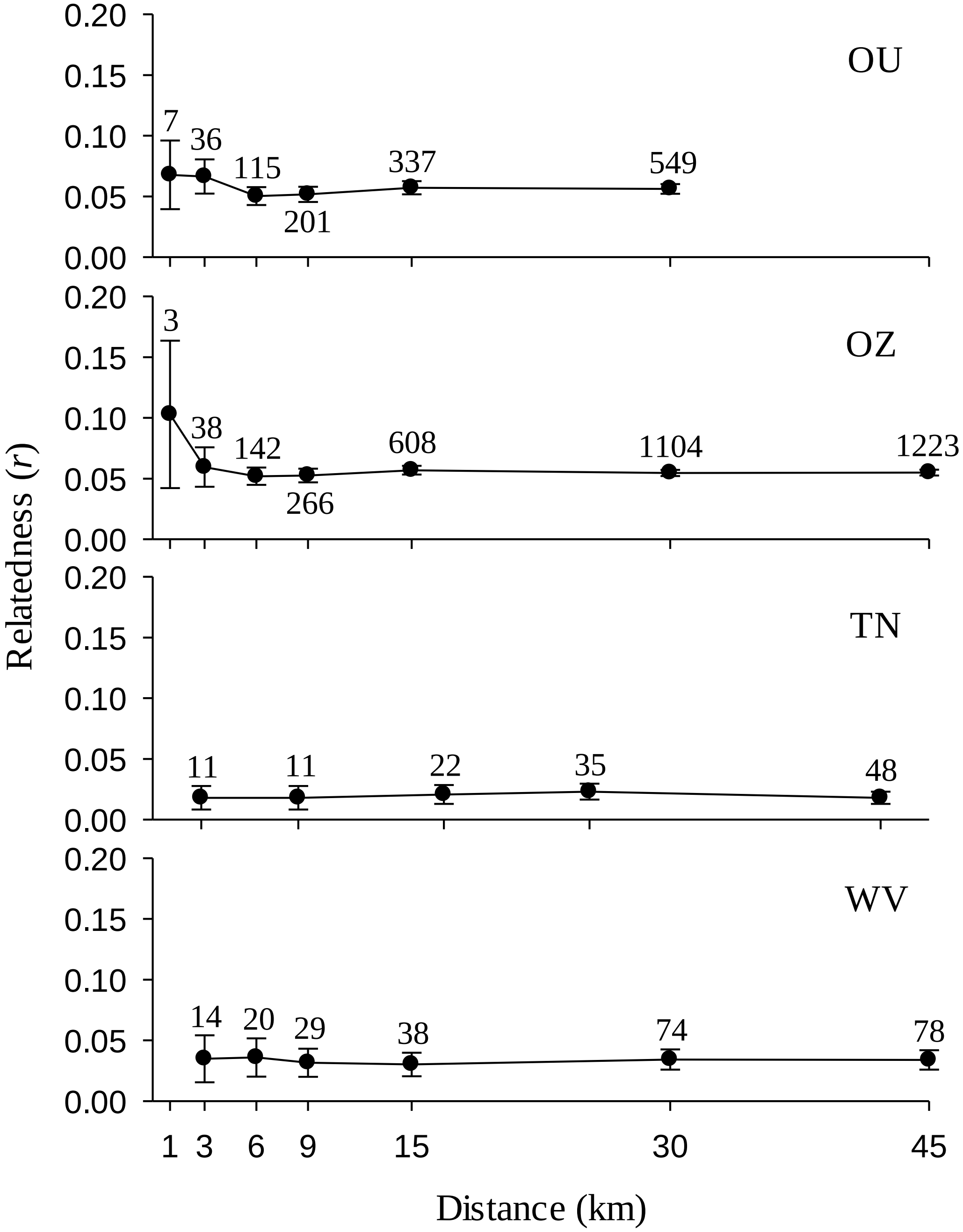

Figure 4. Relationship between distance and average relatedness (r) for male-male dyads, within specific distance categories (1, 3, 6, 9, 15, 30, 45 km) in source black bear populations. Sample size in number of dyads (pairs) is above each average and error bars represent standard error. Samples were collected from 2005-2012 in the Interior Highlands and in the Southern Appalachians. Samples were from: Arkansas Ouachita Mountains (OU) Arkansas Ozark Mountains (OZ), Tennessee (TN), Virginia (VA), and West Virginia (WV).

