2016

ECOLOGY OF TWO REINTRODUCED BLACK BEAR POPULATIONS IN THE CENTRAL APPALACHIANS

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Digital Object Identifier: http://dx.doi.org/10.13023/ETD.2016.076

Recommended Citation

Murphy, Sean McCarthy, "ECOLOGY OF TWO REINTRODUCED BLACK BEAR POPULATIONS IN THE CENTRAL APPALACHIANS" (2016). *Theses and Dissertations--Animal and Food Sciences*. 61.
https://uknowledge.uky.edu/animalsci_etds/61

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ECOLOGY OF TWO REINTRODUCED BLACK BEAR POPULATIONS IN THE CENTRAL APPALACHIANS

DISSERTATION

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
Department of Animal and Food Sciences
at the University of Kentucky

By

Sean McCarthy Murphy

Lexington, Kentucky

Co-Directors: Dr. John J. Cox, Assistant Professor, Wildlife Ecology and Conservation Biology
and: Dr. Michael J. Lacki, Professor, Wildlife Ecology and Management

Lexington, KY

ABSTRACT OF DISSERTATION

ECOLOGY OF TWO REINTRODUCED BLACK BEAR POPULATIONS IN THE CENTRAL APPALACHIANS

Reintroduced populations are vulnerable to demographic and environmental stochasticity, deleterious genetic effects, and reduced population fitness, all of which can increase extinction probability. Population viability is principle to determining the status of reintroduced populations and for guiding management decisions. To attempt to reestablish black bear (*Ursus americanus*) populations in the central Appalachians, two reintroductions using small founder groups occurred during the 1990s in the Big South Fork area along the Kentucky-Tennessee border (BSF) and in the Jefferson National Forest along the Kentucky-Virginia border (KVP). My objectives were to estimate demographic and genetic parameters, and to evaluate long-term viability and reintroduction success for the KVP and BSF black bear populations.

The KVP grew rapidly to 317–751 bears with a significantly female-biased sex ratio by 2013. Spatially explicit capture-recapture models suggested KVP recolonization may continue to the southwest and northeast along linear mountain ridges. Based on radio-monitoring during 2010–2014, high adult female survival and moderate mean litter sizes were estimated in both populations. All mortality was anthropogenic and males were 4.13 times more likely to die than females. Two-cub litters were most probable in the BSF, whereas the KVP had similar probabilities of two- and three-cub litters. The average annual mortality that occurred during the study period was sustainable and allowed for moderate growth ($\lambda_{KVP} = 1.10$; $\lambda_{BSF} = 1.13$). Continued mortality at the higher 2015 rate, however, resulted in probabilities of ≥25% population decline over 10 years of 0.52–0.53 and 0.97–0.98 in the KVP and BSF, respectively.

Rapid population growth during the 13–17 years post-reintroduction and the overlapping generations inherent to bears retained genetic diversity. Cumulative findings indicated both reintroductions were successful at establishing viable, self-sustaining populations over the long-term. The anthropogenic mortality rate during 2015, if sustained, could cause precipitous declines in these populations. Reimplementation of annual vital rate monitoring and conservative harvests should be considered. Connectivity may be established between these two reintroduced black bear populations if growth and recolonization continue.

KEYWORDS: black bear, ecology, population viability, recolonization, reintroduction, *Ursus americanus*
Multimedia Elements Used: JPEG (.jpg)

Sean McCarthy Murphy

April 26, 2016

ECOLOGY OF TWO REINTRODUCED BLACK BEAR POPULATIONS IN THE CENTRAL APPALACHIANS

By

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April 26, 2016

Dedicated to the men and women in the Acknowledgments section of this dissertation who revel in good ol' fashioned hard work

"It is not the critic who counts; not the man who points out how the strong man stumbled or where the doer of deeds could have done them better. The credit belongs to the man who is actually in the arena, whose face is marred by dust and sweat and blood; who strives valiantly; who errs, who comes short again and again because there is no effort without error and shortcoming; but who does actually strive to do the deeds; who knows great enthusiasms, the great devotions; who spends himself in a worthy cause; who at the best knows in the end the triumph of high achievement, and who at the worst, if he fails, at least fails while daring greatly, so that his place shall never be with those cold and timid souls who neither know victory nor defeat."

Theodore "Teddy" Roosevelt
"The Man in the Arena"
Paris, France
1910

Acknowledgments

The studies presented in this dissertation would not have been possible without the curiosity, hard work, and assistance from a number of individuals. The M.S. thesis by J. Hast was the first major step towards characterizing the status of the Kentucky-Virginia and Big South Fork black bear populations, which also filled a long-standing knowledge gap about bear populations in the central Appalachians, and his assistance with field efforts during 2010–2012 were critical to the completion of the studies in Appendix A and Chapter Three. Additionally, B. Augustine provided considerable analytical efforts for the mark-recapture analyses in Appendix A and Chapter Two, and his simulations that were conducted for both of these manuscripts were not only integral to their successful completion but also for mark-recapture analyses of other non-invasive bear studies. Live-trapping and radio-monitoring efforts during the initial years of study for Chapter Three were conducted either entirely (2009) or with assistance (2010–2011) from J. Hast and B. Augustine. Gratitude can therefore not be expressed enough to both of these men, and I look forward to continuing our professional endeavors together.

Opportunistic live-trapping, cavalier free-range darting, and long hikes while constructing and maintaining hair traps in the rugged mountains by T. Curry, J. Guthrie, and M. Strunk during 2010–2013 were some of the most fun and rewarding experiences I had while conducting field research in Kentucky, which also resulted in supplementary data that were used in this dissertation. For that and their long-lasting friendship, I owe them many thanks. The majority of the data used in Chapter Two were collected by J. Wright, S. Maehr, J. McDermott, C. Crawford, and C. Bodkin, who constructed, maintained, and checked hair traps throughout the 4 study areas during 2011–2013. The diligent work ethic and determination displayed by this team of individuals cannot be trumped, and for that, my appreciation is endless.

The success of the studies in this dissertation was substantially influenced by the guidance, support, and tenacity of my advisor, J. Cox, who has been instrumental to my development as a researcher and person during the last 7 years. He helped design all of the studies, acquired the necessary funding to conduct these projects, positively challenged me, and provided me with the independence to learn, understand, and implement my own scientific thought. I am truly grateful for this and for his mentorship, and I look forward to our current and future collaborations together. I hope that what we have collectively produced would provide our late mentor, D. Maehr, with something that he would be proud of if he were still around ranting with us today.

I am extremely grateful to have worked with J. Plaxico and J. Clark during my time as a graduate student and biologist. These men have been outstanding mentors to me and have never failed to lead by example, which I greatly revere and respect. The guidance and friendship of J. Plaxico has been irreplaceable, and I hope the work described herein is what he envisioned 2 decades ago when he first began working on bears. The people and bears of Kentucky, in my opinion, should be eternally grateful for his tireless efforts towards bear recovery and management over the years. My development and maturation as a researcher has been considerably and positively influenced by J. Clark during the last 3 years. He was the principal investigator for the initial reintroduction in the Big South Fork area during the late 1990s, conducted the preliminary mark-recapture analyses for the Tennessee portion of the study in Appendix A, was integral to the successful publication of Appendix A, and provided substantial input and guidance for the analyses and synthesis in Chapter Three. I cannot express enough appreciation for his generosity, patience, and understanding, and I am incredibly thankful to have had the opportunity to learn from him.

Assuredly, a number of individuals to whom I owe the most gratitude, as I would have probably lost my sanity without them, have fostered my personal well-being while a graduate student. My family – P. Murphy, N. Murphy, B. Murphy, U. Franklin, B. Franklin, M. Franklin, and M. Flanders – never failed to provide the support and guidance that, at times, I desperately needed. I would likely not be who or where I am today, or have achieved what I have thus far in life without them. The unwavering friendship provided by B. Murphy, J. Guthrie, J. Hast, B. Augustine, T. Curry, S. Maehr, and J. McDermott over the years has also been critical to my welfare, for which I thank them all. I am especially grateful for the considerable support, appreciation, love, and understanding that R. Rowe has given me during my time as a graduate student. Furthermore, her assistance with formatting of this dissertation was pivotal to getting this document completed in a timely manner. My thankfulness must also be extended to the Rowe and Slaven families – O. Rowe, F. Rowe, A. Slaven, V. Slaven, D. Slaven, and S. Slaven – who provided positive support of my research efforts and personal endeavors, and treated me as family no matter the circumstances. I also thank P. Kalisz, J. Smith, J. Hill, W. Phifer, J. Rabalais, K. Hall, T. Leger, H. Bui, C. Techakanon, B. Miller, B. Curry, A. Curry, T. Dufour, M. Ortego, L. Leger, B. Slabach, T. Maigret, and M. Chevalier for their support and friendship. Even though she will never read this document, I am grateful for the love, amusement, and fun provided by my German shorthaired pointer, Fancy.

I must thank my doctoral committee members – M. Lacki, L. Grabau, P. Crowley, and the late T. Barnes – for their willingness to serve on my committee and for providing valuable guidance. Notably, M. Lacki and L. Grabau have had influential and long-lasting effects on my direction and progression as a student and professional since my time as an undergraduate. T. Barnes provided thought provoking inquiries during my qualifying examination that led to interesting discussions, and P. Crowley thankfully stepped in to fill the role of T. Barnes following his passing. Finally, I thank E. Lyons for serving as the Outside Examiner for my doctoral defense.

Most of the work in this dissertation was funded by Pittman-Robertson (PR) aid administered by Kentucky Department of Fish and Wildlife Resources. Additional funds were provided by the Department of Forestry at the University of Kentucky, and Tennessee Wildlife Resources Agency and United States Geological Survey contributed to the study in Appendix A. Housing was provided by the National Park Service at Cumberland Gap National Historical Park, the United States Forest Service in the Stearns Ranger District of the Daniel Boone National Forest, and on private property owned by J. Hill and J. Smith. I thank these agencies and individuals, as well as J. Beeler and J. Metzmeier, for contributing to the projects. The remaining funds necessary to complete the studies in this dissertation were personally contributed, and for that, I thank myself for working hard to earn the money. Lastly, I thank K. Ribbeck, M. Davidson, F. Kimmel, R. Gosnell, and Louisiana Department of Wildlife and Fisheries for their support of my efforts to complete my doctorate while working full-time as a Large Carnivore Biologist.

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Chapter 1: Introduction

Large Carnivore Reintroductions

Large carnivores are some of the most imperiled wildlife in the world. Species extinctions, population declines, and range reductions of large carnivores occurred globally through the 20th century, primarily because of anthropogenic activities. Habitat loss and fragmentation, and overexploitation were the primary drivers of this process, which continues in some regions of the world as the human population grows by 1.13% per year (Population Reference Bureau 2014, Ripple et al. 2014). Because large carnivores exert ecological effects by contributing to the regulation and structure of ecosystems over broad areas (e.g., trophic cascades), the loss or decline of these species can have detrimental effects on biodiversity (Ordiz et al. 2013). Indeed, large carnivore presence has been linked to abundance and richness of avian, invertebrate, and herpetofauna species, and the occupation of an area by these large-bodied mammals can affect disease dynamics, carbon storage, and stream morphology (Ripple et al. 2014). Restoration of large carnivores may therefore be critical to the reestablishment of functional and diverse ecosystems.

Recolonization is the process by which species or populations grow in number and distribution to reoccupy areas that they were previously extirpated from (International Union for Conservation of Nature [IUCN] 2013), representing the most common process of wildlife restoration. This naturally occurring mechanism can transpire rapidly for r-selected mammals, such as those in the order Rodentia, some of which are capable of producing multiple litters annually and can exploit a variety of habitat types (Kirkland and Layne 1989). Because of low reproductive rates and considerable resource requirements, natural recolonization by K-selected large carnivores occurs slowly in comparison (Hayward and Somers 2009). For example, cougars (*Puma concolor*) have only recently begun recolonizing the Midwestern United States following more than a century-long absence (LaRue et al. 2012). Because of improved wildlife management practices, implementation of game laws and conservation policies, and habitat recovery and restoration during the latter half of the 20th century, some large carnivores successfully recolonized portions of North America and Europe. Gray wolves (*Canis lupus*) and brown bears (*Ursus arctos*), for instance, both naturally recolonized parts of Sweden, Italy, and Greece (Pyare et al. 2004, Fabbri et al. 2014, Votsi et al. 2016), and cougars and American black bears (*Ursus americanus*) are projected to recolonize localized areas of the United States during coming decades (Smith et al. 2015, LaRue and Nielsen 2016). However, the ecological importance and the imperiled status of many large carnivores may necessitate more timely restoration than the rate at which natural recolonization typically occurs for these wide-ranging carnivores.

Reintroduction has become an increasingly used tool for restoring species to their native range, allowing animals to overcome impediments to natural recolonization, such as anthropogenic development (Seddon et al. 2005). Reintroduction is defined as a human-directed attempt to reestablish a species where it was extirpated but which was once part of its historical range (IUCN 2013). Large carnivores are among some of the most frequently reintroduced mammals, surpassed in number only by programs for species in the Cervidae and Bovidae families (Seddon et al. 2007). Most reintroduction programs for large carnivores have been implemented in North America (Breitenmoser et al. 2001). For example, gray wolves, red wolves (*Canis rufus*), Mexican wolves (*Canis* *lupus baileyi*), brown bears, Canada lynx (*Lynx canadensis*) and Louisiana black bears (*Ursus americanus luteolus*) all have populations that were reintroduced in the United States for threatened and endangered species recovery (Servheen et al. 1995, Smith et al. 2003, Devineau et al. 2010, Hinton et al. 2013, Laufenberg and Clark 2014, Hendricks et al. 2016). Most large carnivore reintroductions have occurred for non-imperiled species, though, primarily to attempt to rectify past human transgressions or because these animals were considered important components of ecosystems (Breitenmoser et al. 2001, Seddon et al. 2005, Hayward and Somers 2009).

Success of large carnivore reintroductions has varied among and within species. This is because reintroductions for these animals have often been controversial or, because these programs are time-intensive and expensive, have lacked proper planning or long-term monitoring (Williams et al. 2002, Hayward and Somers 2009, Weise et al. 2014). For example, a brown bear reintroduction in Poland failed because of a lack of monitoring, which did not allow timely implementation of management strategies that were required to mitigate anthropogenic threats (Buchalczyk 1980). Success is generally thought to be enhanced by releasing a large founder group with high genetic variation in suitable habitat where competition for resources is low (Griffith et al. 1989, Thatcher et al. 2006). Definitive criteria for determining reintroduction success for large carnivore programs have been elusive (Hayward and Somers 2009). For wildlife in general, reintroduction success has typically been defined as the establishment of a viable, self-sustaining population (Griffith et al. 1989, Seddon 2015). Although an adequate generality, Sarrazin (2007) posited that this definition did not sufficiently encapsulate all of the characteristics that are representative of healthy, naturally occurring wildlife populations. The author therefore recommended evaluating reintroduced populations during 3 primary phases: 1) population establishment, 2) population growth, and 3) population regulation. Researchers have more recently extended these recommendations, identifying long-term population viability during the regulation phase as the ultimate measure of reintroduction success (Robert et al. 2015).

The population regulation phase is the period during which population dynamics are acutely dependent on the interactions among individuals, habitat characteristics, and anthropogenic activities (Sarrazin 2007, Robert et al. 2015). Life history traits of reintroduced species therefore restrict success evaluations to temporal periods lengthy enough for populations to achieve this phase (Seddon 1999). Intuitively, this requires long-term monitoring for reintroduced large carnivore populations because of their K-selected biological strategy. Demographic information such as abundance, density, and survival and reproductive rates, as well as population genetics characteristics (e.g., genetic diversity and effective population size) should be monitored at pre-defined time intervals after population establishment (De Barba et al. 2010, Robert et al. 2015). Ecological characteristics, such as range expansion patterns and connectivity with neighboring populations, are also key components to reintroduction success. Because most reintroduced populations are small, they are more vulnerable to demographic and environmental stochasticity relative to their larger counterparts, are susceptible to the manifestation of deleterious genetic effects (e.g., inbreeding depression), and consequently have heightened risks of population decline or extinction (Lande et al. 2003, Brook 2008, Johnson et al. 2010). Long-term monitoring is therefore critical for reintroduced large carnivore populations to provide managers with the opportunities to implement conservation strategies that may be necessary to thwart population decline or reintroduction failure.

Bear Reintroductions

Among the 8 extant bear species in the world, five are imperiled and the other three have populations or subspecies that are locally or regionally listed as threatened or endangered (Servheen et al. 1999). Abundance and distribution of bears, in general, has decreased throughout most of their range, and some species have declined in number by ≥50%. Similar to other large carnivores, this resulted primarily because of habitat destruction and anthropogenic persecution. With the exception of polar bears (*Ursus maritimus*) and the giant panda (*Ailuropoda melanoleuca*), most bear species are opportunistic omnivores that are capable of exploiting a variety of habitat types (i.e., not habitat specialists); thus, given the generalist tendencies of these bruins, their global decline is of considerable concern. Bears are typically considered umbrella species, so conservation of these animals and their habitats may preserve more biodiversity than efforts aimed at conserving other large carnivores (Servheen et al. 1999).

Brown bears inhabit more of the world than any other bear species, and American black bears are the most numerous and widely distributed bear in North America. Despite their extensive ranges, most bear reintroductions have been proposed, planned, or implemented for these two species (Clark et al. 2002, Clark 2009). Brown bear reintroductions occurred in both North America and Europe, whereas most American black bear reintroductions were carried out in the eastern and southeastern United States. Although both species are projected to naturally recolonize some historical range during coming decades, a number of their populations remain isolated and threatened by small population size, or habitat fragmentation and loss. Loss of habitat in some areas has been severe enough that connectivity between populations is unlikely to develop in the foreseeable future (Chapron et al. 2014, Scheick and McCown 2014, Smith et al. 2015). Additional reintroductions may therefore be required to surmount threats to population viability at various spatial scales to meet management objectives.

Biological and behavioral characteristics of bears present formidable challenges to successful reintroductions of these animals. Bears exhibit low reproductive rates, low population growth, low genetic variation relative to abundance, and are vulnerable to environmental fluctuations (Bunnell and Tait 1981, Wathen et al. 1985). Homing capabilities and high mortality following translocation can further impede reintroduction efforts for bears (Clark et al. 2002, Clark 2009). Relatively few bear reintroductions have occurred as a result compared to the number of programs for other carnivores (Seddon et al. 2007), and even fewer bear reintroductions have been successful or had monitoring programs intensive enough to evaluate success (Clark et al. 2002). Thus, little is known about the methods that may contribute to reintroduction success for bears, and the demographic, genetic, and spatial expansion characteristics that reintroduced bear populations exhibit following the population establishment phase remains mostly equivocal.

Brown bear reintroductions in Poland, Italy, and Austria failed because of a combination of insufficient habitat availability, high rates of anthropogenic persecution, small founder groups, and the isolated occurrence of these populations relative to other populations in Europe (Clark et al. 2002, Güthlin et al. 2011, Peters et al. 2015). Undoubtedly, all of these factors could have possibly been prevented with better planning and post-release monitoring efforts. The most successful bear reintroduction to-date occurred in the Interior Highlands of Arkansas, where 254 American black bears were released during the 1960s. This population subsequently grew to >2,500 individuals that has since colonized much of the mountainous regions of Arkansas, Missouri, and parts of Oklahoma (Clark and Smith 1994, Bales et al 2005, Wilton et al. 2014). In contrast to the failed attempts in Europe, the Arkansas program was implemented with a large founder group released in an area that had a large quantity of quality habitat, and mortality was low for nearly two decades post-release, all of which likely promoted rapid population growth (λ = 1.26/year; Clark and Smith 1994, Clark et al. 2002). Other bear reintroductions have occurred for which long-term success remains unknown, including those for the American black bear in southern Arkansas, the Asiatic black bear (*Ursus thibetanus*) in South Korea, and the brown bear in portions of Europe (Clark et al. 2002, Wear et al. 2005, Kim et al. 2011).

Black Bears in the Central Appalachians

The American black bear (hereafter referred to as black bear) historically inhabited most of North America (Scheick and McCown 2014). Prior to European colonization, the majority of the eastern United States was forested, with the highly productive mixed-mesophytic forests being the most widespread forest type (Braun 1950). The considerable cover and diverse array of natural foods available in these forests provided the resources necessary to support multiple large mammals other than black bears, including elk (*Cervus elaphus*), gray and red wolves, white-tailed deer (*Odocoileus virginianus*), and cougars (Barbour and Davis 1974). The central Appalachian region, which contained the highest elevations in the East, was no exception and was generally considered a robust hunting area by local and regional Native American tribes because of the abundance of these mammals (Arnow 1960). Historical records suggest the black bear was one of the most important game animals in the central Appalachians, as reflected in the breadth of contemporary place names referencing these species (Swanton 1979, Cox et al. 2002).

Black bear exploitation in the central Appalachians increased considerably following the arrival of European settlers relative to the subsistence nature of Native American use. The fur trade was established in the central Appalachians during the late 17th century, and black bear hides were one of the most sought after items for nearly two centuries thereafter (Unger et al. 2013). Indeed, one account indicates that >8,000 bear hides were exported out of eastern Kentucky to make grenadier hats for the British army during the early 1800s (Collins 1882). Market hunting climaxed at this time, which coincided with an increased rate of large-scale forest clearing in the region for agricultural and wood utilization purposes. This overexploitation and rapid habitat loss, which led to the decline and extirpation of black bears from most of the central Appalachian region by the early 20th century, was exacerbated by the loss of one of the most important hard mast-producing trees for wildlife in the region, the American chestnut (*Castanea dentata*), to chestnut blight (*Cryphonectria parasitica*; Pelton 1996, Clark and Pelton 1999).

Among all central Appalachian states, Kentucky and Ohio were the only ones to experience complete extirpation of the black bear. Small, remnant, and isolated black bear populations persisted in the most rugged and inaccessible mountains of other states throughout the first half of the 20th century, primarily in what is now known as

Shenandoah National Park in Virginia (SNP), Great Smoky Mountains National Park in Tennessee and North Carolina (GSMNP), and the Monongahela National Forest in West Virginia (Maehr 1984, Pelton 2001). The development of the conservation movement during the early 1900s led to the establishment of game laws, natural resource agencies, and national forests and parks by the mid-20th century, which allowed reforestation to occur and some wildlife species to grow in number and distribution (Clark and Pelton 1999). By the 1960s, increased political and public interest in restoring black bears throughout much of their range in the Appalachians resulted in the creation of bear sanctuaries and reserves to serve as source populations for recolonization (Unger et al. 2013).

Although remnant black bear populations that persisted in the high elevation areas of the region recolonized some areas by the 1970s, rapid recolonization was unlikely to occur in most of the central Appalachians because of the disjunct arrangement of suitable habitat and considerable geographic distances between these populations (van Manen and Pelton 1997). Prior to the 1970s, only two concerted and systematic reintroduction projects had ever been conducted to attempt to restore black bears in the United States: 1) as previously mentioned, bears were reintroduced to the Interior Highlands of Arkansas, and 2) bears were reintroduced to the Atchafalaya and Tensas River basins of Louisiana during the 1960s (Taylor 1971, Clark and Smith 1994, Clark et al. 2002). Based on the confirmed long-term success of the Arkansas reintroduction (Clark and Smith 1994), and because of the low probability of rapid and large-scale natural recolonization in the central Appalachians, multiple black bear reintroduction projects were developed and implemented in Virginia, Kentucky, and Tennessee between the 1970s and 1990s.

Central Appalachian Black Bear Reintroductions

The first black bear reintroduction in the region occurred during 1970–1984, when 300 individuals (unknown sex ratio) were captured at SNP by Virginia Department of Game and Inland Fisheries (VDGIF), subsequently moved across the approximately 40-km wide, non-forested Shenandoah Valley, and released in the George Washington National Forest along the Virginia-West Virginia border (Fies et al. 1987; Figure 1.1). All of these translocated bears were hard-released (i.e., released without an acclimation period [Eastridge and Clark 2001]), but none were radio-monitored post-release. Among the 300 bears, 99 were killed an average of 28 km from their release locations, indicating some post-release dispersal occurred (Fies et al. 1987). Of these 99 recovered bears, 23 were thought to have attempted to home back to SNP, and 12 (all males) successfully returned to SNP. Although none of the translocated bears were monitored, this reintroduction probably resulted in the establishment of population connectivity with bears in eastern West Virginia, and range expansion also occurred along the southwest to northeast linearly arranged mountain ridges in western Virginia during later years (VDGIF 2002). Based on population monitoring efforts during 1994–2002, long-term reintroduction success was confirmed for this population (Bridges 2005, Bridges et al. 2011). Perhaps the most important finding from this reintroduction effort was that combined with results from the Interior Highlands reintroduction in Arkansas, reintroduction could be an effective tool to overcome anthropogenic barriers to natural recolonization for black bears.

To attempt to expand on the success of the early Virginia reintroduction, a second reintroduction subsequently occurred in southwestern Virginia during 1987–1992, when

VDGIF captured 221 bears (unknown sex ratio) at SNP and released them >300 km away at Mount Rogers National Recreation Area (Comly-Gericke and Vaughn 1997; Figure 1.1). Similar to the reintroduction in northwestern Virginia, all bears were hard-released, but 43 individuals (19.4%) were radio-monitored post-release in this program. This monitoring allowed documentation of successful reproduction during 1991 and 1992, which confirmed population establishment. Mortality rates were high in the initial founder group ($M = 0.77$), though, as most bears died from automobile collisions during post-release dispersal or while attempting to home back to their capture locations (Comly-Gericke and Vaughn 1997). Although no explicit evaluation of reintroduction success has ever been conducted for this population, anecdotal evidence of bear occurrences and harvests in the area suggests a viable, self-sustaining population was established (VDGIF 2002, 2012).

Notwithstanding the large number of bears that were translocated during these two Virginia reintroductions, black bear populations remained absent from a considerable portion of the central Appalachian region through the 1970s, including all of Kentucky, most of Tennessee, southern West Virginia, and the most southwestern portion of Virginia (West Virginia Division of Natural Resources [WVDNR] 2006, Tennessee Wildlife Resources Agency [TWRA] 2012, VDGIF 2012, Unger et al. 2013). During the 1980s and 1990s, WVDNR translocated an unknown number of conflict bears (i.e., individuals engaged in human-bear conflict behavior) to ≥40 km from the West Virginia-Kentucky border to reduce human-bear conflict complaints in West Virginia (Plaxico and Bonney 2001, Unger et al. 2013). Despite these moves not being part of a concerted reintroduction program, a viable, self-sustaining bear population was established in southern West Virginia (Ryan 2009), which may have been influenced by an influx of bears from Virginia following range expansion that resulted from the early VDGIF reintroduction along the Virginia-West Virginia border. Although Kentucky and Ohio remained devoid of resident bear populations, the first capture of a black bear in Kentucky occurred during 1987 along the Kentucky-West Virginia-Virginia border – likely a bear translocated by WVDNR (Plaxico and Bonney 2001).

A third reintroduction program was conducted during 1990–1997 by VDGIF in which 55 bears (unknown sex ratio) were translocated to southwestern Virginia along the Kentucky-Virginia border from SNP (hereafter referred to as KVP population; VDGIF 2008; Figure 1.1). At least 4 of these 55 bears were females that were hard-released on Pine Mountain (J. Sajecki, VDGIF, personal communication) – a linear geological feature that extends 225 km southwest to northeast from northern Tennessee, through eastern Kentucky, and into southwestern Virginia (Kleber 1992). Although no founders were radio-monitored, successful reproduction was first documented at Cumberland Gap National Historical Park along the Kentucky-Virginia-Tennessee border during 1991 (Simmons 1997), and on Pine Mountain in eastern Kentucky during 2001 (Unger et al. 2013). Increases in confirmed sightings, human-bear conflict complaints, and live-captures through the 2000s suggested a self-sustaining population was established; however, no formal evaluation of population viability or long-term reintroduction success has ever been conducted (Unger et al. 2013).

During 1996–1997, a fourth reintroduction occurred along the Kentucky-Tennessee border at the Big South Fork National River and Recreation Area (hereafter referred to as BSF population; Eastridge and Clark 2001; Figure 1.1). Fourteen adult female bears with 13 cubs were captured at GSMNP and released approximately 150 km away at BSF. All of the adult females were radio-monitored, and by 1998, 6 had either left the reintroduction area or died, resulting in a relatively low survival rate (S = 0.66 [SE = 0.12]; Eastridge and Clark 2001). An additional supplementation was planned during 2000 but was cancelled because of public opposition. As of 1998, 18 bears resided at BSF and the population had a 24% chance of extinction within a century (Eastridge and Clark 2001). A 2010–2012 non-invasive hair sampling study surprisingly estimated the BSF grew by an average of 1.18/year during the 14 years post-reintroduction despite isolation (Murphy et al. 2015 [see Appendix A]). Importantly, this study provided the first insight into the population genetics of a reintroduced bear population founded by a small number of individuals, which demonstrated that high genetic diversity was retained without an influx of genetic material from other populations in the region. However, similar to the KVP, no evaluation of long-term population viability or reintroduction success has been conducted for the BSF during the population regulation phase (Robert et al. 2015).