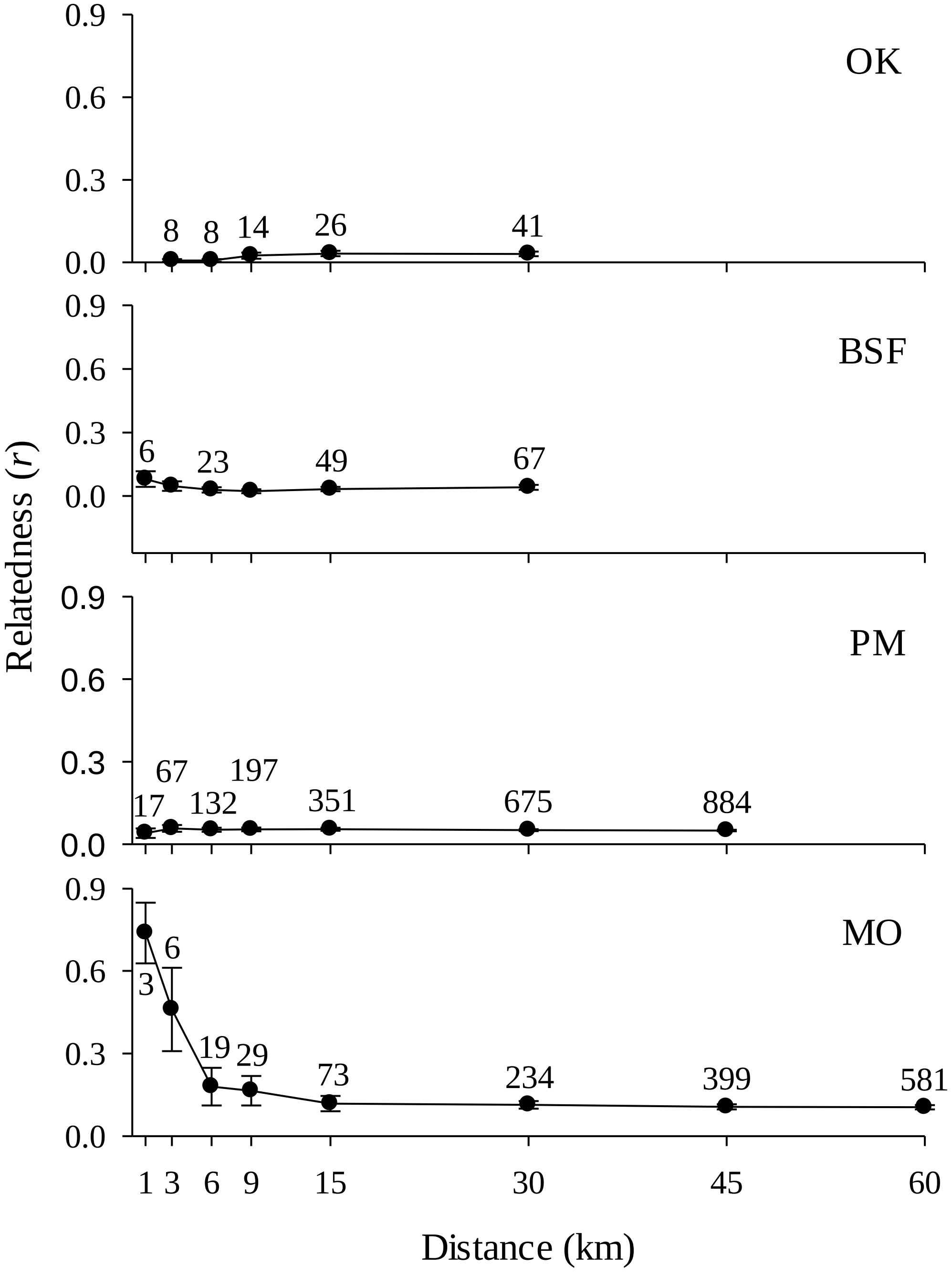

Figure 5. Relationship between distance and average relatedness (r) for male-male dyads, within specific distance categories (1, 3, 6, 9, 15, 30, 45 km) in expanding black bear populations. Sample size is above each average and error bars represent standard error. Samples were collected from 2005-2012 in the Interior Highlands and in the Southern Appalachians. Samples were from: Oklahoma (OK), Missouri (MO), Big South Fork KY (BSF), and Pine Mountain KY (PM).