Status of Reintroduced KVP and BSF Black Bear Populations

Founding of the BSF bear population is well established as having resulted from a limited reintroduction, but incongruences surround studies that reference the origin of the KVP despite the documented 1990s reintroduction efforts. For example, most research to-date has presumed the KVP resulted from natural range expansion by large, extant bear populations in Virginia, West Virginia, and Tennessee (see Jensen 2009, Hast 2010, Frary et al. 2011, Harris 2011, Unger et al. 2013). These studies mistakenly ignored the evidence that bear populations were absent from the surrounding area until the 1990–

1997 reintroduction (WVDNR 2006, TWRA 2012, VDGIF 2012), thus making natural recolonization an unlikely explanation for establishment of the KVP.

Hast (2010) investigated the genetic structure, variation, and origin of the BSF and KVP bear populations using DNA from hair samples collected during 2006–2009. The BSF was comprised almost entirely of genetic material identical to that of the GSMNP source population, and the KVP mostly consisted of genetic material identical to Virginia bears, with some West Virginia influence. Bears at BSF and KVP exhibited negligible genetic differentiation ($F_{ST} \leq 0.04$) from GSMNP and Virginia bears, respectively. Of concern, however, was the finding that the BSF and KVP populations exhibited moderate genetic structuring between them ($F_{ST} = 0.09$) and that gene flow was insufficient (Hast 2010). Genetic connectivity between the KVP and the closest populations in West Virginia and Virginia were low (Nm = 1.5–2.1 bears/generation) but enough to mitigate the loss of genetic diversity (Mills and Allendorf 1990). In contrast, the BSF experienced negligible genetic connectivity with any extant bear populations in the central Appalachians ($Nm<1$ bear/generation) and was therefore genetically isolated (Hast 2010).

Limited demographic information has been collected for the KVP or BSF since their establishment during the 1990s. Based on small sample sizes ($n<16$) of data collected in the KVP during 2003–2007, mean litter size was exceptionally high ($\bar{x}$ = 3.25; SE = 0.11 [Harris 2011]) but adult female survival was relatively low (S = 0.80; SE = 0.14 [Unger 2007]), the latter of which is one of the most important components to bear population growth (Beston 2011). Estimated abundance of the Kentucky portion of the KVP based on systematic mark-recapture hair trapping during 2008 was small (N = 130 bears [Frary et al. 2011]), but the trap spacing, short sampling session, and non-inclusion of lands in Virginia probably negatively biased the estimate. By 2012, the BSF had increased in size to approximately 211 bears; however, no other demographic data were collected in the BSF following the initial 1996–1998 population establishment phase.

Critical to the long-term success of the Interior Highlands reintroduction in Arkansas was the low mortality rate <13 years post-reintroduction, which allowed rapid population growth to occur (Clark and Smith 1994). Despite having minimal demographic information, VDGIF implemented annual 90-day bear harvests in the Virginia portion of the KVP during 2003 (VDGIF 2012). Kentucky Department of Fish and Wildlife Resources (KDFWR) approximated a combined total of 500 bears in the Kentucky portions of both populations during 2011 based on abundance indices even though abundance estimates indicated that only 38 bears resided in the Kentucky portion of the BSF by 2010 and the KVP was thought to be comprised of just 130 bears during 2008 (Frary et al. 2011, Noyce 2011, Murphy et al. 2015). Nonetheless, annual harvests were implemented in the Kentucky portion of the KVP and throughout the BSF during 2009 and 2013, respectively, and all forms of anthropogenic mortality (harvest and non-harvest) increased considerably during 2015 (>259% increase [2014–2015]; KDFWR 2016, TWRA 2016). Demographic monitoring of small bear populations has demonstrated that even marginal increases in mortality can lead to rapid population declines, and the recovery from these reductions can require many years (Dobey et al. 2005, Howe et al. 2007, Clark et al. 2010). The demographic status of the BSF and KVP populations remained mostly unclear prior to initiation of the studies in this dissertation, but estimates indicated their abundances were low and their probabilities of persistence could therefore be threatened by increasing anthropogenic mortality, which may jeopardize ultimate long-term reintroduction success.

Research Objectives

Although some localized or regional large carnivore recolonizations are projected to occur during coming decades, reintroduction will likely be an important tool for the continued restoration of these animals (Ripple et al. 2014). Bears are among the most frequently reintroduced large carnivores in the world, but there is a lack of information on the demographic, genetic, and spatial expansion characteristics of reintroduced and recolonizing bear populations following initial population establishment. Furthermore, few studies have explicitly evaluated long-term bear reintroduction success during the important population regulation phase. Finally, vital demographic information necessary for sustainable management of the KVP and BSF bear populations was lacking despite increased harvest pressure and non-harvest anthropogenic mortality. The overall goal of my research was therefore to estimate the demographics of both the reintroduced KVP and BSF black bear populations, evaluate long-term reintroduction success, and to evaluate the potential effects of anthropogenic mortality on long-term persistence of these populations.

The studies pertinent to this dissertation are comprised of one published manuscript (Appendix A), one accepted manuscript (Chapter Two), and one manuscript in review (Chapter Three) for publication in a peer-reviewed journal. Chapter Two uses non-invasive mark-recapture sampling and novel spatial mark-recapture statistical analyses to provide a comprehensive characterization of the demographics, genetics, and spatial expansion patterns of a recolonizing bear population sourced from reintroduction.

Chapter Three uses demographic data collected over a four-year time period and individual-based population models to provide the first concerted evaluations of long-term black bear reintroduction success during the regulation phase for two populations sourced from small founder groups. Chapter Three also investigates the effects of anthropogenic mortality on persistence and growth of these two reintroduced populations. Collectively, these studies characterize population attributes important to black bear reintroduction success, which should inform management of this species, and may provide guidance in conserving other large carnivores globally.

Chapter 1: Figures

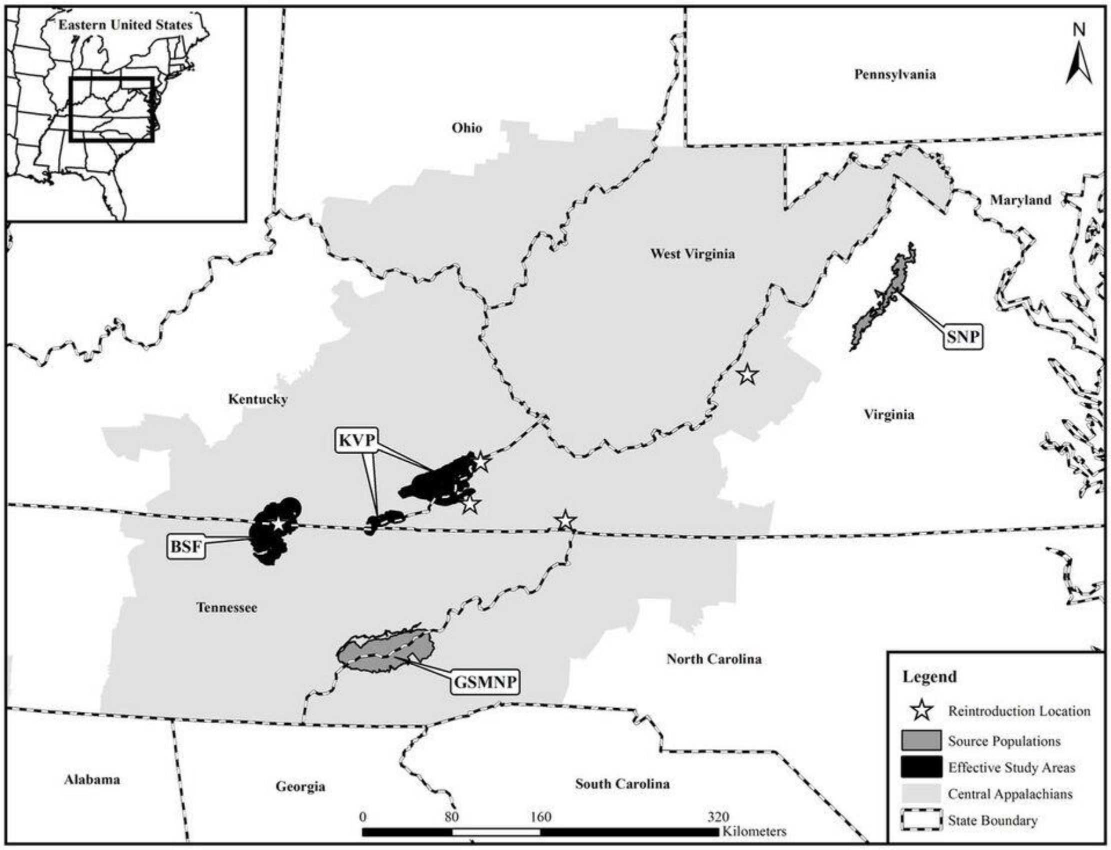

Figure 1.1. Locations of black bear reintroductions, source populations, and effective study areas for this study (2010–2014) in the central Appalachians, USA. Four reintroductions with 5 release locations occurred in Virginia, Kentucky, and Tennessee during 1970–1997. The 3 reintroductions in Virginia were conducted using bears that were translocated from Shenandoah National Park (SNP). One of these reintroductions likely created the Kentucky-Virginia population (KVP) from 55 founders that were released in the Jefferson National Forest along the Kentucky-Virginia border during 1990–1997 (Virginia Department of Game and Inland Fisheries 2008). The Big South Fork population (BSF) was founded by 14 adult females and 13 cubs that were translocated from Great Smoky Mountains National Park (GSMNP) to the Big South Fork National River and Recreation Area along the Kentucky-Tennessee border during 1996–1997 (Eastridge and Clark 2001).

Chapter 2: Recolonization Characteristics of a Reintroduced Black Bear Population Based on Noninvasive Genetic Spatial Capture-Recapture Methods

Abstract

Large carnivores are recolonizing historical range as a result of improved management and conservation policy, habitat restoration, and reintroduction programs. Black bears (*Ursus americanus*) are projected to recolonize large portions of range in the United States, but few studies have characterized or provided practical methods for monitoring this process. We used systematic noninvasive hair sampling at four study areas during 2012–2013 to investigate the demographics, genetics, and spatial expansion patterns of the Kentucky-Virginia black bear population (KVP), which was founded by the reintroduction of 55 bears in a fragmented mountainous landscape during the 1990s and subjected to harvest six years post-reintroduction. Using spatially explicit capture-recapture (SECR) models, we estimated a total density of 0.26 bear/km^2 (95% CI: 0.18–0.37), or a minimum abundance of 482 bears (95% CI: 317–751) distributed among two primary core areas, which were previously identified by occupancy analysis. The southern core area (CG) was likely established by a dispersing founder adult female post-release, but a moderate asymmetrical gene flow (Nm = 6 bears/generation) from the northern core area (PB) mitigated deleterious genetics consequences typical of such founder events. Our estimated effective number of breeders (N_B = 62 bears) was marginally higher than the number of founders, confirming that genetically the KVP remains mostly the product of the original reintroduction. Despite limited connectivity with other bear populations in the region, the KVP retained high genetic diversity (H_E =

0.78), likely because of rapid population growth during the 16 years after reintroduction (λ = 1.14/year). The KVP exhibits demographic characteristics indicative of continued range expansion, including a significantly female-biased sex ratio (0.53M:1.00F) and some support for female density decreasing with distance from the reintroduction area in the larger PB core. Few bear detections at two western study areas and results from anisotropic (non-Euclidean) detection functions in SECR models suggests recolonization may continue to the southwest and northeast along prominent linear mountain ranges. Although the KVP has grown considerably and is genetically stable, because of low population density and recolonization direction propensity, we recommend monitoring of critical demographic vital rates to evaluate harvest sustainability and long-term population viability. Our study demonstrates the utility of noninvasive genetic sampling and SECR models for monitoring reintroduced and recolonizing bear populations at temporal and spatial scales that should be useful for bear management.

Introduction

Anthropogenic activities, including habitat loss and overexploitation, caused range reductions and population declines of large carnivores globally, ultimately resulting in decreased biodiversity and landscape-level ecological changes (e.g., tropic cascades; Ordiz et al. 2013, Ripple et al. 2014). Although wildlife management practices, conservation policies, and habitat improvement during the last half of the 20th century facilitated some large carnivore recolonizations in parts of Europe and North America (e.g., gray wolf [*Canis lupus*] and brown bear [*Ursus arctos*]), these events occurred relatively slowly (Pyare et al. 2004, Fabbri et al. 2014, Votsi et al. 2016). Similar recolonizations will be difficult where human population density is high and habitat is severely degraded, but current predictions indicate regional large carnivore recolonizations may increase in frequency and geographical distribution in portions of the United States and Europe during coming decades (Chapron et al. 2014, Smith et al. 2015, LaRue and Nielsen 2016).

Where natural recolonization seems less probable, reintroduction has become a useful tool for bolstering restoration and enhancing biodiversity by reestablishing top-down ecological processes (Seddon et al. 2005, Estes et al. 2011, Rondinini and Visconti 2015). Many large carnivore reintroductions have been controversial, resulting in complications for single-species and community-level conservation and management (Williams et al. 2002). Reintroduction success has typically been defined as the establishment of a self-sustaining, viable population, but success has varied among and within taxa (Swaisgood 2010, Seddon 2015). Because reintroductions are often time and cost-intensive, most failures have been attributed to poor planning or a lack of post-release monitoring (Clark et al. 2002, Hayward and Somers 2009, Weise et al. 2014). Despite these challenges, multiple reintroductions have been implemented for several large carnivore species throughout the world, but the status of many of these populations remains uncertain (Seddon et al. 2005, Hayward and Somers 2009).

The American black bear (*Ursus americanus*) historically inhabited most of the United States but was extirpated from many areas by the early 1900s because of overexploitation and extensive habitat loss (Hall 1981, Clark et al. 2002). Protection provided by game laws that were implemented during the mid-20th century, habitat restoration, and multiple reintroduction programs have since facilitated resurgence of black bear numbers and an approximate 350% increase in range reoccupation in the eastern and southern United States since 1984 (Maehr 1984, Scheick and McCown 2014). Recent models predict large-scale recolonizations by black bears may occur throughout the country over the next 2 decades (Smith et al. 2015). Understanding how bears recolonize range is therefore important for conservation, but also for management purposes because their presence often results in high rates of conflict with humans (Penteriani et al. 2016).

Previous studies of recolonizing bear populations were based on live-capture, radio-collar, or harvest data, all of which can require multiple years to obtain sufficient sample sizes for population demographic and genetic investigations (Beston 2011, Marucco et al. 2011). Expanding bear populations appear to exhibit female-biased sex ratios and rare female dispersals, the combination of which can drive rapid population growth and range expansion despite habitat fragmentation (Swenson et al. 1998, Bales et al. 2005, Jerina and Adamič 2008). Nonetheless, genetic structuring, small effective population size, decreased genetic diversity, and isolation-accelerated genetic drift could all manifest following founder events, and few studies have investigated the genetic consequences of reintroduction or recolonization for bears (Onorato et al. 2007, Excoffier et al. 2009, Hagen et al. 2015).

During the past 2 decades, bear researchers and managers have increasingly used noninvasive genetic methods, such as hair traps, to sample bear populations (Waits and Paetkau 2005). A wealth of information can be captured from these studies for conducting population genetics tests, and can increase sample sizes for demographic parameter estimation compared to live-capture studies (Mumma et al. 2015). Recent developments in spatially explicit capture-recapture (SECR) statistical models, including the incorporation of landscape and habitat covariates in the density model, non-Euclidean detection functions, and resource selection can reduce parameter estimate bias, inform species-landscape relationships, and result in biologically realistic home range geometry (Efford et al. 2004, Royle et al. 2013, Sutherland et al. 2015). Thus, the combination of noninvasive genetic sampling and SECR models is well suited for evaluating and monitoring reintroduced and recolonizing bear populations.

Extensive deforestation and unregulated harvests caused the extirpation of black bears from the central Appalachian region by the early 1900s, including all of Kentucky and most of Tennessee, Virginia, and West Virginia (Plaxico and Bonney 2001, Wathen 2001, Ryan 2009, Virginia Department of Game and Inland Fisheries [VDGIF] 2012). To attempt to reestablish bear populations in a portion of this range, two separate reintroduction programs were implemented along the southeastern Kentucky border during the 1990s. Fourteen adult female bears and their respective cubs (*n* = 13) were reintroduced to the Big South Fork National River and Recreation Area at the Kentucky-Tennessee border during 1996–1997 (hereafter referred to as BSF population; Eastridge and Clark 2001). During 1990–1997, 55 bears (unknown sex ratio or age class) were reintroduced at two proximal locations in the Jefferson National Forest in southwestern Virginia along the Kentucky-Virginia border (hereafter referred to as KVP population; VDGIF 2008; Figure 2.1). In contrast to the BSF area, which was comprised of contiguous suitable bear habitat, fragmentation from agriculture and surface mining had occurred in the area of the KVP (van Manen and Pelton 1997, Townsend et al. 2009). The next nearest bear population in the region during this time was ~130 km to the East in Virginia, with fragmented mountainous habitat separating them (Comly-Gericke and Vaughn 1997, VDGIF 2012).

Based on population genetics analyses of bear hair samples collected from hair traps and live-captures during 2006–2009, Hast (2010) discovered that these reintroduction efforts created two genetically different allopatric populations with limited connectivity between them and with other populations in the region (e.g., Great Smoky Mountains population [Settlage et al. 2008]). Using noninvasive hair sampling and traditional (non-spatial) mark-recapture models, the BSF was estimated to be comprised of approximately 211 bears by 2012, indicating rapid population growth occurred during the 14 years after reintroduction ($\lambda = 1.18$/year), allowing relatively high genetic diversity ($H_E = 0.712$) to be retained despite demographic and genetic isolation (Murphy et al. 2015). Density estimated during 2008 using noninvasive hair sampling and SECR models was 0.075 bear/km^2 (95% CI: 0.054–0.097), or 130 bears (95% CI: 92–165) in the Kentucky portion of the KVP (Frary et al. 2011). However, based on abundance indices (e.g., frequency and geographical distribution of reported sightings and carcass recoveries), Kentucky Department of Fish & Wildlife Resources (KDFWR) estimated a combined total of 500 bears in the Kentucky portions of BSF and KVP by 2011 despite only ~17% of the BSF population residing in Kentucky ($N = 31$–66 [Murphy et al. 2015]; Noyce 2011). No formal abundance estimates or indices have ever been produced for the Virginia portion of the KVP. The increased frequency and geographical distribution of human-bear conflict incidents and reported sightings led to the presumption that the KVP was rapidly recolonizing westward from the Kentucky-Virginia border notwithstanding the uncertainty surrounding population size (Frary et al. 2011, Unger et al. 2013).

Results from the BSF and Interior Highlands (Arkansas) bear reintroductions indicated protection from harvest during the first 10–14 years following releases was critical to population establishment and growth (Clark and Smith 1994, Murphy et al. 2015). Annual ~90-day non-quota bear harvests were first implemented in the Virginia portion of the KVP during 2003, just 6 years post-reintroduction (VDGIF 2012). The average annual harvest success in this portion of Virginia has remained low relative to other parts of the state, suggesting abundance may be low ($\bar{x}$ = 46 bears harvested/year [2011–2013] or 2% of total Virginia harvest [$\bar{x}$ = 2,159 bears/year]; VDGIF 2016). No bear harvests were allowed in the Kentucky portion of the KVP until 2009 when limited annual quotas were implemented (KDFWR 2009). These quotas were restrictive (≤25 bears/year during our study), but changes to the harvest have occurred annually since 2010, including an increase in the number of annual harvest seasons from one to three (KDFWR 2013).

Population demographic monitoring has shown that even conservative increases in the harvest of small bear populations can result in precipitous population declines, and because of the low reproductive rates inherent to bears, recovery from these reductions can be lengthy (Dobey et al. 2005, Howe et al. 2007, Clark et al. 2010). Small populations are susceptible to heightened levels of demographic and environmental stochasticity compared to their larger counterparts, already prone to increased probabilities of extinction and deleterious genetic effects without being subjected to exploitation (Lande 1993, Mills 2012). Systems comprised of ≥1 reintroduced population may be especially vulnerable because releases often occur in areas that are beyond typical species-specific dispersal distances from source populations, which can decrease the probability of genetic or demographic rescue (Tallmon et al. 2004, Frankham 2015). Furthermore, although the population establishment and growth phases of reintroductions are critical to success, the ultimate success criterion is long-term viability during the regulation phase (Sarrazin 2007, Robert et al. 2015). Given the need for reliable demographic information for the sustainable management of the KVP population, and the impending need for practical and efficient methods to monitor recolonizing bear populations, we used noninvasive genetic sampling and SECR models to investigate the demographics, genetics, and spatial expansion patterns of the reintroduced KVP black bear population. Our objectives were to: 1) estimate population abundance, density, and sex ratio, 2) further investigate the potential for deleterious genetic consequences caused by founder events, and 3) identify the spatial expansion patterns of the KVP black bear population.

Study Area

Research was conducted at four separate study areas located in eastern Kentucky and – to a lesser extent – southwestern Virginia (Figure 2.1). These study areas were identified based on occupancy estimates (Frary et al. 2011) combined with the frequency and distribution of live-capture, mortality, and natal den visit data collected during 2003–2010 (J. Cox, unpublished data). Our Pine-Black (hereafter referred to as PB) and Cumberland Gap (hereafter referrred to as CG) study areas had the highest probabilities of bear use in the area ($\Psi \geq 0.75$), likely constituting core areas of the KVP population (Unger et al. 2013). The Kentucky Ridge (hereafter referred to as KR) and Redbird (hereafter referred to as RB) study areas had moderate probabilities of bear use ($\Psi \geq 0.25 < 0.75$), but were the nearest protected lands to PB and CG in Kentucky that had moderate to high elevations, factors indicative of bear occupancy (Frary et al. 2011). These study areas were located in the Appalachian Plateau physiographic province in the Central Appalachian ecoregion (Figure 2.1; Woods et al. 2002, Appalachian Regional Commission 2016). Study area boundaries included the entirety of Cumberland Gap National Historical Park, three KDFWR Wildlife Management Areas, two Kentucky State Parks, one Kentucky State Nature Preserve, and portions of the Daniel Boone and Jefferson National Forests, embedded within a matrix of forested, agricultural, and surface-mined private lands. The majority of the area was comprised of linear mountains arranged in a southwest to northeast direction (approximately 65° axis), characterized by steep slopes with deep valleys and narrow ridgetops (Campbell 1893, Thornbury 1965). However, the RB study area was comprised of smaller rolling foothills characteristic of the Cumberland Plateau with similar general vegetation types as the other study areas (Kleber 1992). Elevations ranged from 257 m at the RB study area to 1,263 m at the PB study area. Forest composition was mixed-mesophytic and included several species of oak (*Quercus* spp.), hickory (*Carya* spp.), ash (*Fraxinus* spp.), and pine (*Pinus spp.*), as well as American beech (*Fagus grandifolia*), cucumber magnolia (*Magnolia acuminata*), yellow popular (*Liriodendron tulipifera*), and eastern hemlock (*Tsuga canadensis*) throughout all 4 study areas (Braun 1950). The climate in eastern Kentucky was mild and moderately humid, with an average annual temperature of 13ºC and 133 cm of average annual precipitation (Hill 1976); although, cooler temperatures (8ºC) and greater levels of precipition (156 cm) were present on Black Mountain in the PB study area (Hill 1976, Jones 2005). Human population densities were 15/km^2, 11/km^2, and <1/km^2 at the PB, KR and RB, and CG study areas, respectively (United States Census Bureau 2010).

Methods

Sampling

We used barbed wire hair traps in a systematic capture-mark-recapture (CMR) sampling design to collect black bear hair for microsatellite genotyping during 2012 and 2013. We used a trap spacing of 1.58 km x 1.58 km (i.e., 2.50 km^2 area/trap), which ensured four traps were located within an estimated average annual female bear spring-summer home range size ($\bar{x}$ = 10 km^2; J. Cox, unpublished data; Otis et al. 1978). We established the following sampling grids: 1) a 215-km^2 sampling grid of 86 contiguous cells at PB, 2) a 102.5-km^2 sampling grid of 41 contiguous cells at CG, 3) a 95-km^2 sampling grid of 38 contiguous cells at KR, and 4) a 100-km^2 sampling grid of 40 contiguous cells at RB. We constructed a single baited barbed wire hair trap in each sampling cell to collect black bear hair (Woods et al. 1999; Figure 2.1). Hair trap placement was random within a sampling cell but was restricted to >100 m from roads and >500 m from campgrounds, picnic areas, and residential areas to avoid anthropogenic conflicts. We constructed all hair traps using two wires placed at 35 cm and 65 cm above the ground; each was wrapped around 3–5 trees to create an enclosure approximately 25 m^2 in size (Woods et al. 1999). By backdating captures of bears >1 year-of-age from subsequent years, Laufenberg and Clark (2014) found no evidence that these wire heights captured cubs of-the-year. We baited traps with pastries, checking and re-baiting them weekly for eight consecutive weeklong sampling occasions during June–July of each year. Traps were not moved between occasions but were moved within sampling cells between years. Each barb was treated as an individual sample, and hairs were removed using tweezers that were sterilized between collections using flame from a lighter. We placed hair samples in individually labeled paper coin envelopes, which were then stored in desiccant. We used a flame to sterilize barbs following sample collection to prevent cross-contamination of samples during subsequent occasions and to eliminate spurious detections. Hair collection procedures were approved by the University of Kentucky Institutional Animal Care and Use Committee (Protocol #00626A2003).

Laboratory Analyses

All collected samples were sent to Wildlife Genetics International (WGI; Nelson, British Columbia) ≤2 months after collection for DNA extraction and amplification following the protocols of Paetkau (2003). For cost efficiency, we used a subsampling protocol of one sample per trap per occasion (Settlage et al. 2008, Murphy et al. 2015). Following sample randomizations for each trap during each occasion (trap-occasion) by personnel at WGI, technicians selected the first sample encountered at a given trap that contained five guard hair roots or ≥20 underfur hairs for genotyping, and repeated this process for each trap-occasion. If there were no available samples at a trap-occasion that met this threshold, the next best available sample was chosen using a minimum threshold of one guard hair root or five underfur hairs. Standard protocols were followed for DNA extraction by WGI (Woods et al. 1999, Paetkau 2003). Seven black bear-specific microsatellite markers (G10B, G10H, G10J, G10L, G10M, G10P, and MU23) and a sex marker (Ennis and Gallagher 1994) were used to identify individual black bears (Paetkau and Strobek 1994). For genetic differentiation and gene flow tests, we selected an additional four markers (G1A, G1D, G10C, and MU59), or 12 in total, for a subset of 20 individuals from each of the PB and CG study areas (40 total; Excoffier 2001). To reduce the chances of having inflated the number of individuals due to undetected genotyping error, the methods of Paetkau (2003) were used.

Population Genetics

Genotyped samples were grouped and analyzed by the study area in which they originated. We used program Genepop 4.2 to test for Hardy-Weinberg equilibrium (HWE) between genotypes, investigate for linkage disequilibrium (LD) with P-values adjusted using a Bonferroni correction (Rice 1989), estimate genetic diversity as expected heterozygosity (H_{E}), and also calculate observed heterozygosity (H_{O}; Louis and Dempster 1987, Guo and Thompson 1992, Raymond and Rousset 1995). We used the divBasic function in the R software (R Core Team 2012) package diveRsity to estimate allelic richness (R_{A}) using a rarefaction technique that accounts for discrepancies in sample sizes (Hurlbert 1971, Keenan et al. 2013). We compared R_{A}, H_{E}, and H_{O} between study areas with a non-parametric Mann-Whitney U-test to investigate whether or not observed differences in estimates of these parameters were artifacts of sample size discrepancy (i.e., the null hypothesis asserts that the medians of 2 samples are identical [Zar 2010]).

We used the LD method implemented in program NeEstimator v2.01 to provide an estimate of the raw (naïve) effective number of breeders that contributed to the population ($\widehat{N}_B$; Hill 1981, Do et al. 2014). Because the bias in this estimate for iteroparous species (e.g., bears) can be as high as 14%, we applied a 2-vital rate adjustment formula to $\widehat{N}_B$ to calculate the true number of effective breeders (N_{B}; Waples et al. 2014). We then used N_{B} in a separate 2-vital rate adjustment formula for raw effective population size ($\widehat{N}_E$) to calculate true effective population size (N_{E}) – the size of an ideal population that would lose heterozygosity at a rate equal to that of the observed population (Waples et al. 2014). These adjustment formulas have been shown to reduce estimate bias to ≤5% for iteroparious animals, including brown bears, by incorporating 2 vital rates that account for age structure: age at maturity (α) and adult life span (AL = maximum age – α +1). We used 4 years-of-age for α because previously collected reproductive data indicated this was the average age of primiparity in the KVP population (J. Cox, unpublished data [2003–2008]). We used $\alpha = 4$ and a maximum age of 16 (the oldest known bear in the KVP population during our study [J. Plaxico, unpublished data]) to calculate an AL of 13 years. Confidence intervals (95%) were corrected by applying the aforementioned 2-trait adjustment formulas to the lower and upper bounds of $\widehat{N}_B$ and $\widehat{N}_E$ estimates.

We considered an island model of recolonization because previous studies indicated the KVP may be subdivided into 2 core areas (Frary et al. 2011, Unger et al. 2013). We investigated for genetic subdivision by estimating Wright's fixation index (F_{ST} [Wright 1951]) from observed allele frequencies using an analysis of molecular variance in Program GenAlEx 6.5 (Weir and Cockerham 1984, Peakall and Smouse 2012). Although the theoretical maximum of F_{ST} is 1.0 (complete differentiation), we rescaled our maximum F_{ST} to H_{E} to correct for the negative bias caused by the selection of microsatellite markers for neutrality (Hedrick 1999, Balloux and Lugon-Moulin 2002, Jakobsson et al. 2012). We estimated the number of migrants per generation (*Nm*) between study areas using the private allele method in Genepop 4.2 (Slatkin and Barton 1989). To determine if this gene flow (*GF*) between study areas was greater in a particular direction, we used the divMigrate function in the R package diveRsity to quantify the relative migration level, where $GF = 1$ is the maximum and $GF = 0$ is the minimum (Keenan et al. 2013, Sundqvist and Kleinhans 2013). We also calculated Nei's genetic distance (D_{ST}) with GenAlEx 6.5 to evaluate relatedness of individuals between study areas (Nei et al. 1978).

Demographic Estimates and Spatial Patterns

To estimate density ($\widehat{D}$), we used spatially explicit capture-recapture (SECR) models in the R software package secr (Efford 2015). We fit models using a binomial observation model with a half-normal detection function (Efford et al. 2009, Royle et al. 2014). We modeled hair traps as proximity detectors because an individual could be caught at multiple traps during a single occasion and, because subsampling occurred after sample randomization for each trap-occasion, all individuals captured at a trap had an equal probability of being in the subsampled capture history. We developed a set of *a priori* sex-specific models that included expected sources of variation in detection based on previous black bear hair trapping studies in the region (Settlage et al. 2008, Murphy et al. 2015). We modeled a trap-specific behavioral response (bk) on the probability of detection at the activity center of an individual (g_0). We allowed g_0 to be fixed across study areas, vary across study areas (A), or vary across study areas and years (A×Y). We did not allow g_0 to vary by year (Y) and not vary by study area because this did not seem plausible – if g_0 varied by year, it is unlikely it would have varied the same between study areas. We allowed σ, the spatial scale of the detection function, to be shared or to vary by study area. We did not allow $\widehat{D}$ to vary between years because preliminary analyses indicated this change was negligible, but we did allow $\widehat{D}$ to vary between study areas.

Radio-collar data (n = 146 bears [2003–2014]; J. Cox and S. Murphy, unpublished data) indicated that both home range orientation and direction of movement tended to follow the same direction as the linearly arranged mountains in our study areas. We therefore used two different space models: 1) isotropic (Euclidean), and 2) anisotropic (non-Euclidean), the latter of which allowed the detection function to be oriented along the mountain ridges. We used a user-defined distance function to compute the anisotropic distances using the coords.aniso function in the R package geoR (Ribeiro Jr. and Diggle 2001, Diggle and Ribeiro Jr. 2007; Table 2.6). This function has two parameters: an anisotropy angle parameter (Φ_A) and an anisotropy ratio parameter (Φ_R). We set Φ_A to 65 degrees from the y-axis based on the orientation of prominent mountains, and estimated Φ_R by maximum likelihood. Because 1 is the minimum value of Φ_R (i.e., isotropic space), we modeled Φ_R by subtracting 1 and using a log link, then added 1 back to the obtained Φ_R estimates for reporting results (M. Efford, University of Otago, New Zealand, personal communication).

Our study areas were located in a heterogeneous landscape fragmented by agriculture and surface mining, so we used habitat masks for parts of our analyses. Using 2011 National Land Cover Database data at 30-m resolution (Jin et al. 2013), we first reclassified deciduous forest, evergreen forest, mixed forest, shrub/scrub, woody wetlands, and emergent herbaceous wetlands as natural cover, and open water, developed, barren land, grassland, pasture/hay, and cultivated crops as non-natural cover in ArcMap 10.2 (ESRI, Redlands, CA). We then smoothed this reclassified raster by calculating the percent natural cover within a moving circular window with a 1.8-km radius, which corresponded to the average annual female home range size. We reclassified raster pixels that were $\geq 70\%$ natural as bear habitat and $<70\%$ natural as non-bear habitat following smoothing (Hooker et al. 2015). This reclassification was based on the lower range of percent natural land cover within estimated home ranges of male and female black bears in the southeastern United States (Murrow et al. 2013). Finally, we converted the reclassified bear habitat raster to polygon shapefiles to define our habitat masks for each study area (Figure 2.2).

To define the extent and spacing of the state space (i.e., area of integration [AI]) for the PB study area, we increased the discrete space density and associated buffer until $\widehat{D}$ reached an asymptote, which resulted in AIs of 4 km and 9 km for females and males, respectively (Figure 2.1; Borchers and Efford 2008). Inholdings of non-habitat within our sex-specific PB areas of integration were not removed for estimating $\widehat{D}$ because they were surrounded by habitat in a manner that may have led to an activity center occurring in non-habitat (Figure 2.1). We used the same AI distances for the CG study area; however, we excluded areas of non-habitat within these AIs for estimating $\widehat{D}$ because the distribution of non-habitat was such that activity centers could not occur there (Figure 2.1). To produce abundance estimates, we used our habitat masks that excluded non-habitat for both study areas. Data from live-captures and radio-monitoring indicated some female bears resided outside of our 9-km AI at the PB study area (n<15; J. Plaxico and S. Murphy, unpublished data), so we extended this habitat mask to include these confirmed locations after plotting them in ArcMap 10.2 (Figure 2.2).

All combinations of our *a priori* models were fit using isotropic detection functions and then refit using anisotropic detection functions. We evaluated models with Akaike's Information Criterion corrected for small sample size (AIC_c) and model-averaged all models ≤4 $\Delta\mathrm{AIC}_c$ units of the top model to produce estimates of $\widehat{D}$, g_0, and σ (Burnham et al. 2011). We used $\widehat{D}$ estimates to derive sex-specific estimates of abundance as the expected number of individuals ($E[N]$) within our bear habitat masks (Efford and Fewster 2012). We produced combined abundance estimates (both sexes) within study areas and among study areas by adding the individual estimates and obtaining the combined variances, assuming independence (Casella and Berger 2008). To investigate if male to female sex ratios at our study areas differed significantly, we evaluated deviation from an ideal 1:1 ratio based on the presence or absence of 95% confidence interval overlap of sex-specific $\widehat{D}$ estimates. We assumed exponential growth was possible at KVP following the original reintroduction because of the extent of available potential bear habitat in the region (Unger et al. 2008), and therefore used an exponential growth equation to provide an approximate estimate of the mean annual population growth rate (λ) at KVP since 1997, assuming all 55 founders were alive at that time (Gotelli 2008).

Because evidence from previous studies indicated female $\widehat{D}$ may be a decreasing function of distance away from core areas in recolonizing bear populations (Bales et al. 2005, Jerina and Adamič 2008), we created a single covariate that we modeled on $\widehat{D}$ to attempt to investigate this. We calculated the Euclidean distance between the two locations that bears were released in southwestern Virginia and identified the midpoint between them (J. Sajecki and J. Wills, VDGIF, personal communication; Figure 2.2). We then created a Distance from Release Area raster by calculating the circular Euclidean distance from this midpoint. We fit sex- and study area-specific models with a trap-specific behavioral response to capture on g_0, and anisotropic detection functions.

Results

Sampling

During 2012–2013, we collected a total of 1,503 hair samples from 123 hair traps (60% of total traps) among our four study areas, of which 656 (43.6%) samples were genotyped and assigned to 199 (99M:100F) individuals. At PB, we collected 946 samples from 81 traps (94% of total traps), with 912 (96.4%) having met our selection criteria (≥1 guard hair root or ≥5 underfur hairs), and 419 (46%) assigned to 142 (65M:77F) individuals. We collected 544 hair samples from 35 traps at CG (85% of total traps) – 524 (96.3%) of those samples met our selection criteria, and 224 (43%) assigned to 54 (31M:23F) individuals. We collected five samples from two traps at RB (5% of traps), and eight samples from five traps at KR (13% of traps), with nine (69%) samples meeting our selection criteria, and all of which assigned to three male bears. We documented no movement by bears between study areas.

Population Genetics

All individuals identified at PB (n = 142) and CG (n = 54) were successfully genotyped for seven markers with no 1-MM or 2-MM pairs in the datasets. Both samples met the criteria for HWE with no deviations (PB: χ^2_{14} = 13.6, P = 0.48; CG: χ^2_{14} = 13.9, P = 0.46). Of 21 loci pairings for seven markers, five (>23% of total) and two loci pairs (<10% of total) were in linkage disequilibrium at PB and CG, respectively. Allelic richness (R_A), genetic diversity (H_E), and observed heterozygosity (H_O) were similar between both study areas (R_A: U = 30.0, Z = -0.158, P = 0.436; H_E: U = 22.5, Z = -0.192, P = 0.425; H_O: U = 18.0, Z = -0.767, P = 0.221; Table 2.1). The estimated number of breeding individuals that genetically contributed to the PB sample ($N_{B[PB]}$) was 56 bears

(95% CI: 44–72) after 1,021 independent comparisons, which resulted in an effective population size ($N_{\mathrm{E[PB]}}$) of 64 bears (95% CI: 50–82), or an N_E/N ratio of 0.27. The estimated number of breeding individuals that had genetically contributed to the CG core ($N_{\mathrm{B[CG]}}$) was 26 bears (95% CI: 18–36) after 940 independent comparisons, which resulted in an $N_{\mathrm{E[CG]}}$ of 30 bears (95% CI: 21–41), or an N_E/N ratio of 0.45. We detected low but significant genetic differentiation between PB and CG ($F_{\mathrm{ST}} = 0.024$; $P<0.001$), and scaling using H_{E} as the maximum confirmed low subdivision ($F_{\mathrm{ST}} = 0.032$). We estimated the number of migrants per generation (Nm) between these two cores was six bears (SE = 0.58), and genetic distance (D_{ST}) was 0.087 ($P<0.05$). Relative gene flow occurred at a 19% higher rate from PB to CG ($GF_{\mathrm{PB\text{-}CG}} = 1.00$; $GF_{\mathrm{CG\text{-}PB}} = 0.83$). We estimated $N_{\mathrm{B[KVP]}}$ of 62 bears (95% CI: 50–76), $N_{\mathrm{E[KVP]}}$ of 71 bears (95% CI: 57–87), or an N_E/N ratio of 0.23 for the KVP population (PB and CG combined; Table 2.1).

Demographic Estimates and Spatial Patterns

Model selection demonstrated universal preference for models with anisotropic detection functions (Table 2.2, 2.3; Appendix B). Estimates of Φ_{R} for male and female bears at both study areas were 1.66 (95% CI: 1.34–2.28) and 1.98 (95% CI: 1.55–2.74), respectively (Figure 2.3). The top model for male bears included constant $\widehat{D}$ across study areas, a trap-specific behavioral response with study area variation on g_0, an interaction effect between session and study area on g_0, and constant σ (Table 2.2). The top two female-specific models had nearly identical AIC$_c$ values and model weights; both indicated $\widehat{D}$ was constant across study areas, a trap-specific behavioral response with an additive study area effect on g_0, and constant σ (Table 2.3).

We produced parameter estimates by model-averaging only models that included fixed $\widehat{D}$ estimates because of a lack of support for $\widehat{D}$ varying by study area (Table 2.2, Table 2.3). We estimated a significantly higher σ for males than females at both the PB and CG study areas (Table 2.5). Our estimates of g_0 were similar for both sexes at PB, but considerably higher for females than males at CG (Table 2.5). Male and female $\widehat{D}$ were 0.093 bear/km^2 (95% CI: 0.073–0.117) and 0.171 bear/km^2 (95% CI: 0.132–0.219), respectively, resulting in a significantly female-biased sex ratio (0.53M:1.00F [χ_1^2 = 40.66; $P<0.001$]). Combined $\widehat{D}$ for the KVP was 0.26 bear/km^2 (95% CI: 0.18–0.37). We estimated 413 (95% CI: 269–636) and 69 (95% CI: 48–115) total bears within our PB and CG habitat masks, respectively. The combined total *E(N)* estimate for the KVP was 482 (95% CI: 317–751) bears, representing an approximate mean annual population growth rate of 1.14 (95% CI: 1.12–1.18) during 1997–2013. We also found support for female $\widehat{D}$ at PB decreasing with distance from the reintroduction release areas (Table 2.4). Density was highest (0.34 bear/km^2) at the area nearest the midpoint, decreasing to 0.04 bear/km^2 at the southwestern edge of our PB study area (Figure 2.4).

Discussion

Our combined $\widehat{D}$ and *E(N)* estimates were considerably higher and more precise than the 2008 estimates (0.075 bear/km^2 or 130 bears [Frary et al. 2011]). Spatially explicit capture-recapture (SECR) models perform best for noninvasive bear hair trapping studies when σ is at least half the average trap spacing, and negative bias is introduced if traps are too far apart for a given σ (Sollmann et al. 2012, Sun et al. 2014). Trap spacing for the 2008 study was 5 km but σ was only 1.61 km, or 43% smaller than recommended. In contrast, all of our σ estimates for both sexes at both study areas were 13–87% larger than half our 1.58 km trap spacing (Table 2.5). The spatial extents of sampling were also considerably different between studies, which may have influenced the precision of parameter estimates. The 2008 study used an extensive sampling design that covered 7,825 km^2, producing parameter estimates for a 3,000 km^2 area. We instead sampled a smaller total area (513 km^2) using more intensive sampling at four study areas, each covering a 95–215 km^2, but produced estimates for a 1,804 km^2 area (Figure 2.1). Sampling multiple areas with each covering spatial extents ≥1.5 times larger than a female bear home range but smaller than a male bear home range has been shown to yield precise parameter estimates when using SECR models (Sollmann et al. 2012). By converting our σ estimates to home ranges assuming a bivariate normal distribution (Royle et al. 2014), the point estimate of female home range was 15.21 km^2, or 6.74–14.13 times smaller than our study areas. This indicates parameter estimate precision was probably improved without having to cover the extensive area that was sampled during 2008. Finally, we considered both isotropic and anisotropic detection functions in our SECR models, whereas Frary et al. (2011) only used the former. Our model selection demonstrated universal preference for models with anisotropic detection functions, which resulted in less biased parameter estimates assuming our models were correct (Appendix B).

Subsampling is usually required in bear hair trapping studies because of the prohibitive costs of genotyping all samples (*n* = 1,503 in our study), but it can introduce parameter estimate bias in some scenarios. First, bias can be introduced by subsampling through the loss of statistical power to select an appropriate model (e.g., M_h or M_b [Laufenberg et al. 2013]). This is of less concern when using SECR models because the portion of individual heterogeneity stemming from the juxtaposition of animal activity centers and traps is always modeled. More power also exists to detect a trap-specific behavioral response to capture compared to the global behavioral response assumed in non-spatially explicit mark-recapture models, which do not make use of multiple capture events within a given occasion. Second, when using baited traps and SECR models, a trap-specific behavioral response to capture should be assumed *a priori* as we did (Tables 2.2 and 2.3). As a result of not observing some first captures that are subsampled out of the capture history, subsampling in the presence of a behavioral response to capture can introduce potentially large bias in parameter estimates from non-spatially explicit mark-recapture models (Augustine et al. 2014); however, simulations indicated SECR models estimate $\widehat{D}$ with very little bias in the same scenarios (B. Augustine, Virginia Polytechnic Institute and State University, unpublished data). Third, when using the recommended two-wire hair trap design that we used, randomized subsampling may be critical for mitigating the potential bias from individual heterogeneity in g_0 introduced by older, larger males being more likely to encounter the top wire, which was typically the wire that samples were collected from first (Hooker et al. 2015). We therefore believe the potential positive bias in our parameter estimates caused by our subsampling was minimal, but we acknowledge that any subsampling will reduce g_0 and thus decrease the precision of $\widehat{D}$, and in the presence of differential hair deposition rates (e.g., small bears leaving fewer samples than large bears), subsampling can introduce individual heterogeneity and negative bias. Finally, we note that with our subsampling protocol (one sample/trap/occasion) only a single individual can be captured in each trap-occasion. This may appear to change the observation model from proximity detectors to single-catch traps, but because the subsampling process is random, the capture order does not matter as it does in single-catch trap scenarios (B. Augustine, Virginia Polytechnic Institute and State University, unpublished data).

Our *E(N)* estimates are minimums for the KVP because our habitat masks probably did not include the entire extent of this population given the southern reintroduction release area was not included within their bounds (Figure 2.2). However, we could not justifiably extend our habitat masks too far beyond our AIs because of few captures at both the KR and RB study areas and no evidence to support female bears resided between our study areas (J. Plaxico, unpublished data). We also found support for female $\widehat{D}$ in the PB core decreasing with distance away from the reintroduction release areas, but we note that the false positive rate for detecting at least one trend in the four sex-area comparisons was 18.5% (Table 2.5, Figure 2.4). Because of the typically limited dispersal distances for female bears and the larger dataset and spatial coverage of the trapping array at PB compared to CG, we expected to find the most support for a trend in the female component of this area. We did not produce *E(N)* estimates from this $\widehat{D}$ gradient because it required extrapolating to distances that were substantially beyond the extent of our trapping grid, and we did not have enough power to distinguish between different functional forms of the relationship (e.g., transformations off Euclidean distance). Nonetheless, our findings indicated $\widehat{D}$ was likely much lower and not uniform outside of our habitat masks. The female-biased sex ratio (0.53M:1.00F) we estimated for the core areas combined with male-only detections in peripheral areas suggests male bears may reside in the periphery during much of a given year, possibly because of the availability of high quality unoccupied habitat (Swenson et al. 1998, Jerina and Adamič

2008). Our sampling occurred during breeding season when reproductively mature males should be in the core areas seeking mates, so we believe our estimates adequately represent the sex structure of this population.

Because the 2008 study was restricted to the Kentucky portion of the KVP, whereas our study included additional lands in southwestern Virginia, and because the former produced negatively biased parameter estimates resulting from a lower than recommended trap density, we did not approximate population growth (λ) using the 2008 *E(N*) estimate. We instead assumed all 55 founders were alive and present on the study area by the end of the reintroduction project, estimating exponential growth during 1997–2013. Other bear reintroductions experienced a decreased founder group because some founders died, dispersed, or attempted to home back to their respective capture locations (Eastridge and Clark 2001, Wear et al. 2005). Although the original KVP founders were not monitored, our relatively low estimates of effective population size (N_E = 71) and effective number of breeders for the KVP (N_B = 62) suggests most of the 55 founders remained in the general area following releases. Based on our *E(N)* estimates, we conservatively estimated population growth was relatively rapid during the 16 years post-reintroduction (λ = 1.14/year). A reintroduced bear population in the Interior Highlands of Arkansas also exhibited a high growth rate over a 4-year period (λ = 1.26/year [Clark and Smith 1994]), and a 1.18/year λ was estimated for the BSF population over a 14-year period (Murphy et al. 2015). Interestingly, these three studies were all conducted 14–20 years after the reintroduction programs were completed, and none of these populations were subjected to harvest for 6–14 years post-reintroduction. For comparison, estimated growth rates of reintroduced bear populations 2–4 years following releases were 1.03–

1.09 (Eastridge and Clark 2001, Wear et al. 2005, Laufenberg and Clark 2014). Reintroduced bear populations appear to initially experience relatively slow growth during the years immediately following releases, likely because of small founder population size, but our cumulative findings indicate that if protected from harvest and other threats during the initial stages of population establishment, rapid growth may occur 10–14 years post-reintroduction provided sufficient habitat is available.

Our $\widehat{D}$ estimates for the KVP were low compared to estimates for other central and southern Appalachian bear populations (0.03–1.30 bears/km^2 [McLean and Pelton 1994, Bridges 2005, Settlage et al. 2008, Murphy et al. 2015]). None of these studies used SECR models, though, which tend to produce estimates that are more precise because they incorporate the spatial variation in captures and are not dependent on defining an effective sampling area (Borchers and Efford 2008). Considering our estimated λ, the fact that we did not detect any female bears west of our PB and CG study areas, and the support for decreasing female $\widehat{D}$ as a function of distance away from the release areas at PB, our low $\widehat{D}$ estimates indicate bears probably have not yet saturated the core areas and the KVP was not subjected to density-dependent regulatory mechanisms during our study (Czetwertynski et al. 2007). Our $\widehat{D}$ estimates were instead most similar to small bear populations in Arkansas and Georgia that likely experienced overexploitation (Clark et al. 2010, Hooker et al. 2015). However, because harvests were implemented 6 and 12 years post-reintroduction in Virginia and Kentucky, respectively, we believe that Kentucky probably served as a refuge for the initially small bear population, thereby allowing the KVP to avoid overexploitation during the population establishment and growth phases (Sarrazin 2007).

Previous studies suggested that rapid bear recolonizations are primarily driven by infrequent and rare female dispersal, and reintroduction is simply an experimental model of this process (Swenson et al. 1998, Eastridge and Clark 2001, Jerina and Adamič 2008). The sex ratio and age classes of bears released at KVP during 1990–1997 are unknown, but at least four females were released at the northern site in the PB study area (J. Sajecki, VDGIF, personal communication). Our CG study area was 85–105 km from both release sites, but the first confirmed occurrence of bears in this area was of an adult female with cubs during 1991 (Simmons 1997; J. Beeler, National Park Service, personal communication). This indicates that at least one adult female that either mated prior to translocation or did so after release during 1990 subsequently dispersed ≥85 km to found the CG core area. Movements <50 km are more typical following translocation, but female dispersals of up to 192 km from release sites have been documented in other bear reintroductions (Comley-Gericke and Vaughn 1997, Eastridge and Clark 2001, Wear et al. 2005).

Because these founder events often result in initially small and sometimes isolated populations, an unfortunate consequence is an increased probability of deleterious genetic effects (Excoffier et al. 2009, Jaimeson 2010). Despite not documenting movement between any of our study areas, we discovered a low genetic distance ($D_{\mathrm{ST}} = 0.087$) and moderate gene flow between the two core areas ($N\mathrm{m} = 6$ bears/generation), but found evidence of genetic structuring. We suspect this low structuring ($F_{\mathrm{ST}} = 0.032$) is a lingering effect representative of higher differentiation that developed immediately after the 1990–1991 female founder event at CG. A study of recolonizing brown bears in Finland found moderate genetic differentiation ($F_{\mathrm{ST}} = 0.05$) between founder and source populations, but this structuring decreased at a rate of 0.002 per year because of gene flow from the source (Hagen et al. 2015). We did not have genetics information for the original founders nor was the CG core monitored prior to our study, so we could not explicitly investigate this for the KVP. However, assuming similar moderate differentiation had developed between the PB and CG cores within six years after the CG founder event (i.e., by 1997), and assuming this structuring declined at the same rate as what was observed for bears in Finland, F_{ST} within the KVP by the end of our study would have been identical to our estimate. The asymmetrical gene flow from PB to CG that we discovered, which is probably an underestimate because both core areas were closely related (Sundqvist et al. 2013), indicates that if higher genetic structuring existed, it was reduced by immigration into CG from the PB core (i.e., genetic rescue of the CG founder group; Frankham 2015).

We found no evidence of problematic genetics effects in either of the two core areas or the KVP population as a whole (Table 2.1). Conversely, we found the relatively high and equal H_O and H_E (0.78) represent a complete lack of inbreeding and recovery from the reintroduction-induced bottleneck despite all of the original 55 founders being sourced from the same population. It could be argued that this is evidence of immigration and high rates of gene flow into the KVP from other populations (Excoffier et al. 2009). However, genetic connectivity with other bear populations in the region has been low (<2 migrants/generation [Hast 2010]) and our effective number of breeders estimate for the KVP (N_{B} = 62 bears) was only slightly higher than the number of original founders, indicating the KVP remains mostly the product of the reintroduced founder group. Our findings support those of recent studies that suggested for bear populations, rapid population growth can retain genetic diversity and mitigate deleterious genetic effects caused by founder events (Hagen et al. 2015, Murphy et al. 2015). Therefore, the low N_E/N ratio we estimated for the KVP (0.23), which is a maximum, has likely been maintained by limited connectivity with other bear populations in the region and a skewed sex ratio (Schmeller and Merilä 2007, Hoehn et al. 2012).

Because harvest rates were low prior to and during our study, the significantly female biased sex ratio and decreasing female density as a function of distance from the release areas at PB are representative of a bear population still in the process of recolonization (Bales et al. 2005, Jerina and Adamič 2008). Our anisotropic detection function in SECR models demonstrated movements by both sexes at both study areas tended to follow the linear direction of prominent mountains (Figure 2.3). Although we acknowledge that directed movement at the home range level does not always translate to directed dispersal movements, our findings suggest recolonization may be proceeding to the southwest and northeast along these mountain ranges (Figure 2.3). We suspect bears at KVP display preferential movement along the these high elevation mountains because they are comprised of relatively high quality forested habitat, have lower human activity than the valleys, and provide energetically efficient travel corridors that may help bears satisfy resource demands. Because one of the most probable range expansion directions for the isolated BSF population is to the southeast towards Pine and Cumberland Mountains (J. Laufenberg, University of Tennessee, unpublished data), southwestern expansion by the KVP along identical mountains may result in connectivity between these two reintroduced bear populations.

Similar linear movement and population expansion patterns have been identified in other black bear populations using radio-collar data, but to our knowledge, these patterns have never been documented using noninvasive mark-recapture data (Clark and Smith 1994, Bales et al. 2005). Traditional mark-recapture models do not incorporate the spatial distribution of captures, so without SECR models and our use of an anisotropic detection function transformation, we would not have been able to identify this directed movement from our data. Wildlife populations, particularly large carnivores, do not exhibit stationary and symmetric movement often because resources are typically distributed unevenly across heterogeneous landscapes. This biological reality was the justification for the development of the ecological distance function (i.e., least cost path between activity centers and traps [Royle et al. 2013, Sutherland et al. 2015]) and for our use of an alternative detection function. A possibly desirable feature of our approach compared to the ecological distance is that the effective trapping area remains the same for all individuals, which does not violate a potentially compensatory relationship between g_0 and σ (Efford and Mowat 2014). This result stems not from the transformation itself but from the fact that the detection functions for all animals are transformed in the same manner rather than depending on the local landscape. Therefore, our approach may be useful for SECR analyses of bear or other large carnivore populations, most of which are capable of exploiting multiple habitat types but may prefer or have movements restricted by linearly arranged anthropogenic or natural landscape barriers (e.g, roads or mountains; Roever et al. 2010, Clark et al. 2015).

Management Implications

Our findings support those of previous studies that indicated genetic rescue of small founder groups created by female bear dispersal events can occur rapidly if moderate gene flow from the source population exists (Hagen et al. 2015). The significantly female biased sex ratio we estimated, and the support for female density decreasing with distance from the reintroduction areas provides additional characteristics for identifying recolonizing bear populations based on demographics (Bales et al. 2005, Jerina and Adamič 2008). We also found robust population growth occurred in the KVP during the 16 years post-reintroduction despite an early onset of harvest in Virginia, suggesting that for small founder groups established by reintroduction or recolonization, the probability of genetics consequences developing after these events may be reduced if sufficient habitat is available to support rapid growth (Murphy et al. 2015).