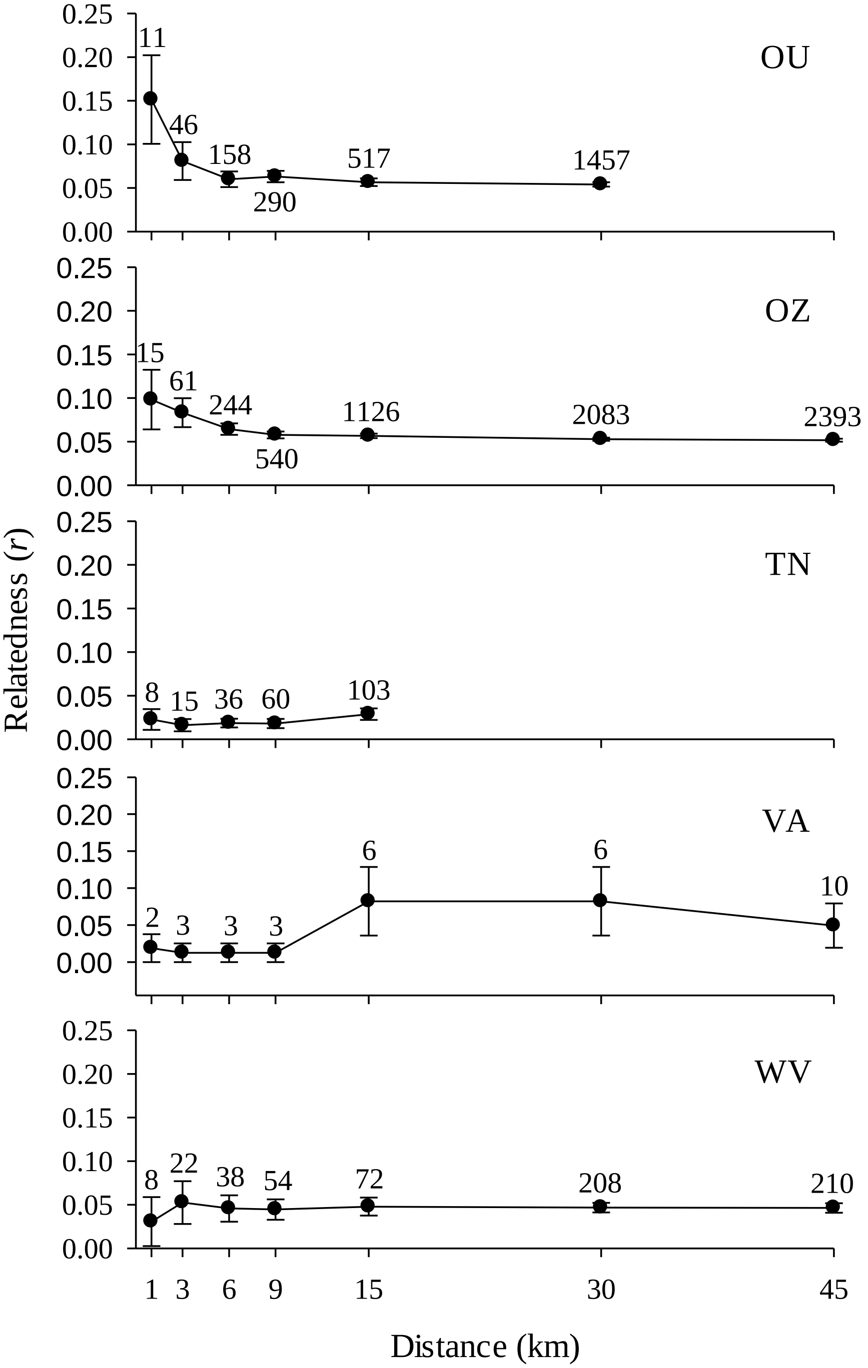

Figure 6. Relationship between distance and average relatedness (r) for female-male dyads, within specific distance categories (1, 3, 6, 9, 15, 30, 45 km) in source black bear populations. Sample size in number of dyads (pairs) is above each average and error bars represent standard error. Samples were collected from 2005-2012 in the Interior Highlands and in the Southern Appalachians. Samples were from: Arkansas Ouachita Mountains (OU) Arkansas Ozark Mountains (OZ), Tennessee (TN), Virginia (VA), and West Virginia (WV).