Our contemporary demographic estimates are more precise and representative of the KVP bear population than prior estimates, and combined with our identification of bear movement direction propensity, should provide wildlife managers with useful information for management of this population. We strongly advise against using our derived time-specific exponential growth rate for management purposes (e.g., for harvest) in lieu of a more accurate and representative asymptotic growth rate obtained from modeling vital rates (Clark et al. 2010). Because adult female survival and fecundity appear to be the primary drivers of bear population growth and viability, we suggest these vital rates be monitored annually in this population (Beston 2011, Harris et al. 2011). Given our low estimated bear densities, projected recolonization directions, and the limited connectivity with other populations in the region, we also suggest managers consider maintaining a conservative approach to annual harvests until the aforementioned vital rate estimates are acquired and a population viability analysis can be completed (Clark and Eastridge 2006, Howe et al. 2007). Repeating our study in the two core areas at regular intervals (perhaps every 2–5 years) combined with recently developed hair trap cluster sampling in peripheral areas could inform mangers when genetic connectivity with other bear populations in the region changes, facilitate monitoring of range expansion rate and direction, and allow identification of this population possibly no longer recolonizing range in the future (Wilton et al. 2014).

Our study demonstrates that noninvasive genetic sampling used in conjunction with SECR models represents a practical method for monitoring reintroduced and recolonizing bear populations at temporal and spatial scales that should be useful for bear management and conservation. Study designs similar to ours but that use appropriate species-specific sampling techniques (e.g., systematic scat collections, hair sampling via rub pads, etc. [Long et al. 2008]) could also be used to monitor expanding populations of other large carnivores, animals that may create management challenges in multiple jurisdictions. We hope our study provides a pragmatic alternative for investigating the demographics, population genetics, and spatial expansion patterns of these sometimes rapidly expanding populations.

Chapter Two has been accepted for publication in the following manuscript:

Murphy, S.M., J.J. Cox, B.C. Augustine, J.T. Hast, J.M. Guthrie, J. Plaxico, and J. Wright. 2016. Recolonization characteristics of a reintroduced black bear population based on non-invasive genetic spatial capture-recapture methods. Journal of Wildlife Management, In Press.

Chapter 2: Figures

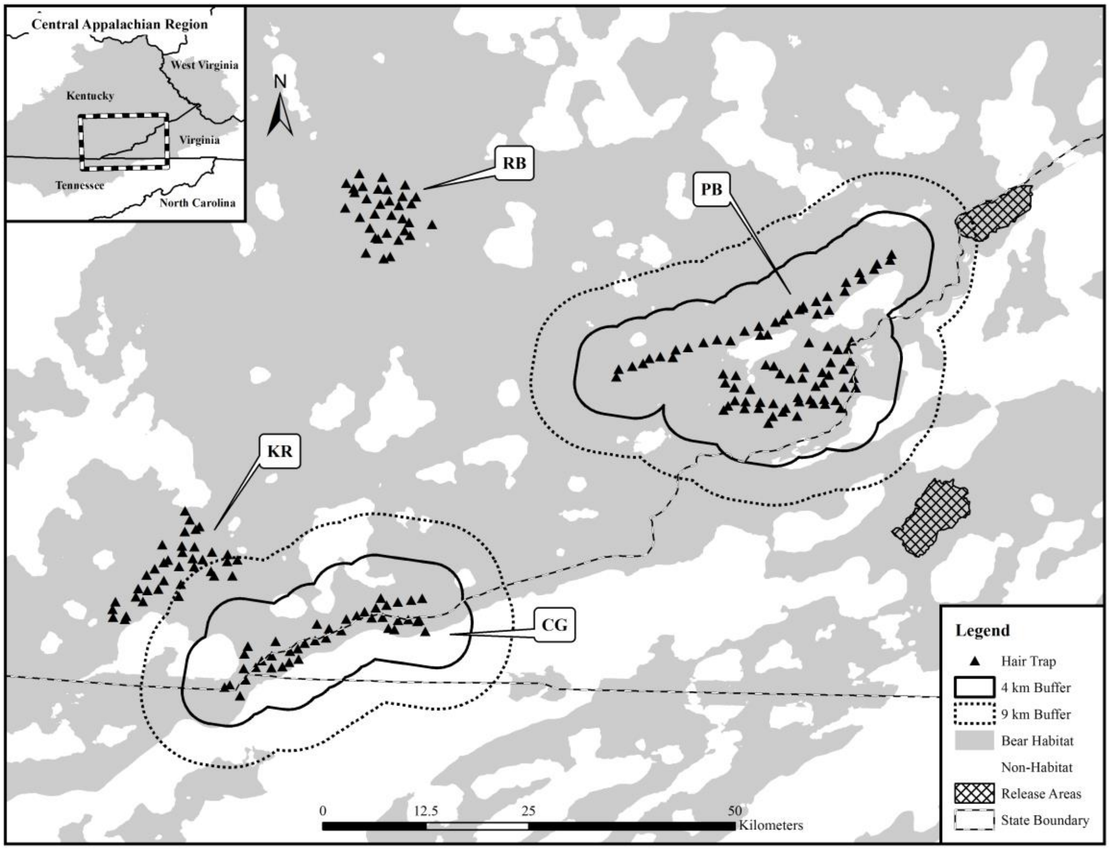

Figure 2.1. Study areas where we conducted mark-recapture hair trap sampling of the Kentucky-Virginia, USA, black bear population (KVP) during 2012–2013. We used 4-km and 9-km buffers as the state spaces for demographic parameter estimates of female and male bears, respectively, at the Pine-Black (PB) and Cumberland Gap (CG) study areas using spatially explicit capture-recapture models (SECR). Insufficient bear detection at the Kentucky Ridge (KR) and Redbird (RB) study areas did not allow demographic parameter estimation, so no state spaces were created.

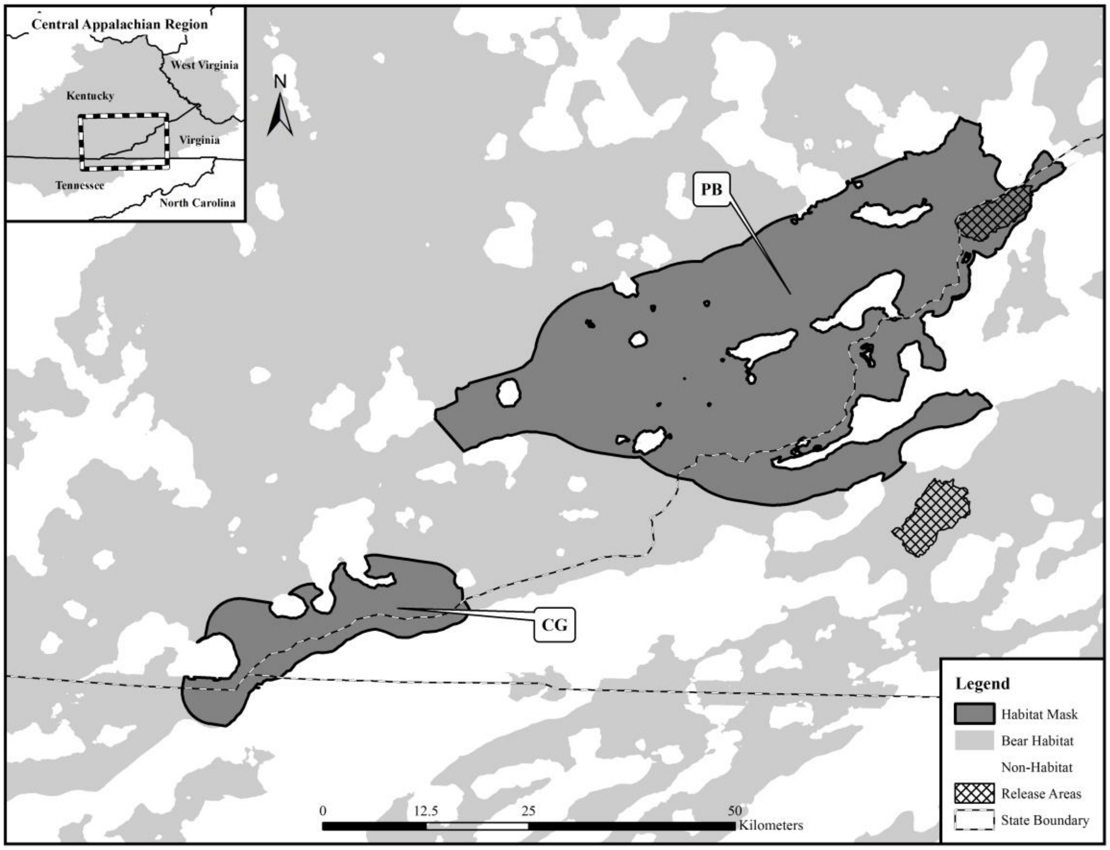

Figure 2.2. Map of available bear habitat and habitat masks that we used for estimating abundance (*E[N]*) of the Kentucky-Virginia, USA, black bear population (KVP) during 2012–2013. Because of negligible bear detection at the Redbird (RB) and Kentucky Ridge (KR) study areas, we only estimated *E(N)* for the Pine-Black (PB) and Cumberland Gap (CG) study areas.

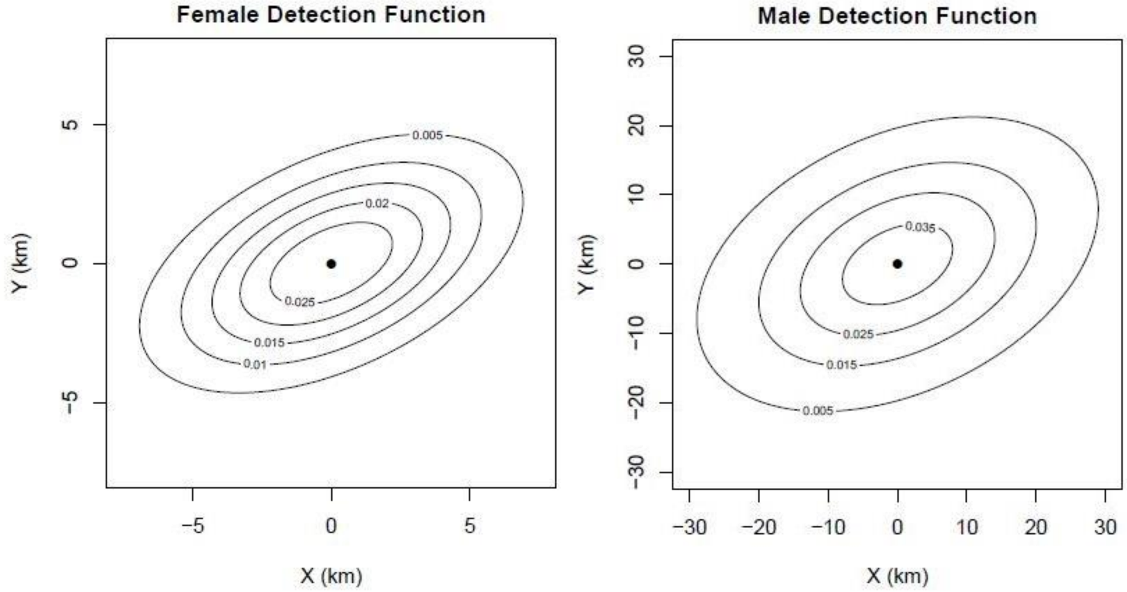

Figure 2.3. Two-dimensional depiction of female and male detection probabilities as functions of distance away from the activity center of an individual (g_0 [• on figure]) from spatially explicit capture-recapture models (SECR) using anisotropic detection functions for estimating density ($\widehat{D}$) of the Kentucky-Virginia, USA, black bear population (KVP) during 2012–2013. We used a user-defined distance function to compute the anisotropic distances by specifying an anisotropy angle (Φ_A) of 65 degrees, which corresponded to the southwest to northeast geographical direction of prominent mountains, and estimating the anisotropy ratio (Φ_R).

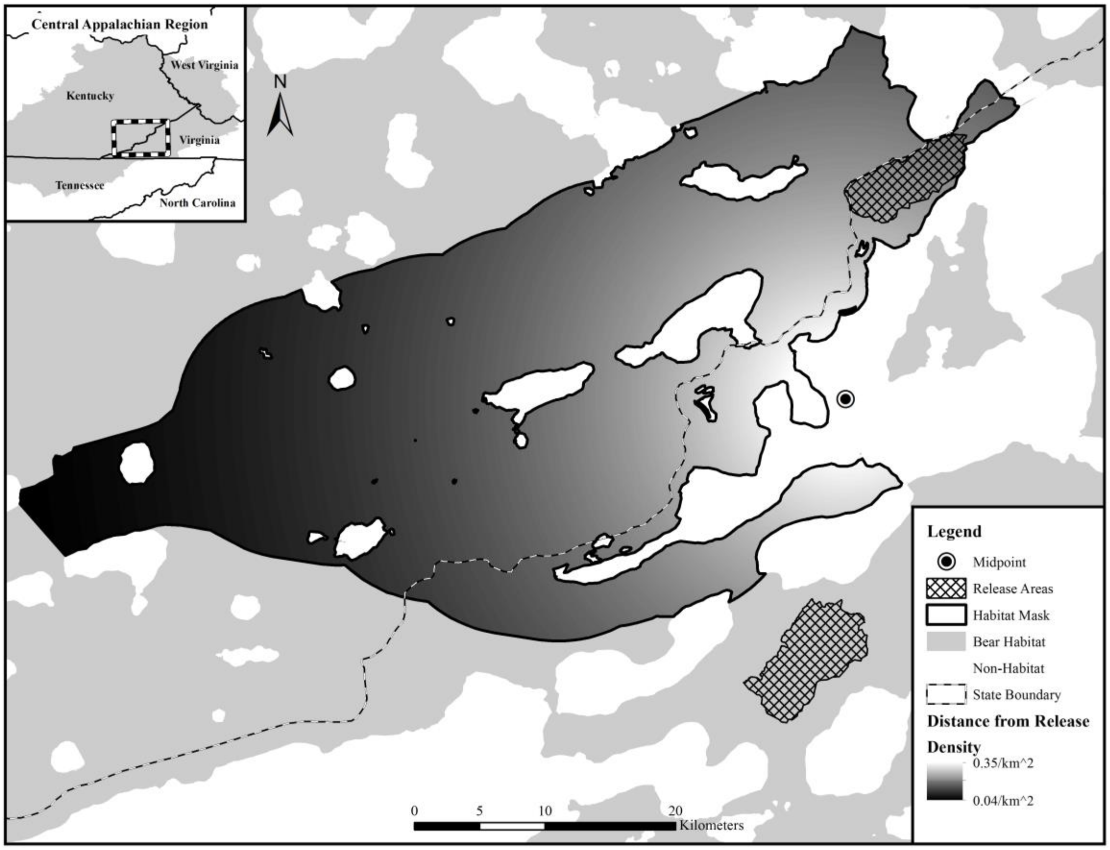

Figure 2.4. Gradient of female bear density ($\widehat{D}$) at the Pine-Black (PB) study area as a function of distance from the 1990s reintroduction (release) areas for the Kentucky-Virginia, USA, black bear population (KVP). We created a Distance from Release Area covariate by calculating the circular Euclidean distance from the midpoint between the 2 release areas in southwestern Virginia, and modeled this covariate on $\widehat{D}$.

Table 2.1. Estimated genetic parameters for the Kentucky-Virginia, USA, black bear population (KVP) from hair samples collected during 2012–2013. We estimated allelic richness (R_A), observed heterozygosity (H_O), expected heterozygosity (H_E), effective number of breeders (N_B), and effective population size (N_E) using eight microsatellite markers.

Location	n[a]	R_A	H_O	H_E	N_B	N_E
Pine-Black Study Area	142	7.38	0.77	0.77	56	64
Cumberland Gap Study Area	54	7.39	0.81	0.77	26	30
Kentucky-Virginia Population[b]	196	7.39	0.78	0.78	62	71

[a]: Number of individual bears in sample.
[b]: Pine-Black and Cumberland Gap combined.

Table 2.2. Spatially explicit capture-recapture (SECR) models used to estimate density ($\widehat{D}$), abundance ($E[N]$), and anisotropy ratio (Φ_R) of male bears in the Kentucky-Virginia, USA, bear population (KVP; 2012–2013). We fit models using a binomial observation model with a half-normal anisotropic detection function. We modeled a trap-specific behavioral response (bk) on the probability of detection at the activity center of an individual (g_0), and allowed g_0 to be fixed across study areas, vary across study areas (A), or vary across study areas and years (A×Y). We did not allow $\widehat{D}$ to vary between years, but we did allow $\widehat{D}$ to vary between study areas (A) or be fixed across study areas (~1). We allowed the spatial scale of the detection function (σ) to be shared (~1) or to vary by study area (A).

Males					
Model	K[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	log[e]
$D(\sim1)\ g_0(\sim bk+A+Y\times A)\sigma(\sim1)\Phi(\sim1)$	8	2368.70	0.00	0.20	-1175.57
$D(\sim A)\ g_0(\sim bk+A+Y\times A)\sigma(\sim1)\Phi(\sim1)$	9	2369.12	0.43	0.16	-1174.58
$D(\sim1)\ g_0(\sim bk+A+Y\times A)\sigma(\sim A)\Phi(\sim1)$	9	2369.43	0.73	0.14	-1174.73
$D(\sim A)\ g_0(\sim bk+A)\sigma(\sim1)\Phi(\sim1)$	7	2369.95	1.26	0.11	-1177.38
$D(\sim1)\ g_0(\sim bk+A)\sigma(\sim1)\Phi(\sim1)$	6	2370.31	1.62	0.09	-1178.71
$D(\sim1)\ g_0(\sim bk+A)\sigma(\sim A)\Phi(\sim1)$	7	2370.69	1.99	0.07	-1177.75
$D(\sim A)\ g_0(\sim bk+A+Y\times A)\sigma(\sim A)\Phi(\sim1)$	10	2370.78	2.09	0.07	-1174.18
$D(\sim1)\ g_0(\sim bk)\sigma(\sim A)\Phi(\sim1)$	6	2371.22	2.52	0.06	-1179.17
$D(\sim A)\ g_0(\sim bk+A)\sigma(\sim A)\Phi(\sim1)$	8	2371.46	2.76	0.05	-1176.96
$D(\sim A)\ g_0(\sim bk)\sigma(\sim A)\Phi(\sim1)$	7	2371.56	2.87	0.04	-1178.19
$D(\sim A)\ g_0(\sim bk)\sigma(\sim1)\Phi(\sim1)$	6	2374.06	5.36	0.01	-1180.59
$D(\sim1)\ g_0(\sim bk)\sigma(\sim1)\Phi(\sim1)$	5	2378.57	9.88	0.00	-1183.97

[a]: Number of model parameters
[b]: Akaike's Information Criterion corrected for small sample size
[c]: Relative difference between AIC_c of model and the highest ranked model
[d]: Model weight
[e]: log Likelihood

Table 2.3. Spatially explicit capture-recapture (SECR) models used to estimate density ($\widehat{D}$), abundance ($E[N]$), and anisotropy ratio (Φ_R) of female bears in the Kentucky-Virginia, USA, bear population (KVP; 2012–2013). We fit models using a binomial observation model with a half-normal anisotropic detection function, modeled a trap-specific behavioral response (bk) on the probability of detection at the activity center of an individual (g_0), and allowed g_0 to be fixed across study areas, vary across study areas (A), or vary across study areas and years (A×Y). We did not allow $\widehat{D}$ to vary between years, but we did allow $\widehat{D}$ to vary between study areas (A) or be fixed across study areas (~1). We allowed the spatial scale of the detection function (σ) to be shared (~1) or to vary by study area (A).

Females					
Model	K[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	log[e]
D(~1) g_0(~bk+A+Y×A)σ(~1)Φ(~1)	8	1918.27	0.00	0.27	-950.41
D(~1) g_0(~bk+A)σ(~1)Φ(~1)	6	1918.33	0.06	0.26	-952.75
D(~A) g_0(~bk+A)σ(~1)Φ(~1)	7	1920.27	2.00	0.10	-952.58
D(~A) g_0(~bk+A+Y×A)σ(~1)Φ(~1)	9	1920.38	2.10	0.09	-950.27
D(~1) g_0(~bk+A)σ(~A)Φ(~1)	7	1920.58	2.31	0.08	-952.73
D(~1) g_0(~bk+A+Y×A)σ(~A)Φ(~1)	9	1920.62	2.35	0.08	-950.39
D(~A) g_0(~bk+A)σ(~A)Φ(~1)	8	1922.42	4.15	0.03	-952.48
D(~A) g_0(~bk+A+Y×A)σ(~A)Φ(~1)	10	1922.63	4.36	0.03	-950.18
D(~1) g_0(~bk)σ(~A)Φ(~1)	6	1922.88	4.61	0.03	-955.02
D(~A) g_0(~bk)σ(~A)Φ(~1)	7	1925.12	6.85	0.01	-955.00
D(~A) g_0(~bk)σ(~1)Φ(~1)	6	1928.64	10.37	0.00	-957.90
D(~1) g_0(~bk)σ(~1)Φ(~1)	5	1928.68	10.41	0.00	-959.05

[a]: Number of model parameters
[b]: Akaike's Information Criterion corrected for small sample size
[c]: Relative difference between AIC_c of model and the highest ranked model
[d]: Model weight
[e]: log Likelihood

Table 2.4. Spatially explicit capture-recapture (SECR) models used to estimate density ($\widehat{D}$) and abundance ($E[N]$) of black bears in the Kentucky-Virginia, USA, bear population (KVP) using a Distance from Release Area covariate (DistRel) to model $\widehat{D}$ (2012–2013). We fit models using a binomial observation model with a half-normal anisotropic detection function (Φ), modeled a trap-specific behavioral response (bk) on the probability of detection at the activity center of an individual (g_0), and a constant (~1) spatial scale of the detection function (σ).

Model	K[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	log[e]
Pine-Black (PB) Females					
D(~DistRel) g_0(~bk)σ(~1)Φ(~1)	6	1519.99	0.00	0.79	-753.44
D(~1) g_0(~bk)σ(~1)Φ(~1)	5	1522.64	2.64	0.21	-755.92
Pine-Black (PB) Males					
D(~1) g_0(~bk)σ(~1)Φ(~1)	5	1203.26	0.00	0.68	-596.09
D(~DistRel) g_0(~bk)σ(~1)Φ(~1)	6	1204.72	1.46	0.33	-595.60
Cumberland Gap (CG) Females					
D(~1) g_0(~bk)σ(~1)Φ(~1)	5	404.79	0.00	0.77	-195.89
D(~DistRel) g_0(~bk)σ(~1)Φ(~1)	6	407.16	2.38	0.23	-195.89
Cumberland Gap (CG) Males					
D(~1) g_0(~bk)σ(~1)Φ(~1)	5	1168.04	0.00	0.76	-578.14
D(~DistRel) g_0(~bk)σ(~1)Φ(~1)	6	1170.30	2.26	0.24	-577.88

[a]: Number of model parameters
[b]: Akaike's Information Criterion corrected for small sample size
[c]: Relative difference between AIC_c of model and the highest ranked model
[d]: Model weight
[e]: log Likelihood

Table 2.5. Parameter estimates for the Kentucky-Virginia, USA, black bear population (KVP) during 2012–2013 from spatially explicit capture-recapture models (SECR) with anisotropic (non-Euclidean) detection functions. We estimated the probability of detection at the activity center of an individual (g_0), the spatial scale of the detection function (σ [km]), and density ($\widehat{D}$ [bears/km^2]) at the Pine-Black (PB) and Cumberland Gap (CG) study areas. We used our $\widehat{D}$ estimates to derive abundance ($E[N]$) at each study area and for the KVP. Confidence intervals (95%) are presented in parentheses.

Location	g_0	σ	$\widehat{D}$	$E(N)$
PB Study Area				413 (269–636)
Males	0.04 (0.03–0.06)	2.01 (1.56–2.56)	0.09 (0.07–0.12)	148 (107–206)
Females	0.03 (0.02–0.05)	0.90 (0.70–1.15)	0.17 (0.13–0.24)	265 (188–374)
CG Study Area				69 (48–115)
Males	0.02 (0.01–0.06)	1.86 (1.50–2.30)	0.09 (0.07–0.12)	23 (17–32)
Females	0.09 (0.04–0.18)	0.90 (0.73–1.11)	0.17 (0.13–0.24)	46 (36–60)
KVP[a]			0.26 (0.18–0.37)	482 (317–751)

[a]: PB and CG combined.

Table 2.6. Program R code for anisotropic transformation of the detection function in spatially explicit capture-recapture (SECR) models using the coords.aniso function in the geor package.

```
distfn <- function (xy1,xy2, mask) {
  xy1 <- as.matrix(xy1)
  xy2 <- as.matrix(xy2)
  psiR <- 1 + covariates(mask)$noneuc[1]
  aniso.xy1 <- geoR::coords.aniso(xy1,aniso.pars=c(65*pi/180, psiR))
  aniso.xy2 <- geoR::coords.aniso(xy2,aniso.pars=c(65*pi/180, psiR))
  distmat <- edist(aniso.xy1,aniso.xy2)
  distmat
}
```

Chapter 3: Reintroduction Success and Potential Effects of Anthropogenic Mortality on Persistence of Two Reintroduced Black Bear Populations

Abstract

Most large carnivore reintroductions in the United States have been conducted to reestablish American black bear (*Ursus americanus*) populations in areas where the species was extirpated by anthropogenic activities. Population viability is used to determine the status of reintroduced populations, and also to evaluate the effects of management on population growth (λ) and persistence. We estimated demographic vital rates and used an individual-based population model to estimate λ of the reintroduced Big South Fork (BSF) and Kentucky-Virginia (KVP) black bear populations during 2010–2014; both of which resulted from small founder groups released along the Kentucky border during the 1990s. We then estimated the probabilities of ≥25% population decline over a 10-year period using multiple observed rates of anthropogenic mortality in each population (both harvest and non-harvest). Based on radio-monitoring, we estimated high adult female survival rates (S_{KVP} = 0.96 [95% CI: 0.89–0.99]; S_{BSF} = 0.99 [95% CI: 0.98–1.00]). All mortality was from anthropogenic causes, harvest was the most probable cause of mortality, and males were more likely to die than females during our study. Litters were male-biased in both populations (KVP = 1.00M:0.50F; BSF = 1.00M:0.70F), and mean litter size was slightly higher at KVP (2.39 [SE = 0.57]) than BSF (2.17 [SE = 0.59]). We estimated average annual λ of 1.10 (SD = 0.08–0.10) and 1.13 (SD = 0.09–0.12) in the KVP and BSF, respectively during 2010–2014. Simulations indicated the average annual mortality that occurred during our study was sustainable and allowed for moderate λ over the long-term. Continued annual mortality at the higher 2015 rate resulted in probabilities of population decline by ≥25% over 10 years of 0.52–0.53 and 0.97–0.98 in the KVP and BSF, respectively. Although our findings indicated the 1990s reintroductions successfully established viable and self-sustaining populations, these populations remain vulnerable to anthropogenic mortality. We therefore suggest mangers consider reimplementation of annual vital rate monitoring in both populations to allow timely management adjustments and consider reducing harvests below the 2015 level.

Introduction

Reintroduction has been integral for restoring many animal species to their native ranges. Most mammalian carnivore reintroductions have been implemented for large carnivores, primarily to rectify widespread range reductions and population declines caused by anthropogenic activities during the 19th and 20th centuries (Seddon et al. 2005, Estes et al. 2011, Rondinini and Visconti 2015). Reintroduction success has typically been defined as the establishment of a self-sustaining, viable population (Griffith et al. 1989, Swaisgood 2010). Although important during the population establishment and growth phases, the ultimate success criterion is long-term viability during the regulation phase (i.e., the period in which population dynamics are acutely dependent on the interactions among individuals, habitat characteristics, and anthropogenic activities; Sarrazin 2007, Robert et al. 2015). Some large carnivore reintroductions have either failed or the status of their resulting populations remains uncertain, mostly because these costly programs lacked sufficient planning or post-release monitoring (Seddon 2007, Hayward and Somers 2009, Weise et al. 2014). Intensive, long-term monitoring programs should be established beyond the initial population establishment phase to allow timely implementation of management strategies that may be needed to avoid population decline (De Barba et al. 2010, Robert et al. 2015).

Among all large carnivore reintroductions in the continental United States, most have been conducted to reestablish American black bear (*Ursus americanus*) populations following considerable range reductions caused by habitat loss and overexploitation that occurred through the early 1900s (Hall 1981, Clark et al. 2002). The most successful black bear reintroduction resulted from the release of 254 founders in the Interior Highlands of Arkansas, which created a population of >2,500 bears within 20 years that has since grown and recolonized the mountains of Arkansas and Missouri, and parts of Oklahoma (Clark and Smith 1994, Bales et al. 2005, Wilton et al. 2014). Multiple other black bear reintroductions occurred in the eastern and southern United States during the last three decades, but none were implemented with founder groups as large as the Interior Highlands program. Large founder group size has been identified as a critical component to improving the probability of reintroduction success (Griffith et al. 1989, Seddon 1999, Frankham 2009). An unfortunate consequence of reintroductions that rely on small founder groups is an increased risk of population decline caused by heightened vulnerability to demographic and environmental stochasticity, deleterious genetic effects, and reduced population fitness (Lande 1993, Allendorf and Luikart 2007). Despite these potential issues, long-term success has not been explicitly evaluated for most reintroduced bear populations during the regulation phase (Clark et al. 2002, Clark 2009).

In an attempt to reestablish black bear populations in a portion of historical range, two reintroductions occurred in the central Appalachians along the Kentucky-Tennessee and Kentucky-Virginia borders during the 1990s. Fifty-five bears (unknown sex ratio and age classes) were captured at Shenandoah National Park in northern Virginia, and were released in southwestern Virginia along the Kentucky border during 1990–1997 (hereafter referred to as Kentucky-Virginia population [KVP]), a translocation distance of about 400 km (Virginia Department of Game and Inland Fisheries [VDGIF] 2008, 2012; Figure 3.1). In a separate reintroduction, 14 adult female bears with 13 cubs were captured at Great Smoky Mountains National Park in eastern Tennessee, and were translocated ~150 km to the Big South Fork National River and Recreation Area along the Kentucky-Tennessee border (hereafter referred to as Big South Fork population [BSF]) during 1996–1997 (Eastridge and Clark 2001; Figure 3.1). The BSF founder group declined to 18 individuals by 1998 because of homing attempts and anthropogenic mortality (J. Clark, unpublished data), and had an estimated extinction risk of 24% at that time (Eastridge and Clark 2001). In contrast, no KVP founders were monitored following releases, but estimated effective population size estimates (N_E = 71 bears [2012–2013]) suggested most of the original founders survived and remained in the general reintroduction area (Murphy et al. 2016 [*in press*]).

Using hair samples collected during 2006–2009, Hast (2010) discovered that both the BSF and KVP remained genetically similar to their respective source populations and had limited gene flow between each other and with other bear populations in the region (0.75–1.5 migrants/per generation [Hast 2010]). Based on abundance estimates from systematic mark-recapture hair trapping, Murphy et al. (2015, 2016 [*in press*]) estimated the BSF and KVP were comprised of 211 (95% CI: 161–287) and 482 (95% CI: 317–751) bears, respectively, by 2010–2013. Both populations exhibited rapid growth (λ_{KVP} = 1.14/year [1997–2013]; λ_{BSF} = 1.18/year [1998–2012]) following the initial population establishment phase, suggesting the reintroductions were successful. A significantly female-biased sex ratio in the KVP population (0.53M:1.00F) combined with the rapid estimated growth indicated the population was in the process of recolonizing vacant range (Murphy et al. 2016 [*in press*]). Annual harvests were implemented throughout the ranges of the KVP and BSF during 2010 and 2013, respectively. Harvest numbers increased from two bears in 2010 to 33 in 2015 in the KVP, and from two bears in 2013 to 58 in 2015 in the BSF (Kentucky Department of Fish & Wildlife Resources [KDFWR] 2016, Tennessee Wildlife Resources Agency [TWRA] 2016). The harvest increase in the KVP was accompanied by higher non-harvest mortality (e.g., management euthanasia, illegal kill, and bear-vehicle collisions) as well, which increased by 86.7% between 2014 (n = 15) and 2015 (n = 28; J. Plaxico, KDFWR, unpublished data). Based on abundance estimates, the 2015 mortality rates were approximately 32.2% and 12.7% in the BSF and KVP, respectively, the former greatly exceeding the recommended maximum sustainable mortality for black bear populations in North America (i.e., 14.2% [Miller 1990]).

Small populations are more vulnerable to demographic and environmental stochasticity relative to their larger counterparts (Lande 1993), and anthropogenic mortality can therefore have strong selective forces on small wildlife populations (Collins and Kays 2011). Increasing anthropogenic mortality can lead to selective pressures on life-history traits of large carnivores, which can not only perturb population growth and persistence but influence evolutionary shifts in behavior and morphology as well (Bischof et al. 2009, Collins and Kays 2011). Prior studies demonstrated that even low mortality increases in small black bear populations can result in precipitating population declines, which can be exacerbated if females comprise a moderate to high proportion of the mortality (Dobey et al. 2005, Howe et al. 2007, Clark et al. 2010). Similar declines in the KVP and BSF populations, the latter of which is isolated, could threaten population growth and long-term persistence (Hast 2010, Murphy et al. 2015).

Population modeling has become an increasingly used tool for planning reintroductions but also for evaluating the success of these programs (King et al. 2013). Population viability is a central tenet to determining reintroduction success, and long-term persistence is one of the most critical concepts for informed management of small and reintroduced populations (Sarrazin 2007). Population viability analyses (PVA) provide a means to evaluate the effects of factors that may influence population dynamics using estimates of demographic vital rates and their respective variances, and can also be used to direct research efforts or management prescriptions (Armstrong et al. 2007, Howe et al. 2007). However, PVA are data-intensive and accurate estimates of demographic parameters and process variance can be difficult to obtain for most reintroduced wildlife populations because of small sample sizes (Nichols and Armstrong 2012). These inherent difficulties can be compounded for analyses of reintroduced populations of large carnivores, including bears, because these animals are long-lived, have relatively low reproductive rates, and tend to inhabit landscapes at low densities (Hayward and Somers 2009, Laufenberg et al. 2016 [*in press*]). Nonetheless, PVA is currently the best available tool for explicitly evaluating reintroduction success, and comparing relative risks of population decline, that given different management scenarios may provide more value than point estimates of extinction probability for small or reintroduced populations (Rueda-Cediel et al. 2015). We therefore conducted a study to investigate long-term population persistence and reintroduction success, and to evaluate the relative risk of decline under different mortality scenarios for the harvested KVP and BSF black bear populations. Our objectives were to: 1) estimate demographic vital rates, 2) estimate population growth rates, 3) quantify the risks of long-term population decline, and 4) investigate the effects of anthropogenic mortality on growth and persistence of these reintroduced black bear populations.

Study Area

We conducted research in the primary core areas of each population along the Kentucky-Tennessee and Kentucky-Virginia borders (Figure 3.1; Murphy et al. 2015, 2016 [*in press*]). The effective sampling areas encompassed 1,415 km^2 (BSF) and 1,489 km^2 (KVP) in the central Appalachian Ecoregion (Appalachian Regional Commission 2016). The KVP study area was located in the Appalachian Plateau physiographic province, characterized by steep mountains and ridges separated by deep, narrow valleys (Woods et al. 2002). The BSF study area was located in the Cumberland Plateau physiographic province, an elevated plateau dissected by deep, narrow ravines cut by multiple rivers and streams (Kleber 1992). Elevations ranged from 220 m to 659 m at the BSF study area, and from 326 m to 1,263 m at the KVP study area. Both study areas had moderately hot, humid climates during summer, and moderately cold winters. Average annual temperatures ranged from -4 to 30°C, and annual precipitation averaged 130 cm in both areas (Hill 1976). Forests were mixed-mesophytic, comprised of multiple species of oak (*Quercus* spp.), hickory (*Carya* spp.), ash (*Fraxinus* spp.), and pine (*Pinus* spp.), and included American beech (*Fagus grandifolia*), cucumber magnolia (*Magnolia acuminata*), yellow popular (*Lirodendron tulipifera*), and eastern hemlock (*Tsuga canadensis*). Study areas included the entirety of the Big South Fork National River and

Recreation Area, Cumberland Gap National Historical Park, four Kentucky Wildlife Management Areas (Beaver Creek, Hensley-Pine Mountain, Martin’s Fork, and Shillalah Creek), Kingdom Come State Park, Bad Branch State Nature Preserve, Pickett State Park, and portions of the Daniel Boone and Jefferson National Forests. Habitats were fragmented by surface mining and agriculture adjacent to both populations (Unger et al. 2008, Townsend et al. 2009). United States Interstate-75 bisected the two bear populations, and human population densities were 5/km^2 and 15/km^2 within our BSF and KVP study areas, respectively (United States Census Bureau 2010). The largest cities nearest to these bear populations were Lexington, Kentucky (290,263 people), to the north-northwest, and Knoxville, Tennessee (558,696 people), to the south-southeast.

Methods

Capture and Handling

From May to September of each year during 2009–2013 and 2010–2011, we conducted live-capture in both populations. Live-capture efforts at BSF primarily occurred along the Kentucky-Tennessee border, whereas bears were captured along the Kentucky-Virginia border in the KVP (Figure 3.1). We used Aldrich spring-activated foot snares (Johnson and Pelton 1980), culvert traps, and free-range darting to capture bears ≥1 year-of-age, and checked traps twice daily. Captured bears were immobilized using Telazol® (Fort Dodge Animal Health, Fort Dodge, Iowa) at a dosage of 5–7 mg per kg of estimated body mass (Kreeger and Arnemo 2007). All captured individuals were marked with unique lip tattoos, ear tags, and subcutaneous passive integrated transponder (PIT) tags (BioMark; Boise, Idaho, USA), and bears of both sexes ≥1 year-of-age were fitted with very high frequency (VHF) radio-collars (Lotek LMRT-4; Newmarket, Ontario, Canada). Radio-collars were programmed with 8-hr mortality switches, and were equipped with a leather spacer to serve as a release mechanism. We recorded existing marks, morphometric measurements, general condition, and reproductive status for all captured bears. A premolar tooth was extracted from each captured bear, and all teeth were sent to Matson's Laboratory (Manhattan, Montana, USA) for age determination via cementum annuli analysis (Willey 1974). Animal capture and handling procedures were conducted in accordance with University of Kentucky Institutional Animal Care and Use Committee Protocol #00626A2003.

Survival and Cause-Specific Mortality

We acquired monthly radiolocations of bears throughout both study areas using aerial telemetry via fixed-wing aircraft. We restricted our survival analyses to the period between April 2011 and March 2014 because aerial telemetry was less intensive outside of this timeframe. We used 1 April as the annual start date for analyses because this coincided with the period when females generally became active following den emergence. We used Cox proportional hazards (CPH) regression models with staggered entry to estimate average annual age- and sex-specific survival rates (Allison 2010). We used the following categorical variables to investigate the factors that may have influenced bear survival: sex, year, age class, and conflict (i.e., whether or not the bear was known to have engaged in human-bear conflict activity during its life). We separated captured bears into the following age classes because sample sizes for specific ages were small: subadult (1–2 years-of-age) and adult (≥3 years-of-age). We included bears three years-of-age in the adult age class because in contrast to prior data that indicated the average of primiparity was four (2003–2008; J. Cox, unpublished data), our reproductive data indicated female bears in both populations produced litters at three years-of-age (*n* = 23 bears [2010–2014]).

Using the coxph function in the R software (R Core Team 2015) package survival (Therneau 2015), we considered single and additive effects of the aforementioned variables on survival. We stratified models by the conflict variable so as not to violate the proportional hazards assumption. Because most bears were monitored during multiple years, we used a clustering method for individuals (Therneau and Grambsch 2000). We estimated both optimistic and pessimistic survival rates by assuming animals whose signals were lost were either alive at the time of censoring (assumed alive, AA) or dead (AD) at the time of signal loss (Clark et al. 2010). We evaluated goodness-of-fit of our CPH models using the cox.zph function to test the proportional hazards assumption (Grambsch and Therneau 1994). We used Akaike's Information Criterion corrected for small sample size (AIC_c) for model selection, and models ≤ 4 $\Delta\mathrm{AIC}_c$ were model-averaged to produce hazard ratio estimates (Burnham et al. 2011).

We used cumulative incidence functions via the Cuminc function in the R package mstate (Putter et al. 2015) to estimate binomial sex-specific probabilities of each mortality type from our radio-monitoring data (Heisey and Patterson 2006, Murray et al. 2010). Potential causes of death included agency euthanasia of conflict bears, illegal kills, bear-vehicle collisions, legal harvests, and natural (e.g., intraspecific strife, disease, starvation, and injury). Radio-collar mortality signals were investigated <12 hrs after detection, and necropsies were conducted at the location of the animal when necessary. Law enforcement personnel investigated suspected illegal kills, and legal harvests were recorded annually by state wildlife agencies (e.g., KDFWR, TWRA, and VDGIF).

Because our telemetry flights were conducted monthly, we used the midpoint between the last active (alive) signal and the date of detection of the first mortality signal as the estimated mortality date when the exact day of death was unknown (i.e., ≤15 days; Sandercock et al. 2011, Wolfe et al. 2015).

Reproductive Rates

We visited natal dens of radio-collared female bears during winter (February–March) of each year (2010–2014) to determine reproductive status. Adult females were immobilized using the same drug and procedures as those used for live-capture. We replaced radio-collars in dens if collars were approaching the end of battery life expectancy. We estimated mean litter size and litter sex ratio from observed litters in each population, and used chi-squared tests to investigate for sex ratio deviations from 1:1. We used multinomial logistic regression via the R package nnet (Ripley 2016) to estimate the following litter size probabilities: 1, 2, 3, and 4 cubs. We estimated litter production rates as the probability that unencumbered females (i.e., without the previous year's cubs) would produce a litter (Clark and Eastridge 2006). Because we only visited dens of female bears that were expected to have cubs of-the-year (COY), and because we did not radio-monitor COY, we could not estimate cub survival. Additionally, our annual sample sizes for litters were relatively small for both populations, so we could not compare litter sizes by year. We therefore used data from a reintroduced black bear population in western Virginia as our cub survival estimate ($S_{\text{cub}} = 0.87$ [Bridges 2005]). We estimated litter survival rates from this estimate, assuming individual cub survival was independent, as the probability that at least one cub in a litter survived using the equation in Clark and Eastridge (2006) and incorporating our estimated litter size probabilities:

$$1 - \sum_{l=1}^{4} \mathrm{P}_l (1 - S_{cub})^l,$$

where l = litter size, P_l = probability of litter size l, and S_{cub} = cub survival. We estimated a pooled (i.e., all years combined) net fecundity rate for each population as the average number of female cubs born per surviving adult female (Skalski et al. 2005).

Population Growth and Viability Analyses

We used a stochastic, individual-based population model implemented in Program RISKMAN (Ontario Ministry of Natural Resources, Toronto, Ontario) to estimate population growth during our study and to evaluate long-term persistence based on our vital rate estimates and average annual mortality rates (Taylor et al. 2003). This model did not account for immigration or emigration, but the BSF was likely both demographically and genetically isolated, and the KVP experienced low gene flow with bear populations in southwestern Virginia and southern West Virginia (Hast 2010, Murphy et al. 2015, 2016). For initial population sizes in our models, we used the abundance estimates produced by Murphy et al. (2015, 2016 [*in press*]) for the BSF and KVP during 2010–2012 and 2012–2013, respectively (Table 3.5). We used our population-specific adult survival rates in our population models, but used subadult male and female survival rates from the KVP for models of both populations because small sample size prohibited estimation of subadult survival for the BSF. Our population models assumed these survival rates were constant in each sex-specific age class, and also assumed that litter production rates were temporally constant.

Program RISKMAN used a Monte Carlo approach to estimate the uncertainty of population trajectories based on our demographic estimates. Because we did not collect data over a time period long enough to accurately distinguish between sampling and process variation (Beston 2011), we partitioned variance as 75% parameter uncertainty and 25% environmental variation, and used the inverse to evaluate model sensitivity (Howe et al. 2007). We used the covariance option in RISKMAN to simulate non-independence of parameter variances because environmental variation likely affected both survival and reproductive rates (Clark and Eastridge 2006, Howe et al. 2007). We did not include density-dependent effects in any of our models because it was unlikely that either population had reached carrying capacity during our study given their relatively low estimated densities (0.03–0.26 bear/km^2 [Murphy et al. 2015, 2016, *in press*).

We estimated the average annual geometric mean population growth rate (λ) of each population during our study period by conducting 1,000 stochastic simulations, beginning with the stable age distribution. We incorporated the average annual harvest ($\bar{x}_{\mathrm{KVP}}$ = 9 bears [SE = 1.03]; $\bar{x}_{\mathrm{BSF}}$ = 12 bears [SE = 1.16]) and non-harvest mortality ($\bar{x}_{\mathrm{KVP}}$ = 17 bears [SE = 2.09]; $\bar{x}_{\mathrm{BSF}}$ = 7 bears [SE = 1.09]) that occurred within our study areas during our study period (2010–2014) to estimate the probability that each population declined by ≥25% or went extinct over a 10-year period by conducting 1,000 stochastic simulations (Clark and Eastridge 2006, Howe et al. 2007). We did not have known ages for many harvested bears, so we only used sex-specific harvest selectivity-vulnerability (S-V) proportions, which dynamically varied the sex distribution of mortalities year-to-year as a function of the S-V and the relative abundance of each sex in the standing age distribution (Taylor et al 2003, Howe et al. 2007). We also conducted 1,000 stochastic simulations to evaluate the probability of decline by ≥25% over a 10-year period assuming the higher 2015 harvest and non-harvest mortality occurred annually in both populations. We restricted 2015 harvest numbers to those that occurred within the counties included in our study areas for each population (i.e., counties that our study areas included or overlapped): 58 bears (32M:26F) at BSF and 33 bears (15M:18F) at KVP (KDFWR 2016, TWRA 2016). We similarly restricted 2015 non-harvest mortality: 26 bears (24:2F) at KVP and 10 bears (7M:3F) at BSF. We report SD instead of SE for our λ estimates because the number of simulation trials does not affect SD.

Results

Capture and Handling

We radio-collared 91 bears (36M:55F) ≥1 year-of-age during 2009–2013: 19 (7M:12F) at BSF and 72 (29M:43F) at KVP. The average age of all captured bears was five, and average sex-specific ages were four and five for male and female bears, respectively. The oldest bear monitored was a 16-year-old female, whereas the oldest male bear in our sample was an 11-year-old, both the KVP population. The oldest female and male bears captured at BSF were 13 and nine years-of-age, respectively.

Survival and Cause-Specific Mortality

Average annual monitoring time until death or censoring for female and male bears was 225 (SE = 7.34) and 160 days (SE = 13.01), respectively. Fourteen (19.4%) bears were censored because of dropped or failed radio-collars, and 18 (25%) bears died (12M:6F), primarily in the KVP population. Two radio-collared male bears died in the BSF population from an illegal kill and management euthanasia, whereas no monitored females died at BSF. We did not document any deaths from natural causes in either population. Harvest was the most probable cause of death in the KVP, followed by management euthanasia, vehicle collisions, and illegal kills (Table 3.4). Female bear mortality in the KVP was most probable from vehicle collisions, whereas male mortality was most probable from harvest. Thirty-two (44.4%) radio-collared bears were known to have engaged in human-bear conflict activity during our study, all but two of which were in the KVP population. Eleven of these conflict bears died (34%); five were euthanized (100% of euthanasia), three were harvested (50% of harvest), and three were illegally killed (100% of illegal kill).

Our CPH models indicated a sex effect influenced *S* regardless of how we treated censors (Table 3.1), and only the hazard ratio for sex was statistically significant among all of our considered variables, which indicated males were 4.13 (SE = 0.56) times more likely to die than females during our study period (Table 3.2). Adult female survival was higher than all other sex and age classes at KVP, whereas subadult male survival was the lowest (Table 3.3). Average annual AA and AD female survival rates for all age classes in the KVP were 0.94 (95% CI: 0.87–0.98) and 0.85 (95% CI: 0.76–0.90), respectively (Table 3.3). We estimated average annual adult female survival rates of 0.99 (95% CI: 0.98–1.00) and 0.79 (95% CI: 0.62–0.89) in the BSF population given AA and AD assumptions, respectively.

Reproductive Rates

The earliest age of successful reproduction by female bears was two (*n* = 2) in the KVP and three (*n* = 8) in the BSF. The average age of primiparity in the KVP and BSF was 2.85 (SE = 0.21) and 3.00 (SE = 0.10), respectively. Based on 48 litters in the KVP, we estimated a mean litter size of 2.39 (SE = 0.59), which was significantly male-biased (1.00M:0.50F [χ^2_1 = 2.36; P = 0.02]). In the BSF, we estimated a mean litter size of 2.17 (SE = 0.57) from 14 litters, which was slightly male-biased but not statistically significant (1.00M:0.70F [χ^2_1 = 1.23; P = 0.27]). We estimated net fecundity was 0.77 in the BSF and 0.52 in the KVP. The probability of KVP females producing 3-cub litters was slightly higher than 2-cub litters, whereas 2-cub litters were most probable for BSF females (Table 5). Our estimated litter production rates were 0.92 and 0.90 in the KVP and BSF, respectively. Litter survival rates were 0.89 (SE = 0.04) and 0.88 (SE = 0.09) in the KVP and BSF, respectively.

Population Growth and Viability Analyses

We estimated an average annual KVP geometric mean population growth rate (λ) of 1.10 (SD = 0.08–0.10) during our study period (2010–2014). Monte Carlo simulations indicated a low probability that the KVP would decline by ≥25% over a 10-year period if subjected to the average annual harvest and non-harvest mortality that occurred during our study period (Table 3.7). The probability of decline over 10 years increased to 0.52–0.53 if the KVP was annually subjected to the higher 2015 mortality (both harvest and non-harvest). Considering only the 2015 harvest (i.e., no non-harvest mortality), the optimistic probability of ≥25% population decline was 0.23–0.27 over 10 years. We estimated an average annual λ of 1.13 (SD = 0.09–0.12) in the BSF during 2010–2014 based on our demographic estimates. Our simulations indicated a low probability of ≥25% decline over a 10-year period in the BSF population if subjected to the average annual mortality that occurred during our study period (Table 3.7). The probability of ≥25% decline over 10 years increased to 0.97–0.98 if the BSF was annually subjected to the higher 2015 mortality (both harvest and non-harvest mortality), and was 0.93–0.94 if the BSF was subjected to only the 2015 harvest. Both the BSF and KVP collapsed in all simulations using pessimistic (AD) survival rates even if no mortality was included in the model and regardless of how we proportioned variance.

Discussion

Previously estimated average annual growth rates were 1.18 (95% CI: 1.17–1.19) and 1.14 (95% CI: 1.12–1.18) in the BSF and KVP, respectively, after the 1990s population establishment phases (Murphy et al. 2015, 2016 [*in press*]). Despite overlapping confidence intervals, our average annual λ point estimates during 2010–2014 were lower (Table 3.6). Although the apparently reduced λ could be representative of density-dependent effects (Czetwertynski et al. 2007), which we did not include in our models, estimated population densities for the BSF (Murphy et al. 2015) and KVP (Murphy et al. 2016 [*in press*]) were low relative to reported estimates for other eastern and southeastern black bear populations (McLean and Pelton 1994, Bridges 2005, Settlage et al. 2008). Considering these estimates, the availability of unoccupied habitat in the region (Unger et al. 2008), and the low female mortality rates during our sampling period, we believe our decision to not model density-dependence was reasonable.

Our live-capture data suggested that both populations had age distributions skewed towards younger bears, and our optimistic point estimates of survival for all age classes were higher than the averages for bear populations in the eastern United States (Table 3.3; Beston 2011); both of which should have resulted in relatively high λ estimates. Therefore, if density-dependent effects influenced these bear populations, the reductions of λ were possibly caused by decreased reproductive rates. A previous study of reintroduced bear populations in the Interior Highlands of Arkansas, which our study was most similar to, also suggested reproductive rates may have partially influenced the decreased λ that was estimated in one population (Clark and Smith 1994). Although these vital rates were not monitored in the BSF prior to our study, nor did we monitor cub survival in either population, estimated mean litter size in the KVP during 2003–2006 was 3.25 (SE = 0.11; Harris 2011). Our fecundity estimates were similar to the average for other eastern black bear populations, but we acknowledge that this may have been influenced by the relatively high survival estimates that we used in our calculations (Beston 2011). Nonetheless, our mean litter size estimates in the BSF and KVP were lower than that of Harris (2011), we documented no 4-cub litters at BSF, and the litter sex ratio in the KVP was skewed towards males. These findings provide some, although limited support for lower reproductive rates as potential contributors to the reduced λ we estimated if density-dependence was acting on these populations.

Perhaps the most interesting finding of our study was the presence of male-biased cub sex ratios in both populations. This ratio was closer to 1:1 in the BSF (1.00M:0.70F), but approximately twice as many male than female cubs were born in the KVP during our study (1.00M:0.50F). Our estimated cub sex ratio in the BSF differing from 1:1 was probably influenced by our small litter sample size (n = 14 litters) and sampling error; however, the substantially skewed cub sex ratio in the KVP was based on a much larger sample size (n = 48 litters). The KVP had a significantly female-biased combined subadult and adult sex ratio (0.53M:1.00F [Murphy et al. 2016, *in press*]), which suggests the population had high productivity (Caughley 1977). Significantly male-selected mortality occurred during our study period (2010–2014) in the KVP, and previous research has shown that even low levels of male-selected mortality can result in male-biased offspring sex ratios for large carnivores, which can lead to reduced fecundity, recruitment, and population growth (Milner et al. 2007, Wielgus et al. 2013). Alternatively, bears exhibit male-biased dispersal, and if the estimated density for the KVP is the highest that available habitat can support, then producing more male than female cubs would be advantageous (Rogers 1987). This would also partially explain the female-biased adult and subadult sex ratio estimated by Murphy et al. (2016 [*in press*]) because dispersing yearling males may have resided outside of our study areas (Swenson et al. 1998, Jerina and Adamič 2008).

The validity of model output is dependent upon the quality of the parameter estimates used (Rueda-Cediel et al. 2015). The point estimates of survival rates that we used in our population models may be biased high because we only considered AA estimates for which lost signals were censored. We attempted to also use pessimistic survival estimates (AD) for each sex and age class to provide a conservative synopsis (Clark and Eastridge 2006, Laufenberg et al. 2016), but regardless of how variance was partitioned, both the KVP and BSF collapsed prior to the end of the 10-year simulation period using these estimates. This is concerning because some of the lost signals for which we could not recover radio-collars may have represented illegal kills that we did not account for, which may have been of importance in the BSF because of the large difference between AA and AD survival rates for females (Table 3; Howe et al. 2007, Kindall et al. 2011). We also used a cub survival estimate from a separate study in Virginia in our population models, an approach that has been employed in previous bear PVAs to provide population persistence evaluations (Wear et al. 2005, Howe et al. 2007).

Cub survival and recruitment are critical to black bear population growth and sustainability, and the estimate we used may have been overly optimistic (Bridges 2005, Beston 2011). Additionally, our survival analysis did not support a temporal effect (Table 3.1), and our average annual sample sizes for litter size were too small to investigate a year effect in either population. We could not accurately quantify temporal process variance in these parameters as a result, so we instead partitioned total variance as 75% parameter uncertainty and 25% environmental variation, and also considered the inverse to evaluate sensitivity (Howe et al. 2007). This approach may produce optimistic estimates of growth and persistence for studies with short durations (<10 years) because of the inability to accurately quantify environmental and total variances (Taylor et al. 2006). Furthermore, and perhaps most importantly, we assumed a stable age distribution in all of our population models. Despite this being an accepted and often used assumption in PVA, it is an unlikely scenario for most wildlife populations because fecundity and mortality rates are rarely temporally constant (Akçakaya 2000). Although we did not detect any temporal differences in our survival rates, mortality increased annually in both populations and considerably between our monitoring period and 2015. We therefore caution that our growth and probability of decline estimates are probably optimistic. A longer-term dataset would have more power to detect annual variation in demographic vital rates, so we encourage managers to continue monitoring efforts to add to our dataset (Harris et al. 2011, Laufenberg et al. 2016 [*in press*]).