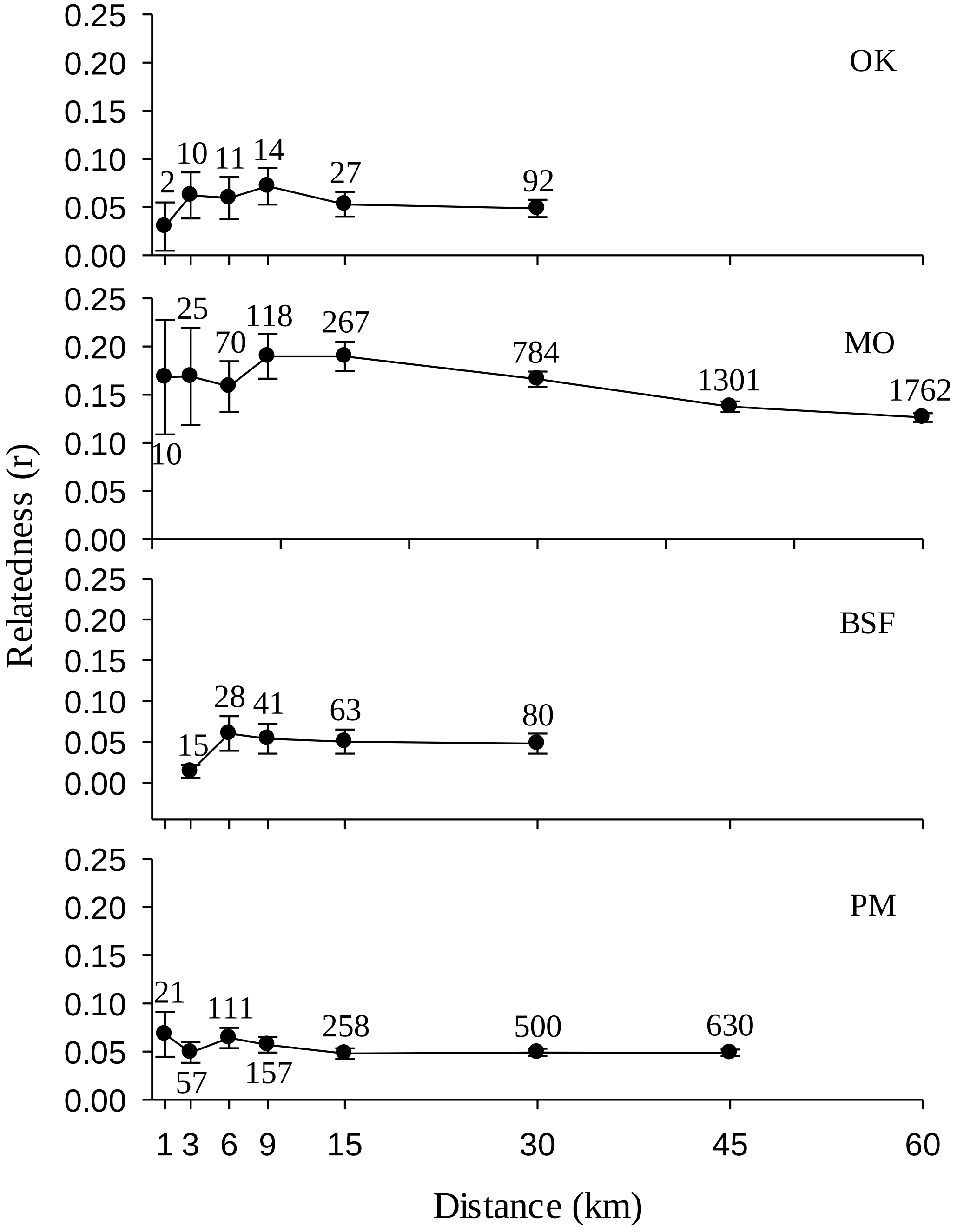

Figure 7. Relationship between distance and average relatedness (r) for female-male dyads, within specific distance categories (1, 3, 6, 9, 15, 30, 45 km) in expanding black bear populations. Sample size is above each average and error bars represent standard error. Samples were collected from 2005-2012 in the Interior Highlands and in the Southern Appalachians. Samples were from: Oklahoma (OK), Missouri (MO), Big South Fork KY (BSF), and Pine Mountain KY (PM).

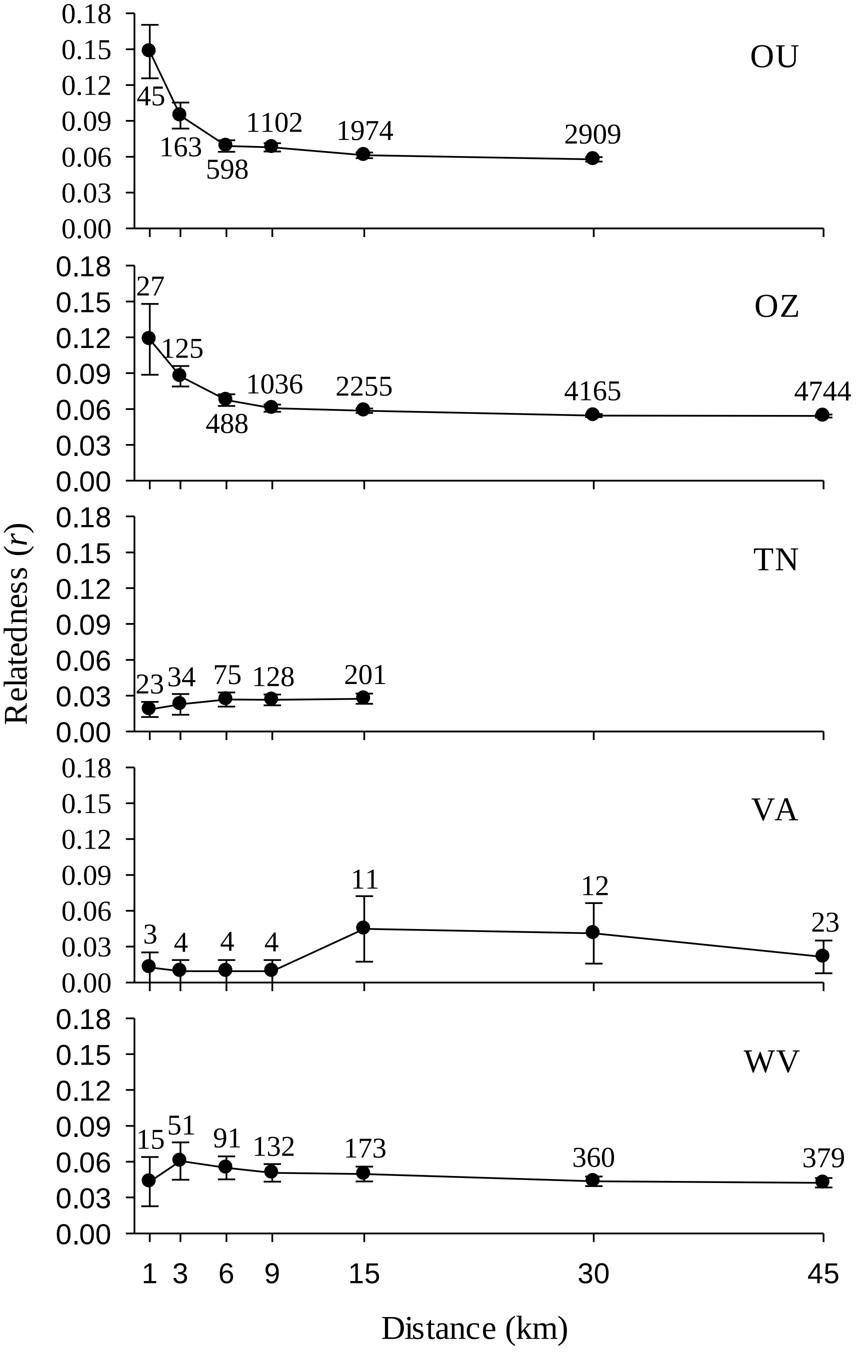

Figure 8. Relationship between distance and average relatedness (r) for all dyads, within specific distance categories (1, 3, 6, 9, 15, 30, 45 km) in source black bear populations. Sample size in number of dyads (pairs) is above each average and error bars represent standard error. Samples were collected from 2005-2012 in the Interior Highlands and in the Southern Appalachians. Samples were from: Arkansas Ouachita Mountains (OU) Arkansas Ozark Mountains (OZ), Tennessee (TN), Virginia (VA), and West Virginia (WV).