Our simulations suggested that both populations had high chances of persistence over the next 10 years based on our estimated demographic parameters and the mortality that occurred during our study period (2010–2014; Table 3.7). Both reintroductions were therefore successful at establishing viable and self-sustaining populations over the long-term. Our study represents only the third such study that explicitly evaluated and confirmed long-term success of black bear reintroductions based on vital rates estimated during the population regulation phase (e.g., Arkansas [Clark and Smith 1994] and Louisiana [Laufenberg et al. 2016, *in press*]). Importantly, the cumulative findings of our study and those of Murphy et al. (2015, 2016 [*in press*]) contradict some of the criteria that are presumably crucial to wildlife reintroduction success, which were also thought to apply to successful bear reintroductions. Primarily that large founder groups should be used for population establishment, and these founders should be released in areas that have a high probability of resulting in connectivity with nearby populations (Thatcher et al. 2006, Clark 2009, De Barba et al. 2010). In contrast to the 1960s reintroductions in Arkansas and Louisiana that used founder groups of 254 and 130 bears, respectively, both the BSF and KVP populations were established using small founder groups ($N = 14$ and 55 adult bears, respectively [Eastridge and Clark 2001, VDGIF 2008]). Despite the BSF being demographically and genetically isolated, and the KVP having experienced limited immigration, no evidence of deleterious genetics effects were found in either population (Hast 2010, Murphy et al. 2015, 2016 [*in press*]). Rapid population growth following the establishment phase, the overlapping generations inherent to bears, and the availability of suitable but unoccupied habitat in the release areas were important factors in these findings (Murphy et al. 2015, 2016 [*in press*]). Thus, our findings combined with those from reintroduced populations in Arkansas and Louisiana (Clark and Smith 1994, Laufenberg and Clark 2014, Puckett et al. 2014) provide support for the possibility that reintroduced black bear populations may be robust to the factors that are often detrimental to reintroduced populations of other wildlife species. A perhaps overlooked but important caveat to this is that the BSF, KVP, and reintroduced populations in Arkansas were not subjected to high levels of harvest or non-harvest mortality ≤13 years post-reintroduction (Clark and Smith 1994), which allowed rapid growth to occur.

Notwithstanding moderate λ and low risks of decline during our relatively short study period, both the KVP and BSF bear populations remain vulnerable to anthropogenic mortality. All documented deaths during our study period were anthropogenic; suggesting additive instead of compensatory effects influenced survival and ultimately population growth (Czetwertynski et al. 2007, Bischof et al. 2009). Harvest was the leading cause of mortality among our sample of radio-monitored bears at KVP, but management euthanasia comprised a surprisingly high proportion of mortalities, and vehicle collisions were the most probable cause of death for female bears (Table 3.4). Our simulations indicated that non-harvest mortality may have a greater impact on growth and persistence of the KVP population than harvest (Table 3.7), which we suspect may have been because of an increased proportion of females in the non-harvest mortality relative to harvest during our study period. Howe et al. (2007) discovered a similar scenario in a small, isolated black bear population in Canada, and McLoughlin et al. (2003) cautioned that increased non-harvest mortality could cause larger population reductions than mortality from harvest because of proportionally more females in the non-harvest mortality. Although we could not investigate cause-specific mortality in the BSF because of small sample size, carcass recovery data suggested that harvest was probably the leading cause of mortality in the BSF (J. Plaxico, unpublished data), and our simulations indicated harvest had a greater effect on persistence of the BSF than did non-harvest mortality (Table 3.7). Our findings therefore importantly demonstrate that mortality in both populations could be directly manipulated by management actions. These actions could include reducing harvest rates in the core population areas, mitigating bear access to anthropogenic food sources to decrease the frequency of and need for management euthanasia of conflict animals, slowing vehicular speed limits on roadways that have high rates of bear-vehicle collisions, or increasing law enforcement presence in areas where illegal kills are prevalent. Annual mortality rates of 10% ($n \approx 48$ bears) and 13% ($n \approx 27$ bears) may be sustainable within our KVP and BSF study areas, respectively. Although these yields are average compared to sustainable rates reported for other black bear populations (Miller 1990), we caution managers that our estimated rates are optimistic and include both harvest and non-harvest mortality.

Simulations using the higher 2015 mortality projected high probabilities of ≥25% decline over a 10-year period in both populations despite the use of optimistic survival rates in our models (Table 3.7). We acknowledge that our probability of decline estimates may be slightly biased because we did not incorporate age class-specific S-V proportions but instead only considered sex-specific S-V in our models. We suspect this bias was low, though, because despite weight and size restrictions for bears available for harvest (KDFWR 2015, TWRA 2015), two cubs were harvested in the KVP and at least nine cubs died from other anthropogenic causes of mortality during 2015, suggesting all age classes may have had comparable S-V that year (J. Plaxico, unpublished data).

Multiple factors likely influenced the increased harvest and non-harvest mortality that occurred during 2015. First, harvests prior to 2015 were during late fall and early winter (November–December), whereas an early fall (September–October) season was implemented during 2015 in addition to the later season (KDFWR 2015, TWRA 2015). This early season probably increased the chances of hunter success because, based on radio-collar data, bears did not enter the denning period prior to November in either population (J. Cox, unpublished data). Second, the addition of the early season resulted in more female bears being harvested relative to prior years, as reflected by the 1:1 sex ratio in the 2015 harvest. Female bears are perhaps the most critical component of bear populations, and population growth is largely dependent on their survival and successful reproduction (Beston 2011, Harris et al. 2011). Finally, oak-hickory hard mast is the most important autumn food source for black bears in the central and southern Appalachians (Pelton 1989, Vaughan 2002), and both KDFWR and TWRA reported either poor hard mast availability or complete failure within or near our study areas during 2015 (J. Plaxico, personal communication; D. Gibbs, TWRA, personal communication). A negative relationship between black bear mortality (both harvest and non-harvest) and hard mast availability has been previously documented in the region, and we suspect a similar scenario may have occurred during 2015 in the KVP and BSF populations (Pelton 1989, Ryan et al. 2004, Ryan et al. 2007). Such oscillations in mast availability are to be expected in natural systems.

Our simulations indicated that if the 2015 level of mortality occurs during successive years, both populations may decline rapidly (Table 3.7). Although it is unlikely that the 2015 mortality alone had a significant long-term effect on λ or persistence of either population, similar mortality over multiple years would likely have such an effect on the BSF. The probability of decline was much higher in the BSF than the KVP under all mortality scenarios, and we believe multiple factors influenced this.

Estimated abundance for the KVP was >2 times larger than the BSF, which we used as the initial population sizes in our models (Murphy et al. 2015, 2016 [*in press*]). The size of the specified initial population can have considerable influence on growth and risk estimates in individual-based PVA models (Howe et al. 2007), and larger populations are buffered against stochastic deviations (Lacy 2000). With the exception of fecundity, reproductive rates were also slightly higher in the KVP and the age of primiparity was younger. These factors may collectively improve the ability of the KVP to recover from unsustainable mortality rates more quickly, but our simulations suggested the BSF could be reduced to as few as 100 bears within 6 years if annually subjected to the 2015 mortality rate. Despite the BSF being approximately 78% smaller than the KVP, the former was subjected to a 55% higher harvest rate during 2015, and the proportion of females harvested in the BSF was greater. Both of these factors and smaller population size all probably contributed to the higher risks of decline for the BSF bear population (Howe et al. 2007). Assuming our demographic estimates are temporally constant, recovery from the 2015 mortality should occur in the BSF if mortality is reduced to <13% of the recently estimated BSF abundance instead of the approximately 32% rate that occurred during 2015, most of which was from harvest.

Management Implications

Our findings indicated that both the reintroduced KVP and BSF bear populations were viable and self-sustaining 13–17 years post-reintroduction, confirming reintroduction success. The average annual mortality that occurred during our study period (2010–2014) was sustainable in both populations and allowed for population growth. Our simulations demonstrated that continued mortality at the level that occurred during 2015 could result in overexploitation, especially in the isolated BSF population. If continued population growth is desired, then during years of high non-harvest mortality, we suggest managers contemplate reducing harvests within our KVP study area to below our estimated sustainable yield. We strongly suggest managers consider a more conservative approach to annual harvests over the long-term in the smaller, isolated BSF population relative to what occurred during 2015 to allow continued population growth and not threaten long-term persistence.

We acknowledge that our λ estimates may be positively biased and our probability of decline estimates optimistic, primarily because of our short study period and inability to estimate temporal process variance, which heightens the need to collect additional demographic data over a longer temporal period in the KVP and BSF (Rueda-Cediel et al. 2015). Vital rate monitoring in both populations ended with the completion of our research efforts during 2014, but simulations by Harris et al. (2011) indicated that annual radio-monitoring of 30 adult females, 10 subadults, 10 cubs, and 20 litters over 10 years in each population could provide adequate vital rate estimates for black bear population modeling. We therefore suggest re-implementing the annual vital rate monitoring program with the addition of investigating cub survival in order to detect significant population declines and to adjust harvests accordingly. Harvest can have considerable conservation value, often garnering local support for bear management, but conservatism may be crucial for sustainable management of these reintroduced bear populations over the next decade if continued growth and recolonization are desired. Our study demonstrates how pivotal annual vital rate monitoring of relatively small, exploited bear populations can be for affording managers the opportunity to make timely management adjustments. Similar monitoring efforts may become more important as black bears recolonize additional portions of the United States during coming decades (Scheick and McCown 2014, Smith et al. 2015).

Chapter Three is in review in the following manuscript:

Murphy, S.M., J.J. Cox, B.C. Augustine, J.T. Hast, J. Plaxico, J.M. Guthrie, T. Curry, M. Strunk, and S.C. Maehr. 2016. Potential effects of anthropogenic mortality on persistence of two reintroduced black bear populations. Journal of Applied Ecology.

Chapter 3: Figures

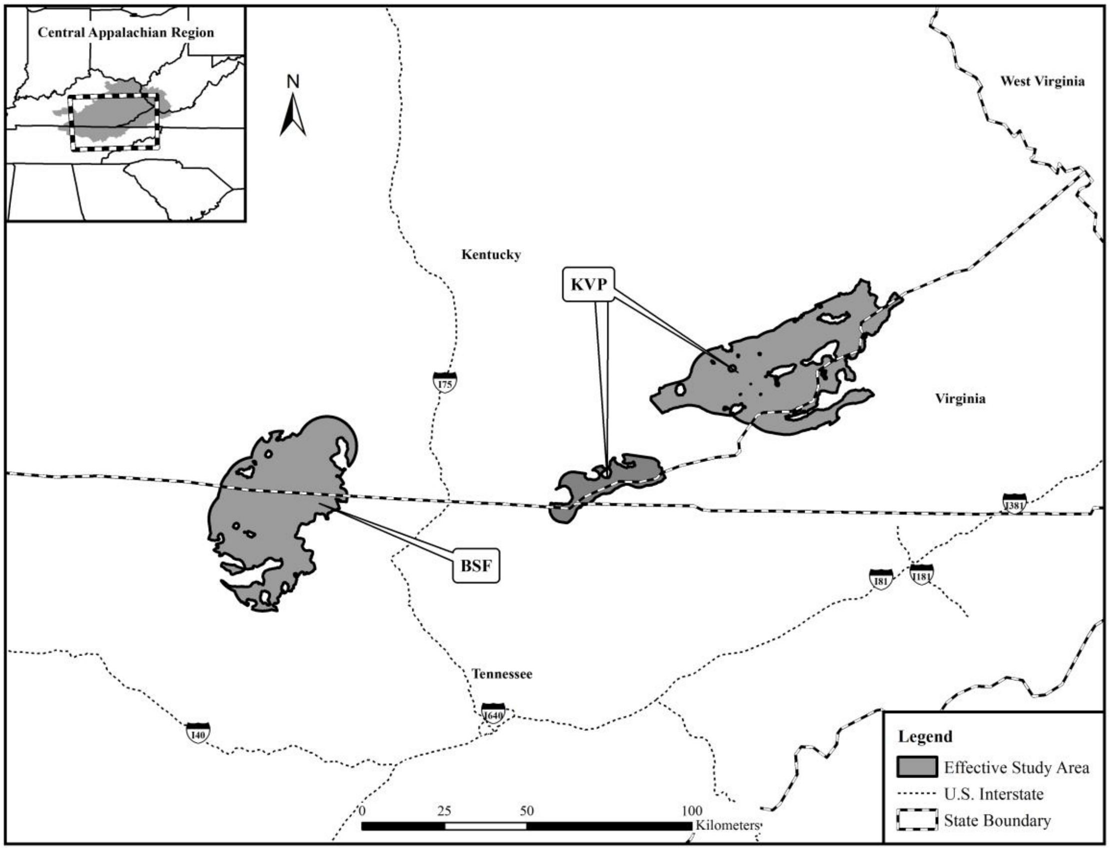

Figure 3.1. Study areas where we live-captured and radio-monitored black bears in the reintroduced Kentucky-Virginia (KVP) and Big South Fork (BSF) populations in the central Appalachians, USA, for demographic parameter estimation and population viability analyses (2010–2014).

Table 3.1. Cox proportional hazards (CPH) model selection used to estimate survival rates (*S*) of radio-monitored black bears in the reintroduced Kentucky-Virginia (KVP) and Big South Fork (BSF) populations in the central Appalachians, USA (2011–2014). We considered both optimistic (AA; assumed alive) and pessimistic (AD; assumed dead) survival in both populations. We modeled the following single and additive effects on *S*: Population (Pop), Sex, Age Class, Year, and a Conflict strata. For brevity, we only present the top models based on our model selection criteria (i.e., ≤4 ΔAIC_c).

Model	K^a	$AIC_c{}^b$	$\Delta AIC_c{}^c$	$w_i{}^d$	log^e
AA					
Sex	1	164.62	0.00	0.16	-81.28
Age Class + Sex	2	165.07	0.40	0.13	-80.45
Sex + Pop	2	165.39	0.71	0.11	-80.61
Age Class + Sex + Pop	3	165.82	1.20	0.09	-79.82
AD					
Sex	1	353.71	0.00	0.12	-175.83
Age Class + Sex	2	355.00	1.27	0.06	-175.45
Sex + Year	3	355.27	1.47	0.06	-174.51
No effect	0	355.52	1.81	0.05	-177.75
Sex + Pop	2	355.69	1.93	0.04	-175.78
Age Class	1	355.83	2.08	0.04	-176.87
Age Class + Sex + Year	4	356.06	2.28	0.04	-173.88
Age Class + Year	3	356.38	2.66	0.03	-175.11
Year	2	356.77	3.02	0.03	-176.32

[a]: Number of model parameters
[b]: Akaike's Information Criterion corrected for small sample size
[c]: Relative difference between AIC_c of model and the highest ranked model
[d]: Model weight
[e]: log Likelihood

Table 3.2. Variables related to time to death from Cox proportional hazards (CPH) models of survival (*S*) of radio-monitored black bears in the reintroduced Kentucky-Virginia (KVP) and Big South Fork (BSF) populations in the central Appalachians, USA (2011–2014). One level of each categorical variable was used as a control.

Variable	Hazard Ratio	SE	Z	P>|z|	95% CI
Sex					
Males	4.13	0.56	2.27	0.02	1.21–14.01
Year					
2012–2013	1.20	0.62	0.30	0.77	0.35–4.14
2013–2014	1.55	0.62	0.68	0.50	0.44–5.50
Population					
KVP	2.18	0.76	1.06	0.29	0.52–9.18
Age Class					
Adults	2.11	0.52	1.19	0.23	0.61–7.27

Table 3.3. Estimated sex and age class-specific average annual survival (S) rates for black bears in the Kentucky-Virginia (KVP; *n* = 72) and Big South Fork (BSF; *n* = 19) populations during 2011–2014. Using Cox proportional hazards (CPH) models, we produced optimistic (AA) and pessimistic (AD) estimates, standard errors, and 95% confidence intervals depending on how censors were treated. Because of small sample size, we only produced BSF survival estimates for adults.

Sex and Age Class	S_{AA} (SE)	95% CI	S_{AD} (SE)	95% CI
KVP Population				
Female	0.94 (0.02)	0.87–0.98	0.85 (0.04)	0.76–0.90
Adult (≥3)	0.96 (0.02)	0.89–0.99	0.86 (0.04)	0.76–0.91
Subadult (1–2)	0.81 (0.15)	0.42–0.95	0.75 (0.17)	0.39–0.91
Male	0.73 (0.09)	0.58–0.83	0.67 (0.09)	0.52–0.75
Adult (≥3)	0.75 (0.10)	0.56–0.86	0.66 (0.12)	0.48–0.79
Subadult (1–2)	0.65 (0.21)	0.32–0.85	0.62 (0.21)	0.32–0.82
BSF Population				
Female (Adult [≥3])	0.99 (0.01)	0.98–1.00	0.77 (0.12)	0.53–0.89
Male (Adult [≥3])	0.88 (0.09)	0.60–0.97	0.81 (0.11)	0.54–0.93

Table 3.4. Average annual cause-specific mortality binomial probabilities for 72 radio-monitored black bears (29M:43F) in the reintroduced Kentucky-Virginia population (KVP; 2011–2014). Estimates with standard errors (SE) in parentheses are presented for all documented causes of mortality (*n* = 18). Only 2 radio-monitored bears (both males) died in the Big South Fork population (BSF), so we could not estimate cause-specific mortality for the BSF. No bears in our sample died from natural causes.

Cause of Mortality	Male	Female	KVP
Vehicle Collision	0.15 (0.10)	0.40 (0.22)	0.22 (0.10)
Harvest	0.38 (0.13)	0.20 (0.18)	0.33 (0.11)
Illegal Kill	0.15 (0.10)	0.20 (0.18)	0.17 (0.09)
Management Euthanasia	0.32 (0.13)	0.20 (0.18)	0.28 (0.10)

Table 3.5. Black bear demographic parameter estimates used for simulations of the reintroduced Kentucky-Virginia (KVP) and Big South Fork (BSF) populations in the central Appalachians, USA (2010–2014). We considered both optimistic (AA) and pessimistic (AD) scenarios depending on how we treated censored bears for survival analyses (i.e., assumed alive or assumed dead by the end of our study).

Parameter	AA (SE)	Estimate (SE)	AD (SE)
Cub survival[a]		0.87 (0.21)[b]	
KVP Population			
Abundance (*N*)		482 (62.7)[c]	
Litter survival		0.89 (0.04)	
Subadult (1–2) survival (M)	0.65 (0.21)		0.62 (0.21)
Subadult (1–2) survival (F)	0.81 (0.15)		0.75 (0.17)
Adult (≥3) survival (M)	0.75 (0.10)		0.66 (0.12)
Adult (≥3) survival (F)	0.96 (0.02)		0.79 (0.09)
Litter production rate		0.92	
Probability of litter = 1		0.13	
Probability of litter = 2		0.39	
Probability of litter = 3		0.44	
Probability of litter = 4		0.04	
Mean litter size		2.39 (0.59)	
BSF Population[d]			
Abundance (*N*)		211 (39.2)[e]	
Litter survival		0.88 (0.09)	
Adult (≥3) survival (F)	0.99 (0.01)		0.79 (0.09)
Adult (≥3) survival (M)	0.88 (0.09)		0.81 (0.11)

Table 3.5 (continued)

Litter production rate	0.90
Probability of litter = 1	0.08
Probability of litter = 2	0.67
Probability of litter = 3	0.25
Probability of litter = 4	0.00
Mean litter size	2.17 (0.57)

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[a]: Used in population models for both the KVP and BSF populations.

[b]: Estimate from a black bear population in western Virginia (Bridges 2005).

[c]: Estimated during 2012–2013 (Murphy et al. 2016 [*in press*]).

[d]: We used our subadult (both male and female) survival rates from KVP for the BSF because of small sample size at BSF.

[e]: Estimated during 2010–2012 (Murphy et al. 2015).

Table 3.6. Estimated geometric mean population growth rates (λ) of the reintroduced Kentucky-Virginia (KVP) and Big South Fork (BSF) black bear populations (2010–2014). Estimate ranges are based on our proportionment of variance as 75% parameter uncertainty and 25% environmental variation, and 25% parameter uncertainty and 75% environmental variation. Standard deviation (SD) of estimates is presented in parentheses instead of standard error because SD is unaffected by the number of simulation trials.

Year	λ_{KVP} (SD)	λ_{BSF} (SD)
2010–2011	1.11 (0.10–0.12)	N/A
2011–2012	1.10 (0.08–0.10)	1.13 (0.12–0.20)
2012–2013	1.10 (0.07–0.10)	1.13 (0.09–0.12)
2013–2014	1.10 (0.06–0.10)	1.13 (0.08–0.10)
$\bar{x}$	1.10 (0.08–0.10)	1.13 (0.10–0.14)

Table 3.7. Estimated probabilities of ≥25% population decline over a 10-year period and corresponding average annual geometric mean population growth rates (λ) for the reintroduced Kentucky-Virginia (KVP) and Big South Fork (BSF) black bear populations based on different mortality scenarios. Estimate ranges are based on our proportionment of variance as 75% parameter uncertainty and 25% environmental variation, and 25% parameter uncertainty and 75% environmental variation. We conducted 1,000 stochastic simulations for each scenario using the average annual harvest and average annual non-harvest mortality, and the higher 2015 harvest and non-harvest mortality that occurred in both bear populations.

Mortality Scenario	10-year Average Annual λ	10-year Probability of ≥25% Decline
KVP Population		
2010–2014 average harvest	1.09	0.01–0.03
2010–2014 average harvest and non-harvest	1.07	0.07–0.13
2015 harvest	1.02	0.23–0.27
2015 harvest and non-harvest	0.95	0.52–0.53
BSF Population		
2013–2014 average harvest	1.10	0.01–0.02
2013–2014 average harvest and non-harvest	1.06	0.04–0.08
2015 harvest	0.78	0.93–0.94
2015 harvest and non-harvest	0.62	0.97–0.98

Chapter 4: Conclusions

Population declines, range contractions, and extinctions of large carnivores have occurred globally, primarily because of anthropogenic activities (Ripple et al. 2014). Restoring large carnivores to their historical range can improve the structure and function of ecosystems and ultimately enhance biodiversity, which makes reestablishing populations of these animals a worldwide conservation objective (Ordiz et al. 2013, Ripple et al. 2014). Extensive habitat loss and fragmentation, and the inherent biological characteristics of large carnivores render natural recolonization of historical range slow and often unlikely for many of these species. Reintroduction has therefore received increased consideration as a tool for restoring large carnivores throughout the world, but relatively few studies have investigated the characteristics of successful reintroductions for these animals (Seddon et al. 2007, Hayward and Somers 2009). Long-term viability and persistence during the population regulation phase is the ultimate measure of reintroduction success (Robert et al. 2015). The status of most reintroduced large carnivore populations remains unknown, and some reintroduction programs have failed because of poor planning or a lack of post-release monitoring (Clark et al. 2002, Hayward and Somers 2009).

Despite being one of the most frequently reintroduced large carnivores in the world, only two prior studies have explicitly evaluated success of American black bear reintroductions during the regulation phase (Clark and Smith 1994, Laufenberg et al. 2016 [*in press*]), and few studies have investigated the success of reintroductions of other bear species (Clark et al. 2002, Clark 2009). Furthermore, there is a lack of information about the demographic, population genetic, and spatial expansion characteristics of reintroduced and recolonizing large carnivore populations. The work in this dissertation was designed to investigate these processes for, and evaluate reintroduction success of, two reintroduced black bear populations that were created by small founder groups 13–14 years prior. Collectively, the findings in this dissertation: 1) represent the first comprehensive characterization of recolonization for a reintroduced black bear population, 2) provide the first investigations of the long-term genetic effects of reintroducing bears using small founder groups, 3) demonstrate sampling and analytical methods that can be applied to studies of other recolonizing or reintroduced large carnivore populations to efficiently monitor these populations, and 4) cumulatively represent the first holistic demographic and genetic synthesis of reintroduction success for two black bear populations sourced from small founder groups.

A female-biased sex ratio is often indicative of a population that is actively in the process of recolonizing range, and represents one that presumably has high productivity (Miller and Inouye 2013). A recolonizing black bear population in Oklahoma and expanding brown bear populations in Scandinavia and Slovenia all exhibited sex ratios skewed towards females (Swenson et al. 1998, Bales et al. 2005, Jerina and Adamič 2008). These studies were all based on data collected via either live-capture or harvest, which reduces the reliability of conclusions because of the inherent bias in these data types. We instead used noninvasive genetic sampling over a relatively large area and recently developed spatially explicit capture-recapture (SECR) models to estimate a significantly female-biased sex ratio in the Kentucky-Virginia (KVP) black bear population, providing more empirical support for this being a characteristic of recolonizing populations. Additionally, studies of the brown bear in Scandinavia and

Slovenia used harvest data to posit that female density being a decreasing function of distance from the core area was indicative of a recolonizing population (Swenson et al. 1998, Jerina and Adamič 2008). Using our non-invasive sampling, SECR models, and a distance covariate, we explicitly modeled and identified a decreasing female density as a function of distance from the reintroduction area in the larger Pine-Black (PB) core area of the KVP population (Figure 2.4). Finally, because we knew the number of KVP founders, we were able to produce an estimate of the average annual population growth rate between the establishment and regulation phases, which was moderate (λ = 1.14/year). Cumulatively, our findings provide additional and perhaps more dependable evidence for identifying bear populations that are in the process of actively recolonizing range based on demographic characteristics. The ability to do so in a timely manner as we did will likely become more important in the near future when a number of bear populations in the world are projected to recolonize native range, especially since these animals have high rates of conflicts with humans (Chapron et al. 2014, Smith et al. 2015, Penteriani et al. 2016).

In general, bears exhibit male-biased dispersal, whereas females are highly philopatric. Previous studies suggested that rare female dispersal events were crucial to the rate at which bear populations successfully recolonized range (Jerina and Adamič 2008). Bears often exhibit post-release dispersal or attempt to home back to their capture location following reintroduction events (Eastridge and Clark 2001, Wear et al. 2005). Records indicate that at least one female post-release dispersal event likely led to the initial establishment of bears in the Cumberland Gap (CG) core area of the KVP during the early 1990s (Simmons 1997). Inbreeding depression, loss of variation, and reduced effective population size can all manifest following founder events, and can be exacerbated if the founding population is small (Excoffier et al. 2009, Jaimeson 2010). Only one study prior to ours (i.e., brown bears in Finland [Hagen et al. 2015]) had investigated the potential genetic consequences of recolonization for bears. Similar to Hagen et al. (2015) we found no evidence of adverse genetic effects in the CG core or the KVP and Big South Fork (BSF) populations, but instead estimated high genetic diversity. Thus, our findings add to a mounting body of evidence that suggests rapid population growth and the overlapping generations inherent to bears may collectively retain genetic diversity and mitigate the manifestation of deleterious genetic effects following founder events even if the population remains isolated for an extended period (Puckett et al. 2014, Hagen et al. 2015, Murphy et al. 2015). This is a promising finding that could have substantial influence on the decision-making process for reintroducing bear populations elsewhere.

Prior studies of recolonizing bear populations used live-capture, radio-collar, or harvest data to characterize the demographics and spatial expansion patterns of recolonization (Swenson et al. 1998, Bales et al. 2005, Jerina and Adamič 2008, Hagen et al. 2015). Data collection in these types of studies can require multiple years to obtain adequate sample sizes and can be cost-prohibitive (Marucco et al. 2011). In Chapter Two, we instead used noninvasive genetic sampling in a systematic pseudo-clustered grid design to collect robust sample sizes over a short timeframe (i.e., 8 weeks during each of 2 consecutive years) in a recolonizing bear population sourced from reintroduction (Waits and Paetkau 2005, Wilton et al. 2014). By genotyping these noninvasively collected hair samples with microsatellite markers, we obtained considerable demographic and genetic information that allowed us to conduct population genetics tests, estimate demographic parameters, and investigate spatial recolonization patterns (Mumma et al. 2015).

Our use of recently developed correction formulas allowed us to estimate critical conservation genetics parameters – the effective number of breeders (N_B), effective population size (N_E), genetic diversity (H_E) – from these data with minimal bias (≤5%) using the linkage disequilibrium method (Do et al. 2014, Waples et al. 2014). Because of this, we were able to determine that the KVP bear population, long considered to have resulted from natural recolonization (Unger et al. 2013), was instead mostly the product of the original 55 reintroduced founders and retained high genetic diversity. Further, the novel SECR models that we used estimated more precise density and abundance estimates than would have been expected from traditional (non-spatial) mark-recapture models by incorporating the spatial distribution of captures (Efford et al. 2004). By using new developments in SECR models, such as anisotropic transformation of the detection function, and by incorporating potential bear habitat within our study areas, we were able to reduce parameter estimate bias and identify the most likely directions of recolonization by the KVP population (Royle et al. 2013, Sutherland et al. 2015).