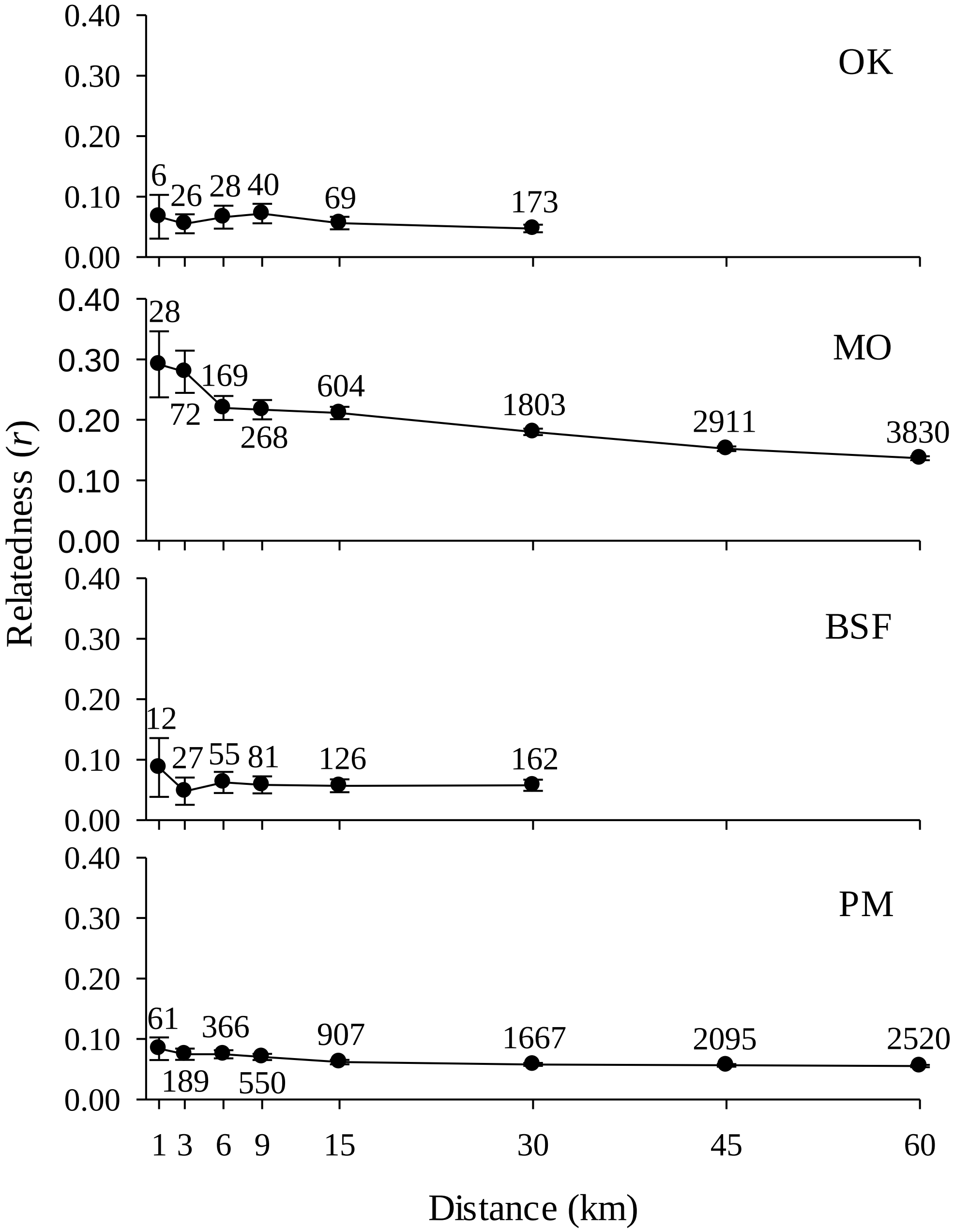

Figure 9. Relationship between distance and average relatedness (r) for all dyads, within specific distance categories (1, 3, 6, 9, 15, 30, 45 km) in expanding black bear populations. Sample size is above each average and error bars represent standard error. Samples were collected from 2005-2012 in the Interior Highlands and in the Southern Appalachians. Samples were from: Oklahoma (OK), Missouri (MO), Big South Fork KY (BSF), and Pine Mountain KY (PM).

CONCLUSIONS

In the Interior Highlands of Arkansas, Missouri, and Oklahoma, overharvest, extensive logging, and reductions of habitat availability by other means contributed to the decline of black bears (Clark 1991, Smith and Clark 1994). Bears were extirpated from the majority of the region by the 1940's Oklahoma by 1915 and from Missouri by 1931 (Bennitt and Nagel 1937, McCarley 1961, Smith and Clark 1994). From 1958-1968, the Arkansas Game and Fish Commission undertook a reintroduction to the Ouachita and the Ozark National Forests in Arkansas (Rogers 1973, Smith and Clark 1994). The successful growth and expansion of the released population caused these efforts to be considered one of the most successful reintroductions of carnivores (Smith and Clark 1994). Evidence of a population in Oklahoma was recorded by the 1980's, (Bales et al. 2005) and in by the 1990's (Titus et al. 1993). By the early 1990's, approximately 2500 bears were present in the Interior Highlands of Arkansas, Oklahoma, and Missouri (Smith and Clark 1994).

One purpose of the research towards this dissertation was to estimate population abundance and density at two locations in the Interior Highlands: the Ouachita Mountains (2006-2008) and the Ozark Mountains (2009-2011), utilizing the Robust model in program MARK (Kendall et al. 1995) and spatially explicit capture-recapture (SECR) methods (Efford 2004, Borchers