Black bears are expected to recolonize portions of the United States during coming decades (Smith et al. 2015), and the status of two reintroduced black bear populations in southern Arkansas and east-central Louisiana are either entirely or partially unknown (Wear et al. 2005, Laufenberg and Clark 2014). Cougars and brown bears are also expected to recolonize parts of the Midwestern and northwestern United States, respectively (LaRue and Nielsen 2016, United States Fish and Wildlife Service

[USFWS] 2016). Recolonizations by brown bears, gray wolves, and Eurasian lynx (*Lynx lynx*) are predicted for parts of Europe (Chapron et al. 2014, Karamanlidis et al. 2015, Ordiz et al. 2015), and Asiatic black bears were recently reintroduced in South Korea (Kim et al. 2011). Study designs and methods similar to what we used in Chapter Two could be employed for studies of the aforementioned large carnivore populations if appropriate species-specific sampling methods are used. For example, hair traps can be used for both black and brown bears, ground-based rub pads have been effective for collecting hair samples from wolves, post or tree-based rub pads and snow tracking have proven reliable at collecting hair samples from cougars, and scat transects have become an increasingly used method for noninvasively collecting genetic samples from all of these species (Long et al. 2008, Ausband et al. 2011, Sawaya et al. 2011). The SECR models we used are well suited for estimating demographic parameters from systematic grid sampling that uses these collection methods, and recently developed SECR models now allow parameter estimation from transect sampling (Efford 2015). Therefore, the collective methods used in Chapter Two may be practical and efficient alternatives for determining the status of and for monitoring recolonizing and reintroduced populations of bears and other large carnivores.

Perhaps most importantly, our collective findings indicated that small founder groups can be used to successfully establish viable, self-sustaining bear populations over the long-term. Using individual-based population viability (PVA) models, we estimated moderate growth rates and simulated low probabilities of decline for both the KVP and BSF bear populations during the population regulation phase (Robert et al. 2015) using our demographic vital rates that were estimated 13–17 years post-reintroduction. Clark and Smith (1994) and Laufenberg et al. (2016 [*in press*]) were the only prior studies that confirmed reintroduction success during the regulation phase for black bear populations (i.e., Interior Highlands populations in Arkansas and Upper Atchafalaya River Basin population in Louisiana). However, only the Three Rivers Complex population in Louisiana was created using an adult founder group (*n* = 48 adults and 104 cubs) of similar size to that of the KVP and BSF populations, but the Three Rivers Complex population was likely not in the regulation phase when the recent evaluation was conducted (during to 3 years post-reintroduction; Laufenberg et al. 2016 [*in press*]). A separate bear reintroduction that also used a small adult founder group (*n* = 23 adults and 56 cubs) occurred during 2000–2002 at Felsenthal National Wildlife Refuge in Arkansas (Wear et al. 2005), but the status of this population remains unknown (J. Clark, United States Geological Survey, personal communication). Therefore, the studies in this dissertation represent the only confirmed long-term successes during the regulation phase of black bear reintroductions that originated from small founder groups.

Based on the findings in Chapters Two and Three, and in Appendix A, three primary factors may have been critical to the success of the BSF and KVP black bear reintroductions. First, despite females being the only reproductively mature sex released at BSF, reproduction was documented during 1999 and rapid growth occurred during later years (Eastridge 2000, Murphy et al. 2015). This indicates that male cubs reached sexual maturity at 2 years-of-age and successfully sired litters. Although this is not typical of most black bear populations (Rogers 1987), given competition for resources and density-dependent effects were non-existent at the time, such early sexually maturity is not implausible (Eiler et al. 1989). Second, harvest was not implemented in the BSF or the Kentucky portion of the KVP for 16 and 12 years post-reintroduction, respectively. This probably allowed bears to become settled and more accustomed to the location of resources within the release areas, and provided an opportunity for mating and subsequent population growth to occur. Finally, both reintroductions occurred in areas that were comprised of a large, relatively contiguous area of forested lands that probably exhibited high productivity (van Manen and Pelton 1997). The availability of high quality habitat in sufficient quantity has been posited as the most critical component to reintroduction success for wildlife (Griffith et al. 1989).

Simulations in Chapter Three suggested that the success of the KVP and BSF black bear reintroductions has resulted in both populations reaching the stage at which they can sustain a small harvest relative to population size. Based on the estimated vital rates in each population, λ estimates revealed that mortality rates (both harvest and non-harvest) of 10% and 13% may stabilize λ of the KVP and BSF, respectively. If management objectives are to reduce populations, then higher rates could be prescribed; although we caution that mortality at the 2015 rate in the BSF could result in a precipitous decline. On the other hand, if larger populations are desired, simulations indicated that the average annual mortality that occurred during our study period would result in positive average annual λ of 1.07 and 1.06 in the KVP and BSF, respectively. Two important caveats must be stated, however: 1) our growth and probability of decline estimates are optimistic and have relatively low precision, and should therefore be used conservatively, and 2) our estimated potential sustainable mortality rates do not solely represent harvest, but include non-harvest mortality as well. Collectively, these findings should provide wildlife managers with an empirical basis to manage the KVP and BSF black bear populations. We importantly suggest that state wildlife agencies consider continuing long-term population monitoring to allow adaptive management of these relatively small populations and improve the precision of our estimates.

Limitations

The study in Chapter Two is limited by the uncertainty of bear distribution outside of our study areas. We sampled the known core areas of the KVP as well as peripheral areas to the west that were predicted to have moderate probabilities of bear occupancy based on a 2008 study (Frary et al. 2011). We captured few male and no female bears in the two western peripheral areas. However, we did not sample the areas immediately to the east and north of the PB core where anecdotal information suggests reproductively mature female bears may reside (J. Plaxico, KDFWR, unpublished data; J. Wills, VDGIF, personal communication). Our abundance and density estimates should therefore be considered minimums for the KVP and not representative of the entire population. We do not believe this to be a major issue for management if our findings are conservatively applied given the vulnerability of these relatively small bear populations to mortality, and assuming the desire to maintain existing bear numbers or allow population growth. Management of both the KVP and BSF populations has not been a coordinated multi-state endeavor, but has instead been state agencies independently managing the portions of each population that reside within their respective jurisdictional boundaries. Given the differences in vulnerability to anthropogenic mortality as indicated by our population models, we suggest that wildlife managers in Kentucky consider managing the BSF and KVP as separate populations until there is sufficient evidence of demographic connectivity between them. Further, we also suggest that KDFWR, NPS, and TWRA consider coordinated and cooperative management of the BSF bear population that in our models appears vulnerable to overexploitation.

Some uncertainty in our survival and reproductive rate estimates in Chapter Three was a limitation because it reduced the reliability of our population growth and risk estimates. The primary data limitations were the inability to estimate temporal process variance because of short study duration and, at BSF, small sample sizes (Harris et al. 2011). Although vital rate monitoring in the KVP began during 2003, annual sample sizes were far too small to produce reasonably precise vital rate estimates until the initiation of this study in 2010 (Unger 2007, Harris 2011). Furthermore, no vital rates were monitored in the BSF between 1998 and 2010. An additional 6–7 more years of demographic vital rate data may need to be collected in both populations to account for the estimate variation issue and alleviate parameter uncertainty. Our growth estimates are probably also biased because we did not monitor cub survival in the BSF or KVP. This vital rate probably needs to be quantified in both populations to produce more accurate growth and probability of decline estimates.

Further Research

The findings in this dissertation have answered a number of questions and filled long-standing knowledge gaps about reintroduced and recolonizing bear and large carnivore populations, and the BSF and KVP populations specifically; however, additional studies are needed. Foremost would be an investigation of the demographic and genetic characteristics that reintroduced bear populations exhibit between the establishment and regulation phases when rapid growth appears to occur. Demographic research was not initiated in the KVP until 2003; ensuing annual bear capture numbers consequently remained low (<20) until 2009, likely because of the small population size during this period. Small sample sizes during the initial years of research and low monitoring intensity prohibited an evaluation of demographics and genetics during the growth phase for the KVP, and the BSF was not monitored after the establishment phase until our studies were initiated during 2010. To our knowledge, only one such study has been designed and implemented that should allow such an investigation to occur. Vital rates and genetics in the reintroduced Three Rivers Complex black bear population in Louisiana were annually monitored during the establishment phase (2001–2009 [Benson and Chamberlain 2007, Laufenberg et al. 2016, *in press*]), have been monitored each year since (S. Murphy and M. Davidson, Louisiana Department of Wildlife and Fisheries, unpublished data), and a 7-year monitoring plan beginning during 2016 has been developed (USFWS 2015). This will cumulatively result in 22 years of annual monitoring for this reintroduced population that was sourced from a small adult founder group, which should result in the first comprehensive characterization of each reintroduction phase for a bear population.

A pseudo-cluster sampling design and SECR models were used to estimate abundance and density of the recolonizing, reintroduced KVP bear population. This sampling design was used to attempt to sample a large geographical area while also producing parameter estimates that were less biased and more reliable compared to those of Frary et al. (2011). Although our study achieved these objectives, since completion of our sampling, recent studies have demonstrated that clustered sampling less intensive than what we used can allow researchers to sample an even larger area and produce reasonably precise density and abundance estimates for black bear populations (Wilton et al. 2014, Sun et al. 2014). These findings could have major implications for monitoring recolonizing and reintroduced bear populations, primarily by possibly allowing researchers to sample the entire extent of these populations to produce population-wide or regional estimates. The work in Chapter Two represents one example of the initial step towards achieving this. A current study designed to estimate abundance and density of the 7 extant Florida black bear (*Ursus americanus floridanus*) subpopulations serves as the first application of these methods over a broad regional scale (Humm et al. 2015). Importantly, continued development of SECR model types will be critical to achieving this potentially pivotal methodological development (Royle et al. 2014).

This dissertation represents work that was designed to determine the contemporary status of both the reintroduced KVP and BSF black bear populations. Although this primary objective was attained, the findings in this dissertation have revealed additional research that may be needed for continued management of these populations. As noted elsewhere in this dissertation, longer-term vital rate datasets are needed for both populations to reduce parameter estimate bias, quantify process variance, and to produce more precise λ estimates. Given the moderate to high probabilities of decline for both populations were optimistic, this is of primary importance to sustainable management and long-term persistence. The general recommendation is that such studies should be conducted for a minimum of 10 years or up to 3 generations, whichever is longer considering the life history traits of the species of interest (Rueda-Cediel et al. 2015). Simulations by Harris et al. (2011) showed that for black and brown bears, parameter estimate precision was more sensitive to adding to the duration of short studies such as ours, and adding additional bears to sample sizes as small as our BSF sample size. Radio-monitoring 30 adult females, 10 subadults, 10 cubs, and 20 litters annually in each population over 10 years would likely produce optimal parameter estimate precision, but this may be so time and cost-intensive that it is unfeasible (Harris et al. 2011). Instead, given the logistical and financial constraints that most state wildlife agencies are subjected to, allotting additional resources to monitor recruitment, cub survival, and adult female survival of the same individual females over a long temporal period may be more efficient than attempting to substantially increase sample sizes (Beston 2011, Harris et al. 2011).

The BSF population remains demographically and genetically isolated, and the KVP experiences limited connectivity with other bear populations in West Virginia and Virginia (Hast 2010, Murphy et al. 2015, 2016). The impetus therefore exists for state wildlife agencies to consider managing these populations as separate entities in a coordinated multistate effort. Tennessee Wildlife Resources Agency currently manages the Tennessee portion of the BSF separate from the eastern Tennessee bear population (TWRA 2015), but KDFWR prescribes singular management actions that make no distinction between the BSF and KVP (KDFWR 2015), and VDGIF mostly conducts statewide, not population-specific, bear management (VDGIF 2012). Despite being bisected by a major highway (Interstate 75), which can inhibit bear movement and population connectivity, suitable habitat exists in the area between the BSF and KVP populations (Unger et al. 2008). One of the most probable directions of range expansion for the BSF is to the southeast towards Pine and Cumberland Mountains (J. Laufenberg, University of Tennessee, unpublished data), and the findings in Chapter Two indicate the KVP may recolonize range towards the southwest along these same linear mountain ridges. Continued genetic monitoring in both populations would allow researchers and managers to determine if connectivity is established between these two populations in the future, assuming management allows growth and range expansion to occur. If these are not management objectives for the BSF, then demographic and genetic monitoring may become vitally important to the conservation of this population, and augmentation efforts may one day be necessary to assuage potential deleterious genetics effects that can develop from prolonged isolation (Edwards 2002, Triant et al. 2004, Dixon et al. 2007).

Appendix A: Rapid Growth and Genetic Diversity Retention in an Isolated Reintroduced Black Bear Population in the Central Appalachians

Abstract

Animal reintroductions are important tools of wildlife management to restore species to their historical range, and they can also create unique opportunities to study population dynamics and genetics from founder events. We used non-invasive hair sampling in a systematic, closed-population capture-mark-recapture study design at the Big South Fork (BSF) area in Kentucky during 2010 and Tennessee during 2012 to estimate the demographic and genetic characteristics of a black bear (*Ursus americanus*) population that resulted from a reintroduced founding population of 18 bears in 1998. We estimated 38 (95% CI: 31–66) and 190 (95% CI: 170–219) bears on the Kentucky and Tennessee study areas, respectively. Based on the Tennessee abundance estimate alone, the mean annual growth rate was 18.3% (95% CI: 17.4–19.5%) from 1998 to 2012. We also compared the genetic characteristics of bears sampled during 2010–2012 to bears in the population during 2000–2002, 2 to 4 years following reintroduction, and to the source population. We found that the level of genetic diversity since reintroduction as indicated by expected heterozygosity (H_{E}) remained relatively constant ($H_{\mathrm{E(source,\ 2004)}} = 0.763$, $H_{\mathrm{E(BSF,\ 2000–2002)}} = 0.729$, $H_{\mathrm{E(BSF,\ 2010–2012)}} = 0.712$) and the effective number of breeders (N_{B}) remained low but had increased since reintroduction in the absence of sufficient immigration ($N_{\mathrm{B(BSF,\ 2000–2002)}} = 12$, $N_{\mathrm{B(BSF,\ 2010–2012)}} = 35$). This bear population appears to be genetically isolated, but contrary to our expectations, we did not find evidence of genetic diversity loss or other deleterious genetic effects typically observed from small

founder groups. We attribute that to high initial genetic diversity in the founder group combined with overlapping generations and rapid population growth. Although the population remains relatively small, the reintroduction using a small founder group appears to be demographically and genetically sustainable.

Introduction

Reintroduction has been successfully used to restore many animal species to their historical ranges, typically with the goal of establishing self-sustaining, viable populations (Griffith et al. 1989, Seddon 1999, Swaisgood 2010). In general, the probability of reintroduction success is improved with large founder population size, high genetic variation in the founder group, availability of high quality habitat, high initial population growth rates, low mortality, and low intraspecific competition (Griffith et al. 1989, Earnhardt 1999, Seddon 1999, Frankham 2009*b*). Therefore, reintroduction efforts with small founder population sizes should establish intensive monitoring programs during and beyond the initial reintroduction phase to determine if further management intervention is necessary to ensure long-term population viability (Frankham 2009*b*, De Barba et al. 2010). Nonetheless, many reintroduction programs have failed to determine whether the criteria for success were met, not only during the focal reintroduction phase, but also at any time post-reintroduction (Beck et al. 1994, Sarrazin and Barbault 1996, Clark et al. 2002). Ultimately, a lack of monitoring can limit science-based assessment and management of often time- and cost-intensive efforts, and risk damage to species conservation programs and public confidence in such activities (Seddon et al. 2007, Armstrong and Seddon 2008, Seignobosc et al. 2011).

The American black bear (*Ursus americanus*) has been subjected to anthropogenic exploitation and habitat destruction throughout North America. Consequently, bear populations in the eastern United States reached historic lows by the early 1900s (Hall 1981, Pelton 2001). Although habitat recovery and population expansion occurred in some areas over the last half-century, a number of smaller black bear populations in the eastern United States remained isolated within fragmented landscapes (Hellgren and Maehr 1992, Pelton and van Manen 1997, Clark et al. 2002, Dixon et al. 2007, O'Connell-Goode et al. 2014). The popularity of the black bear as a game species and the recognition of its important ecological and cultural roles have led to multiple reintroduction efforts within its historical range (Alt 1995, Comly-Gericke and Vaughn 1997, Clark et al. 2002, Wear et al. 2005, Benson and Chamberlain 2007). Perhaps the most successful black bear reintroduction occurred in Arkansas where 254 individuals were translocated from Minnesota and Canada, creating a population of >2,500 within 20 years (Smith and Clark 1994). However, the fate of most black bear reintroductions in the United States remains unknown because of the lack of post-release monitoring, and few black bear reintroduction successes have been documented to date (Clark et al. 2002, Clark 2009).

In the late 1990s, a limited black bear reintroduction took place in an attempt to reestablish the species in a portion of its historical range in the central Appalachians (Eastridge 2000, Eastridge and Clark 2001). During 1996 and 1997, 14 adult female black bears with 13 cubs were captured at Great Smoky Mountains National Park (hereafter referred to as GSMNP) in Tennessee, and were released in the Big South Fork National River and Recreation Area (hereafter referred to as BSF) along the Kentucky-

Tennessee border (11 adult females in Tennessee and 3 in Kentucky), a translocation distance of more than 150 km (Eastridge and Clark 2001). No effort was made to maximize genetic diversity of the original founder group, but all of the founders were sourced from different sites within GSMNP (J. Clark, United States Geological Survey, personal communication). By 1998, 6 adult founders had either left the area or died (Eastridge 2000), and adult female survival including emigration was estimated at 0.66 (SE = 0.12; Eastridge and Clark 2001). A recommended supplementation to this population during 2000 was disallowed because of public opposition, and no supplementation occurred at any time following the initial release of founders. Approximately 18 bears (4 subadult females, 6 subadult males, and 8 adult females) resided in and around the BSF by 1998 (J. Clark, unpublished data), and Eastridge and Clark (2001) estimated that the population had a 24% chance of extinction within 100 years. Persistent observations of adult female bears with cubs in the study area from 1999 to 2009 suggested that either individuals from the original founder population or their descendants remained at BSF, or the area had been colonized by bears from relatively distant (>70 km) neighboring populations.

Hast (2010) investigated the genetic structure of black bears at BSF and other areas of southeast Kentucky by analyzing hair samples collected from hair traps and live captures during 2006–2009. Whereas bears in the neighboring southeast Kentucky population were primarily an admixture of genotypes from Virginia and West Virginia, Hast (2010) determined that bears in the BSF population were comprised almost entirely of genetic material identical to bears in the GSMNP source population, a phenomenon observed in other reintroduced bear populations (Puckett et al. 2014). Hast (2010) identified only 2 migrants in the BSF population; both individuals were males with genotypes similar to the neighboring southeast Kentucky population located approximately 70 km to the east, possibly the result of a nuisance translocation (J. Plaxico, Kentucky Department of Fish & Wildlife Resources, personal communication). Additionally, none of the 146 bears that were radio collared in the nearest southeast Kentucky population during 2000–2014 were known to have successfully traveled to the BSF area (S. Murphy and J. Cox, University of Kentucky, unpublished data). Collectively, this evidence suggests that bears at BSF primarily are descendants of the original translocated founders with minimal gene flow having occurred between BSF and other central Appalachian bear populations since reintroduction.

The winter soft-release method employed by Eastridge and Clark (2001) to initiate the BSF population focuses on the translocation of adult females with cubs to avoid emigration from the release area and to increase settling rates. Although effective (Alt 1995, Eastridge and Clark 2001, Wear et al. 2005, Benson and Chamberlain 2007), the method results in an initially skewed sex ratio and, because it is labor intensive, the number of founders is typically low. A consequence of such reintroductions that rely on small numbers of founder individuals is an increased likelihood of population bottlenecks (Jaimeson 2010) characterized by heightened vulnerability to demographic and environmental stochasticity (Lande 1993, Lande et al. 2003), and the deleterious genetic effects of inbreeding depression, genetic drift, and loss of genetic diversity (Allendorf and Luikart 2007, Brook 2008). Additionally, without immigration from nearby populations, the male component of the population consists of cubs born to founding females, thereby enhancing the prospects for inbreeding. Although bears typically avoid inbreeding because subadult males disperse (Rogers 1987, Clevenger and Pelton 1990, Lee and Vaughn 2004), without unrelated sexually mature males present in the population to replace these offspring, inbreeding can occur (Kasbohm et al. 1994, Zedrosser et al. 2007). Collectively, these inherent consequences of small founder sizes can lead to the loss of fitness and adaptive potential, and an increased risk of population extinction.

Given the lack of critical biological information for the BSF bear population, our goals were to evaluate its demographic and genetic status to provide wildlife and land managers with information for the establishment of management efforts for bears in this area, and to provide further insight into the genetic consequences of reintroducing a large mammal based on a small founder group size. Therefore, we used DNA obtained with non-invasive hair sampling in a systematic, closed-population mark-recapture study design to 1) estimate population abundance and growth rate, 2) determine the potential for deleterious genetic effects resulting from the low number of original founders, and 3) evaluate reintroduction success (i.e., establishment of a self-sustaining population [Griffith et al. 1989]) of black bears at BSF.

Study Area

The 1,915-km^2 study area was located on the western edge of the Cumberland Plateau physiographic region of the Appalachian Plateau physiographic province in the Central Appalachian ecoregion (Thornbury 1965, Smalley 1986, Woods et al. 2002). Study area boundaries included the entirety of the Big South Fork National River and Recreation Area in south-central Kentucky and north-central Tennessee, the Stearns Ranger District of the Daniel Boone National Forest, a portion of Pickett State Park in

Tennessee, a portion of Cumberland Falls State Park in Kentucky, and a matrix of forested and agricultural private lands in McCreary, Whitley, and Wayne counties, Kentucky, and Scott, Fentress, Pickett, and Morgan counties, Tennessee. The area was topographically characterized as a plateau, dissected by deep, narrow ravines cut by multiple rivers and streams, such as the Big South Fork of the Cumberland River (Kleber 1992). Elevations in the study area ranged from 220 m to 659 m above sea level. Vegetation was predominantly mixed-mesophytic forest characterized as having up to 30 co-dominant canopy tree species (Braun 1950, Safley 1970). Forest composition included several species of oak (*Quercus* spp.), hickory (*Carya* spp.), ash (*Fraxinus* spp.), and pine (*Pinus spp.*), as well as American beech (*Fagus grandifolia*), cucumber magnolia (*Magnolia acuminata*), and eastern hemlock (*Tsuga canadensis*). Climate was hot and humid in summer and mild during winter with a typical mean annual temperature of 13º C, and 133 cm of average annual precipitation (Shaw and Wofford 2003). The Daniel Boone National Forest was managed for multiple uses, including timber, water, wildlife, fish, minerals, and recreational activities (United States Forest Service 2009). Active management plans commonly implemented included prescribed burning and timber harvesting. Forests in Big South Fork National River and Recreation Area were managed for multiple uses as well, primarily recreation and conservation but did not include timber harvesting (National Park Service 2005). Removal of timber was permitted only for development of public and administrative facilities by the National Park Service. Prescribed burning, however, was permitted and used as a management tool. Bear harvests did not occur in the study area following reintroduction or during this study. Human population density averaged 15 per km^2 across the entire study area.

Methods

Study design

Black bears are elusive, cryptic, and occur at low density, which introduces difficulty in collecting demographic data (Mowat and Strobeck 2000, Coster et al. 2011). As a result, live-trapping often yields sample sizes too small for reasonably precise demographic estimates (Coster et al. 2011, Marucco et al. 2011). Non-invasive genetic capture-mark-recapture (CMR) methods have become increasingly used among bear researchers and managers as practical and economic alternatives for estimating demographic and genetic characteristics of populations (Woods et al. 1999, Waits and Paetkau 2005, Clark et al. 2010). These methods can increase trapping efficiency and capture probabilities, reduce bias, and mitigate the loss of marks common in live-trapping studies (Woods et al. 1999). The advent of highly variable molecular markers, such as microsatellites, and the ability to amplify the DNA in small quantities of tissue, such as hair, have further increased the applicability and usefulness of non-invasive genetic sampling methods (Taberlet and Luikart 1999, Waits and Paetkau 2005).

Our CMR dataset was the result of 2 independent studies conducted in Kentucky (2010) and Tennessee (2012). We used non-invasive hair traps randomly placed in systematic grids to collect black bear hair for microsatellite DNA analysis. In Kentucky, we established a 1,260-km^2 sampling grid composed of 126 contiguous 10 km^2 cells that covered all of McCreary County, Kentucky, and included the Kentucky portion of Big South Fork National River and Recreation Area. We established a single baited, barbed wire hair trap in each sampling cell to collect black bear hair for microsatellite DNA analysis (Figure A.1; Woods et al. 1999). Hair trap placement was restricted to >100 m from roads and trails, and >500 m from campgrounds, picnic areas, and residential areas. A hair trap consisted of 1–2 barbed wire strands wrapped around 3–5 perimeter trees to create an enclosure about 25 m^2 in size (Woods et al. 1999). We secured wire 65 cm above the ground but added a second wire to some traps at a height of 35 cm above the ground. Laufenberg and Clark (2014) identified no captures of cubs based on backdating captures of bears >1 year of age from subsequent years using these wire heights, so our population estimates probably did not include cubs. Each trap was baited with a combination of sardines and pastries suspended between 2 trees using a string secured approximately 3 m above the ground. From May 2010 to July 2010, we checked and re-baited all hair traps every 7 days for 7 consecutive sampling sessions. We did not move traps between or during any sampling sessions.

In Tennessee, we created a hair trap sampling grid composed of 107 contiguous sampling cells that covered a 645-km^2 area. We used a grid cell size of 6.7 km^2 instead of the 10 km^2 spacing used in Kentucky in an effort to increase capture probabilities and minimize capture heterogeneity (Settlage et al. 2008). As in Kentucky, we constructed a single baited, barbed wire hair trap within each sampling cell to collect black bear hair and adhered to the same placement restrictions (Figure A.1). We constructed all hair traps on the Tennessee study area using 2 wires placed 35 cm and 65 cm above the ground; we wrapped each around 3–5 perimeter trees to form an enclosed polygon. We again baited with sardines and pastries and checked traps weekly for 8 consecutive weeks from May 2012 to July 2012. Again, we did not move traps between or during any sampling sessions. For both studies, we treated each barb on the barbed wire as an individual sample, and removed hairs using tweezers that we sterilized between collections.

Procedures were approved by the University of Kentucky Institutional Animal Care and Use Committee (Protocol #626A2003). We placed collected hair samples in individually labeled paper coin envelopes that were stored at room temperature. We used a flame to sterilize barbs following individual sample collections to prevent cross-contamination of samples.

Although no genetic samples were available from the original founders at BSF, we acquired a dataset consisting of black bear hair samples that were collected during 2000–2002 (i.e., 2-4 years post-reintroduction) from bears at BSF. We used these samples to investigate potential changes in genetic characteristics of the BSF population since reintroduction. These samples were collected opportunistically year round at randomly placed non-invasive hair traps in the Kentucky portion of BSF by Kentucky Department of Fish & Wildlife Resources and National Park Service personnel. The frequency of trap checks for this dataset was variable; otherwise, hair traps and collection methods were similar to those used for the 2010–2012 CMR samples.

We also acquired an additional dataset of black bear hair samples from the GSMNP source population that were collected during 2004 by University of Tennessee researchers as part of a mark-recapture study (Settlage et al. 2008). Although these samples were collected 6 years after the BSF reintroduction, to our knowledge the GSMNP population has not endured any severe reductions in population size in recent history that would alter the estimates of genetic parameters for this source population. Furthermore, Hast (2010) determined that the genotypes of BSF bears and GSMNP bears remained nearly identical. Therefore, we considered these samples representative of the genetic characteristics of the GSMNP source population that the original BSF founders originated from.

Laboratory Analyses

Following sample collection, we sent all hair samples to Wildlife Genetics International (WGI; Nelson, British Columbia) for DNA extraction and amplification. We shipped samples to WGI within 1 month of collection, and data quality was managed by WGI using the methodology described in Paetkau (2003). All samples collected during 2004 at GSMNP, 2000–2002 at BSF, and 2010 in Kentucky were selected for genotyping. However, because a large number of samples were collected in Tennessee during 2012, we established a subsampling protocol to mitigate the financial costs of genotyping. We selected 1 sample per hair trap per week for genotyping (Settlage et al. 2008, Laufenberg 2010) to reduce the number of duplicate samples analyzed from an individual trap site while maximizing the success rate of genotyped samples. Personnel at WGI randomized samples from each site-week and selected the first sample encountered containing 5 guard hair roots or ≥20 underfur hairs. If no samples at a site-week met this threshold, they chose the best available sample using a threshold of 1 guard hair root or 5 underfur hairs. If none of the samples at a site-week met the more lenient threshold, they did not genotype any hair samples for that site during that capture session (D. Paetkau, WGI, personal communication).