and Efford 2008, Efford et al. 2009, Efford 2013). Under the Robust model, capture probabilities were influenced by sex, year, and time for the Ozarks, but there was no strong top model for the Ouachitas. Year, sex, and trap-specific behavior were all important components of density models. Top models for regional density included percent forested landscape cover and density of roads as covariates of density, with percent forest having a positive association and road density having a slightly negative association. Density estimates are comparable to or above previous estimates done in the late 1980's/early 1990's. The population appears to have maintained or exceeded previous density estimates, but should be monitored further since the year of the highest harvest did not occur until the middle of this study.

With respect to dispersal patterns, females showed declining relatedness with increasing distance in both source and expanding populations. Average relatedness of female-female dyads declined significantly up through about 30 km between pairs. All pairs and female-male dyads displayed a similar pattern, though with a less-pronounced decline. Males in source populations did not differ in relatedness across space, however, in some expanding populations, this was not the case. In recently expanding populations, male-male dyads followed a similar pattern to female-female dyads, with relatedness decreasing with distance. Female-female dyads in expanding populations also had higher levels of closely related dyads than female-female dyads in source populations. With these deviations from more typical expectations of dispersal patterns, exploration of such variation in expanding populations may have important management implications, particularly because some American black bear populations have expanded in recent years.

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