Following the protocols described by Woods et al. (1999) and Paetkau (2003), DNA was extracted using QIAGEN DNeasy Blood and Tissue spin columns (Qiagen, Valencia, CA). Seven black bear-specific microsatellite loci (G10B, G10H, G10J, G10L, G10M, G10P, and MU23) were used to identify individual black bears using the polymerase chain reaction (PCR) and genotyping methods described by Paetkau and Strobek (1994). A sex marker was used to delineate sex of identified individuals (Ennis and Gallagher 1994). To minimize genotyping error and mitigate incorrect identification of individuals, WGI discarded samples that failed at >3 markers on the first pass of amplification. Additionally, samples with 1–3 misidentified pairs were reanalyzed, and samples without complete genotypes for all markers were discarded. Finally, error checking was completed by reanalyzing pairs of samples with genotypes matching at all-but-one (1-MM pairs) or all-but-two markers (2-MM pairs) to determine if differences existed at each locus (D. Paetkau, personal communication). This process effectively ensured that the number of individuals identified had not been inflated through undetected genotyping error (Paetkau 2003).

Population Genetics

We tested Hardy-Weinberg equilibrium (HWE) between genotypes with Program Genepop 4.2 using the complete enumeration method and a Markov Chain sampling process (Louis and Dempster 1987, Guo and Thompson 1992, Raymond and Rousset 1995). Linkage disequilibrium, the failure of alleles at 2 loci to be statistically independent, was investigated using the linkage disequilibrium test in Genepop 4.2 (Raymond and Rousset 1995) with *P*-values adjusted using a Bonferroni sequential correction (Rice 1989). We estimated genetic diversity as expected heterozygosity (H_E) using the allele identity method in Genepop 4.2 (Raymond and Rousset 1995). We used the R statistical program (R Core Team 2012) package diveRsity to estimate allelic richness (R_A) using a rarefaction technique (Hurlbert 1971, Keenan et al. 2013). We then compared R_A and H_E of the BSF population during 2000–2002 to that during 2010–2012 with a non-parametric Mann-Whitney U-test in R to investigate whether or not observed changes of these measures of genetic health were the result of differing sample sizes (i.e., the null hypothesis asserts that the medians of the 2 samples are identical [Zar 2010]).

Effective population size (N_E) is the size of an ideal population (i.e., a population with an equal sex ratio of reproducing individuals that are equally likely to reproduce, that exhibits random mating, and in which the number of reproducing individuals is constant among generations) that experiences the same rate of random genetic change over time as the population under consideration (Wright 1931, 1938), and is one of the most important parameters to estimate for conservation and management of wildlife populations (Frankham 2005). This is especially true for reintroduced populations because they are typically vulnerable to deleterious genetic effects, such as founder effect, genetic drift, and a loss of diversity due to small population size (Frankham et al. 2003). Estimating the effective population size and deriving an estimate of the ratio of N_E to abundance (N) can help researchers understand the relative risk that genetic factors may pose for population fitness and persistence (Frankham 2009*a*, Luikart et al. 2010, Palstra and Fraser 2012).

Multiple methods exist to estimate N_E, all of which must be appropriately applied. The standard genetic drift method is temporally based, requiring estimates of allelic or genetic diversity at 2 time points (Kempthorne 1957). Although this method appears to produce precise estimates of N_E for semelparous species, it often biases estimates high for iteroparous species that have overlapping generations such as bears (Palstra and Fraser 2012). An ecological method to estimate N_E developed by Nunney and Elam (1994) performs well for iteroparous organisms (De Barba et al. 2010) but requires long-term demographic data that were not available for the BSF population. In contrast, the linkage disequilibrium method (Hill 1981) requires only a single sample of genetics data, and when used for iteroparous species, it provides an estimate of the number of breeding individuals that have genetically contributed to the population, thereby reflecting N_E of the current generation (Waples 2005, Antao et al. 2011, Palstra and Fraser 2012). Therefore, we estimated effective population size as the number of breeding individuals that have contributed to the population (hereafter referred to as N_B; Waples and Teel 1990) using the linkage disequilibrium method in NeEstimator v2.01 (Ovenden et al. 2007, Do et al. 2014) for the 2000–2002 and 2010–2012 microsatellite data from BSF, as well as the 2004 microsatellite data from GSMNP.

Demographic Estimates

To estimate abundance (N), we employed closed-population models in Program MARK for the 2010–2012 CMR data (White and Burnham 1999). Closed-population models are based on the assumptions of 1) demographic and geographic closure (i.e., no births, deaths, immigration, or emigration during sampling), 2) animals do not lose their marks during sampling, 3) marks are recognized and recorded correctly, and 4) all animals have an equal opportunity of being captured during each sampling session. Closed-population models assume equal capture probability (p; assumption 4 above), but variation often exists (Otis et al. 1978). To address sources of variation in p, models that account for temporal variation (time), behavioral response to capture ($p \neq c$; where c is the recapture probability), and individual heterogeneity (π) have been developed (Otis et al. 1978, Huggins 1989, Pledger 2000).

However, in the presence of missing data introduced by processes such as subsampling hair samples and DNA amplification failure, models that include a behavioral response to capture can sometimes produce biased high *N* estimates because subsequent captures can erroneously be identified as first captures (Augustine et al. 2014). Alternatively, excluding a behavioral response to capture when there is indeed a positive behavioral response to capture leads to an overestimation of *p* and therefore an underestimation of *N*. Methods have recently been developed to fit behavioral response models in the presence of missing data (Augustine et al. 2014), but the methodology has not yet been extended to the subsampling protocol we used in this study for the 2012 Tennessee CMR dataset (i.e., select 1 sample per trap per capture occasion). Therefore, we chose to exclude the behavioral response to capture and time effects for the 2012 Tennessee CMR dataset to produce conservative estimates of *N* and λ.

We used a method to account for individual heterogeneity by modeling capture probability as coming from a 2-class mixture with different capture probabilities for each mixture (Pledger 2000). We did not use individual covariates to model capture heterogeneity (Huggins 1989). For the Kentucky dataset, we considered various combinations of models accounting for individual heterogeneity with a 2-class mixture, sex, behavioral response to capture, and time. For the Tennessee dataset, we considered similar models as those used for the Kentucky dataset but excluded a behavioral response to capture and a time effect. We evaluated models with Akaike's Information Criterion corrected for small sample size ($\mathrm{AIC_c}$; Burnham and Anderson 2002). We averaged models with ≤ 4 $\Delta\mathrm{AIC}_c$ values (i.e., no subsetting) according to the methods outlined in Burnham et al. (2011) to produce final, model-averaged parameter estimates. Because a small number of bears were released in suitable habitat (van Manen and Pelton 1997) that was likely void of resident bears prior to the reintroduction (Eastridge 2000, Eastridge and Clark 2001), we used the exponential growth equation from Gotelli (2008) to estimate the mean annual population growth rate since 1998.

Results

During 2000–2002 at BSF, 83 hair samples were collected, 64 of which assigned to 19 individuals (13M:6F). Twelve (15%) samples failed during genetic analysis and 7 (8%) samples lacked sufficient DNA for analysis. All individuals sampled were successfully genotyped for 7 microsatellites with no 1-MM or 2-MM pairs in the dataset. The sample met the criterion for HWE (c^{2}_{14} = 6.82, P = 0.98), although 4 of 21 loci pairings (19% of total) for the 7 markers were in linkage disequilibrium ($P < 0.05$) following Bonferroni sequential correction. Allelic richness (R_A) from the 7 markers was 6.30 (SE = 0.22), genetic diversity as indicated by expected heterozygosity (H_E) was 0.729 (SE = 0.033), and observed heterozygosity (H_O) was 0.822 (SE = 0.023; Table A.1). The estimated number of breeding individuals that had genetically contributed to the population (N_B) for the 2000–2002 sample was 12 bears (95% CI: 7–18) following 696 independent comparisons (Table A.1).

We acquired data from 39 hair samples from bears at GSMNP during 2004, 24 of which assigned to 22 individuals (10M:12F). Thirteen (33%) samples failed during genetic analysis and 2 (5%) samples lacked sufficient DNA for analysis. All individuals sampled were successfully genotyped for 7 microsatellites with no 1-MM or 2-MM pairs in the dataset. The sample met the criterion for HWE (c^{2}_{14} = 13.3, P = 0.65) and had no signs of linkage disequilibrium ($P < 0.05$) following Bonferroni sequential correction.

Allelic richness (R_A) from the 7 markers was 6.58 (SE = 0.014), genetic diversity as indicated by expected heterozygosity (H_E) was 0.763 (SE = 0.026), and observed heterozygosity (H_O) was 0.787 (SE = 0.018; Table A.1). The estimated number of breeding individuals that had genetically contributed to the population (N_B) for the 2004 GSMNP sample was 142 bears (95% CI: 49–225) following 1,131 independent comparisons (Table A.1).

During summer 2010, we collected 156 bear hair samples in Kentucky from 23 individual hair trap sites (mean = 3.3 visited sites/sampling session). We captured only males ≥15 km from the original BSF reintroduction area (Figure A.1). Of those hair samples, 25 (16%) lacked sufficient DNA for analysis, and 44 (28%) failed during genetic analysis. The laboratory extracted DNA from the remaining 87 (56%) samples, which produced successful identities for 29 (16M:13F) individual bears. During summer 2012, we collected 1,508 bear hair samples from 83 sample sites (mean = 10.4 visited sites/sampling session) in Tennessee (Figure A.1). Of those samples, 1,491 met our predetermined selection criteria to produce a genotype and we selected 295 samples for extraction and genotyping. Technicians at WGI then selected an additional 34 samples for genotyping, beginning with sites with the most multiple samples. A total of 307 (93%) genotyped samples were assigned to 124 (60M:64F) individuals. In sum, 20.3% of collected samples produced an individual identification for the Tennessee dataset. Two male bears (M516 and M510) were sampled during both 2010 and 2012, and 1 male (M610) was sampled in Kentucky during 2009 by Hast (2010) and also during 2012 in Tennessee. No bears sampled during 2000–2002 were resampled during 2010–2012 in either Kentucky or Tennessee.

All individuals sampled in Kentucky and Tennessee during 2010–2012 (n = 153) were successfully genotyped for 7 microsatellites with no 1-MM or 2-MM pairs in the dataset. The pooled sample (n = 153) met the criterion for HWE (χ^2_{14} = 19.1, P = 0.16); however, 1 individual locus (G10L) deviated from HWE ($P \leq 0.001$). Of 21 loci pairings for 7 markers, 11 pairs (> 51% of total) were in linkage disequilibrium ($P < 0.05$) following Bonferroni sequential correction. Allelic richness (R_A) from the 7 markers was 7.81 (SE = 0.53), genetic diversity as indicated by expected heterozygosity (H_E) was 0.712 (SE = 0.025), and observed heterozygosity (H_O) was 0.739 (SE = 0.033; Table A.1). When we compared these results with those from BSF during 2000–2002, we did not detect differences (R_A: U = 23.0, Z = 0.893, 1-tailed P = 0.187; H_E: U = 29.5, Z = 0.210, 1-tailed P = 0.417). The estimated number of breeding individuals that had genetically contributed to the population (N_B) for the 2010–2012 sample was 35 bears (95% CI: 26–47) after 1,062 independent comparisons (Table A.1).

Sex-specific, closed-population CMR models without some form of heterogeneity in capture probability received essentially no support, which conforms to what has typically been the case for most non-invasive bear CMR studies (Boulanger et al. 2004). Therefore, we excluded non-heterogeneity models from model averaging. The top model for the Kentucky (2010) dataset included a mixture effect on capture probability and a behavioral response to capture that varied by mixture group, whereas the top model for the Tennessee (2012) dataset included a mixture effect on capture probability with mixture proportions varying by sex (Table A.2). Model-averaged abundance estimates for males and females in Kentucky were 21 (SE = 5.79, 95% CI = 17–42) and 17 (SE = 9.84, 95% CI = 14–42), respectively, or 38 in total (95% CI = 31–

66). Model-averaged abundance estimates in Tennessee were 103 (SE = 39.2, 95% CI = 73–202) and 87 (SE = 45.2, 95% CI = 71–142) for males and females, respectively, or a total of 190 (95% CI: 170–219). Beginning with 18 bears in 1998 and using only the Tennessee total abundance estimate, the estimated annual population growth rate was 18.3% (95% CI: 17.4–19.5%).

Discussion

Our findings conservatively indicated that bears at BSF exhibited very robust population growth that averaged 18.3% across the 14-year period since reintroduction (1998–2012). This rate is conservative because, although possible, the cub component of the population was not likely captured using our hair trap design (Laufenberg and Clark 2014), and we did not include the 2010 estimate from Kentucky. Moreover, the estimate of abundance in Kentucky may have been negatively biased because the trap site density was lower than that used in Tennessee, which can result in undetected heterogeneity (Settlage et al. 2008). Furthermore, the exclusion of a behavioral response to capture in Tennessee probably resulted in a negative bias (Augustine et al. 2014). Although our estimated rate of population growth is one of the highest reported, especially over such an extended period of time, it is within the biological capabilities of black bears (Bunnell and Tait 1981). The relatively low initial growth rate of 2.6% estimated for this population by Eastridge and Clark (2001) was substantially exceeded over subsequent years possibly because male cubs became reproductively mature, and because bears became settled and more accustomed to the location of resources within the large forested area. Additionally, no bear harvests were permitted at BSF during the 14-year period following reintroduction. Perhaps the most critical component to population growth at

BSF was the availability of a large, contiguous area of state and federally managed forested lands that reached high productivity soon after the bear reintroduction; van Manen and Pelton (1997) predicted 49% of all hard mast producing tree species at BSF would reach the optimal production age within 10 years of the 1996–1997 bear reintroduction. Griffith et al. (1989) posited the availability of sufficient habitat quality and quantity was more critical to reintroduction success than supplementation strategies. Assuming the predictions of van Manen and Pelton (1997) are valid, success of the BSF bear reintroduction supports that postulation.

The decision to soft-release adult females with cubs during the winter (Eastridge and Clark 2001), which suppresses homing behavior common in bears and conversely increases settling rates (Clark et al. 2002), likely promoted successful establishment of resident bears at BSF during the initial reintroduction phase. Although most of the bears released during summer either died or left the reintroduction area, the majority of bears released during winter remained at BSF (Eastridge and Clark 2001). The winter soft-release technique using adult females with cubs has been successfully used for other bear reintroductions (Clark et al. 2002, Wear et al. 2005, Benson and Chamberlain 2007), and results from our study indicate it is an effective technique to establish resident bears and promote subsequent population growth.

Biologists generally agree that reintroductions should be initiated with a large founder population that exhibits high genetic diversity to facilitate resiliency to environmental stochasticity and to avoid deleterious genetic effects (Griffith et al. 1989, Earnhardt 1999, Frankham 2009*b*). Although genetic diversity of the founders was probably high based on our estimate from the 2004 GSMNP dataset ($H_E = 0.763$), the size of the founder group of the BSF bear population declined to as few as 18 individuals by 1998. Our estimate of the effective number of breeders for the 2000–2002 BSF dataset ($N_{\mathrm{B(BSF,\ 2000–2002)}}$ = 12) supports the presumption of a small founder size. Yet, contrary to traditional population genetics theory, genetic diversity of the BSF population remained relatively constant since reintroduction and compared to the source population, and N_{B} increased at BSF ($N_{\mathrm{B(BSF,\ 2010–2012)}}$ = 35; Table A.1).

Although it is widely accepted that small founder groups are at an increased risk of diversity loss (Allendorf and Luikart 2007), recent studies have posited that this may not always be the case for iteroparous mammals because the loss of alleles may be reduced because of generation overlap (Kaeuffer et al. 2007, Kekkonen et al. 2012, Nyman et al. 2014). Additionally, because offspring diversity (i.e., heterozygosity) depends on the genetic composition of parents, and 2 homozygous parents can produce heterozygous offspring, repetitive selection for heterozygotes could increase diversity in reintroduced iteroparous species (Kaeuffer et al. 2007). For example, Kekkonen et al. (2012) conducted a genetics study of an introduced white-tailed deer (*Odocoileous virginianus*) population in Finland sourced from a founder group size of 4 individuals. They discovered that even though the population experienced a historical bottleneck and no supplementation, high levels of genetic diversity were retained in this isolated population more than 75 years after the founder event. Kekkonen et al. (2012), attributed this to overlapping generations, but more importantly, also to a high initial population growth rate that caused the population to remain small for a relatively short time period, thereby retaining diversity. Similarly, Kaeuffer et al. (2007) investigated the genetic consequences of an isolated island population of moufflons (*Ovis aries*) founded by only

2 individuals. They found that genetic diversity increased in the absence of supplementation and attributed this to a high population growth rate along with the natural selection of heterozygotes.

Our results indicate that the deleterious genetic effects commonly observed in reintroduced populations sourced from small founder groups have not occurred in the BSF bear population. Typically, in the absence of supplementation, this would suggest that immigration and resulting gene flow into the population has occurred at a level substantial enough to mitigate these effects. Supporting this is the identification of 2 male migrants during 2009 in BSF by Hast (2010). Yet, the level of immigration estimated by Hast (2010; N_{m} = 0.735) was below the minimum threshold of 1–10 migrants per generation that is needed to effectively mitigate deleterious genetic effects (Mills and Allendorf 1996). Furthermore, even if both migrants identified by Hast (2010) were completely heterozygous, and assuming both individuals successfully reproduced, their genes would likely have had a negligible impact on diversity considering the rapidly growing founding population of bears (Nei et al. 1975, Kekkonen et al. 2012). Though possible because of new allele admixtures from immigration (Hartl 2000, Frankham et al. 2003), the level of linkage disequilibrium we observed in the 2010–2012 dataset (>51% of pairings) would be accompanied by increased H_E and H_{O}, and the effective number of breeders would likely be higher than what we observed (Nunney 1993, Miller et al. 2009). A low number of breeders at BSF was supported by a parentage analysis conducted by Murphy (2011) during 2009–2010, which indicated that roughly 30% of the sampled individuals (n = 48) were descendants of a single father-son pair of male bears.

Although the 2 migrants identified by Hast (2010) could have introduced new alleles into the BSF population thereby increasing R_A, we found no differences between 2000–2002 and 2010–2012. Therefore, similar to Kaeuffer et al. (2007) and Kekkonen et al. (2012), we suggest that the overlapping generations of bears and high population growth rate at BSF, combined with the natural selection of heterozygotes in the absence of adequate gene flow, caused genetic diversity to be retained in the BSF population. Our postulation is further supported by Groombridge et al. (2012) who noted that rapid population growth of iteroparous mammals was associated with no difference in genetic diversity between reintroduced and source populations. More recently, Puckett et al. (2014) discovered that a reintroduced black bear population in Arkansas exhibited relatively constant genetic diversity since reintroduction as well, and posited that this may have been the result of a high population growth rate.

Classical population genetics theory was developed based on semelparous species and, therefore, may not be applicable to iteroparous species that have overlapping generations, such as bears (Johnson 1977). Our findings combined with those of Puckett et al. (2014) support this postulation for bears but also accentuate the interplay of variables in reintroductions, some of which may be beyond management control (i.e., immigration). Additionally, Palstra and Fraser (2012) posited that the incorrect application of methods to estimate genetic parameters for iteroparous species with overlapping generations has remained a problem in wildlife studies. Methods developed for semelparous species are often used for iteroparous species but can produce biased estimates and inaccurate inferences about the genetic health of iteroparous species, particularly long-lived species such as black bears, which are capable of many litters over a lifetime, often with multiple paternities in a single litter (Schenk and Kovacs 1995). Therefore, we caution that classical population genetics theory was not developed for iteroparous organisms and as a result may not apply to large mammals with overlapping generations.

Management Implications

Success of the BSF bear reintroduction demonstrates the importance of investigating habitat characteristics of the release area prior to reintroduction, the use of species-specific release techniques that suppress emigration, and the release of founders that exhibit high genetic diversity. Although our findings combined with that of Hast (2010) indicate that gene flow into BSF from neighboring populations remains minimal, we do not perceive this issue as necessitating immediate action but instead should be monitored and considered for future management. We therefore suggest non-invasive CMR sampling be repeated to evaluate changes in abundance and growth, which would also allow monitoring of population genetics, thereby affording the opportunity to investigate if gene flow into BSF has increased. Based on our findings, we agree with Kekkonen et al. (2012) that future reintroduction programs for iteroparous large mammals should consider prioritizing efforts towards maximizing population growth of founders regardless of founder group size. This may include allocating financial resources to restore or improve habitat, and providing the population with protection from harvest and illegal kills.

Appendix A is published in the following manuscript:

Murphy, S.M., J.J. Cox, J.D. Clark, B.C. Augustine, J.T. Hast, D. Gibbs, M. Strunk, and S. Dobey. 2015. Rapid growth and genetic diversity retention in an isolated reintroduced black bear population in the central Appalachians. Journal of Wildlife Management 79:807–818.

Appendix A: Figures

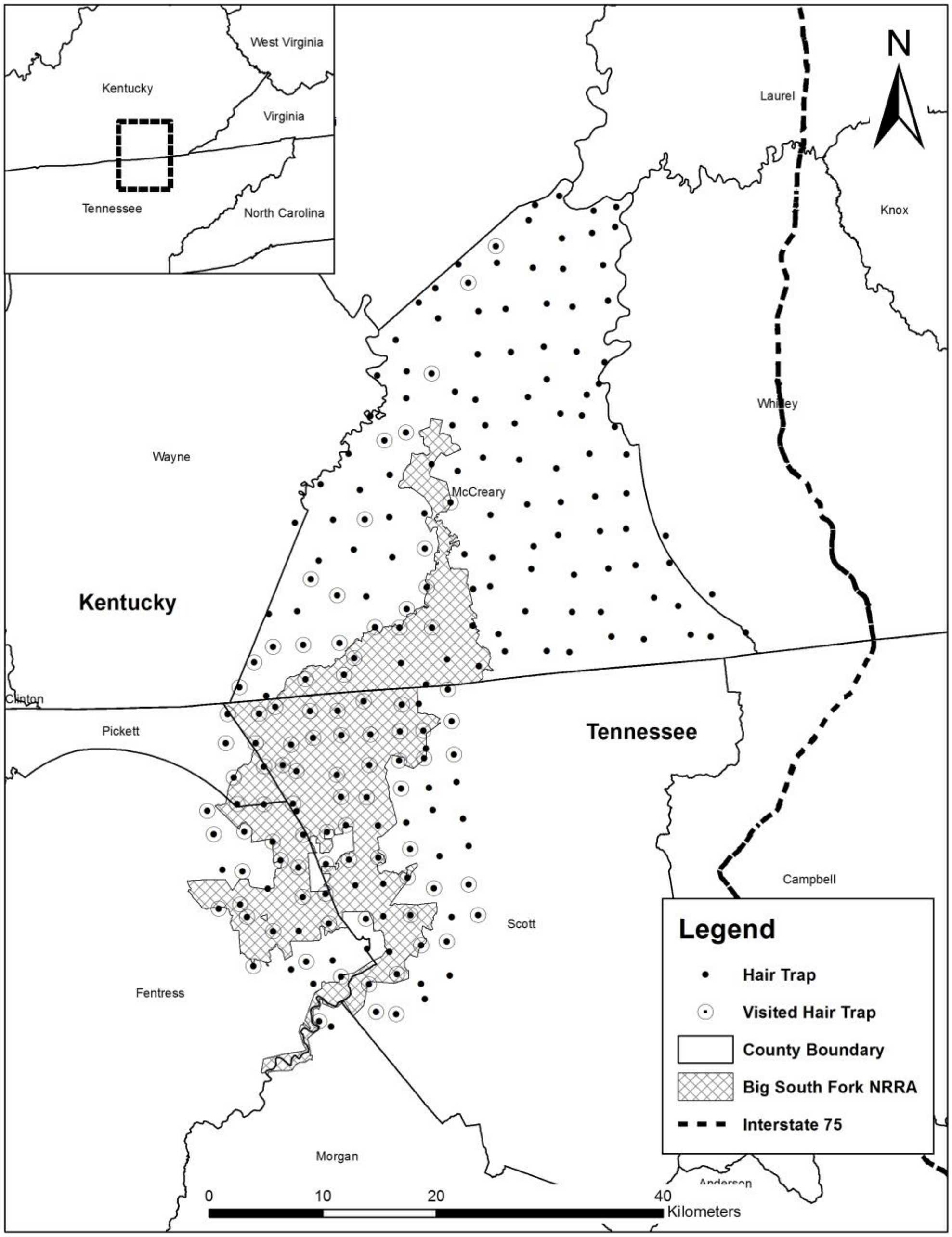

Figure A.1. Locations of 233 black bear hair traps and 106 visited hair traps where we collected hair samples at the Big South Fork study area in Kentucky (2010), and Tennessee (2012), USA. Hair trap density was 1 trap/10 km^2 in Kentucky and 1 trap/6.7 km^2 in Tennessee.

Table A.1. Estimated genetic parameters of 3 independent datasets comprised of black bear hair collected at Big South Fork in Kentucky (2000–2002), USA, Great Smoky Mountains National Park in Tennessee (2004), USA, and Big South Fork in Kentucky and Tennessee (2010–2012), USA. We estimated allelic richness (R_A), observed heterozygosity (H_O), expected heterozygosity (H_E), and the effective number of breeders (N_B) for each dataset using 7 microsatellite markers.

Location	Year	n^a	R_A	H_O	H_E	N_B
Big South Fork	2000–2002	19	6.30	0.822	0.729	12
Great Smoky Mountains	2004	22	6.57	0.787	0.763	142
Big South Fork	2010–2012	153	7.81	0.739	0.712	35

[a] Number of individual bears in sample.

Table A.2. Closed population sex-specific models used to estimate abundance (*N*) of the Big South Fork black bear population in Kentucky (2010), and Tennessee (2012), USA. We modeled individual heterogeneity with a 2-class mixture (π), capture probability (*p*), and abundance (*N*) as functions of sex (sex), a mixture effect (mixture), a null effect (~1), and a time effect (time; Kentucky [2010] only). We accounted for a behavioral response to capture ($p \neq c$) only for the Kentucky (2010) dataset by using additive and interaction effects of the recapture probability (*c*).

Model	K^a	$AIC_c{}^b$	$\Delta AIC_c{}^c$	$w_i{}^d$	Deviance
Kentucky (2010)					
π (~1) *p*(~mixture×c) *N*(~sex)	7	126.13	0.00	0.42	81.32
π (~1) *p*(~mixture) *N*(~sex)	5	127.49	1.36	0.22	86.95
π (~sex) *p*(~mixture×c) *N*(~sex)	8	127.50	1.37	0.21	80.52
π (~1) *p*(~mixture×sex) *N*(~sex)	7	129.94	3.81	0.06	85.13
π (~1) *p*(~mixture×sex+time) *N*(~sex)	13	130.55	4.41	0.05	72.39
π (~sex) *p*(~mixture×sex) *N*(~sex)	8	132.08	5.94	0.02	85.10
Tennessee (2012)					
π (~sex) *p*(~mixture) *N*(~sex)	6	304.34	0.00	0.33	261.09
π (~1) *p*(~mixture+sex) *N*(~sex)	6	304.43	0.09	0.31	261.18
π (~sex) *p*(~mixture+sex) *N*(~sex)	7	305.88	1.54	0.15	260.61
π (~1) *p*(~mixture×sex) *N*(~sex)	7	306.45	2.11	0.11	261.18
π (~sex) *p*(~mixture×sex) *N*(~sex)	8	307.88	3.54	0.06	260.57
π (~1) *p*(~mixture) *N*(~sex)	5	308.43	4.09	0.04	267.21

[a] Number of model parameters.

[b] Akaike's Information Criterion corrected for small sample size.

[c] Relative difference between AIC_c of model and the highest ranked model.

[d] Model weight.

Appendix B: All Considered Spatially Explicit Capture-Recapture (SECR) Models with Isotropic and Anisotropic Detection Functions Used to Estimate Demographics in Chapter Two

Table B.1. We fit models using a binomial observation model with a half-normal detection function. We modeled a trap-specific behavioral response (bk) on the probability of detection at the activity center of an individual (g_0), and allowed g_0 to be fixed across study areas, vary across study areas (A), or vary across study areas and years (A×Y). We did not allow density ($\widehat{D}$) to vary between years, but we did allow $\widehat{D}$ to vary between study areas or be fixed across study areas (~1). We allowed the spatial scale of the detection function (σ) to be shared or to vary by study area. Models that included anisotropic transformation of the detection function are indicated by Φ in the model structure.

Model	K[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	log[e]
Males					
$D(\sim1)\ g_0(\sim bk+A+Y\times A)\sigma(\sim1)\Phi(\sim1)$	8	2368.70	0.00	0.20	-1175.57
$D(\sim A)\ g_0(\sim bk+A+Y\times A)\sigma(\sim1)\Phi(\sim1)$	9	2369.12	0.43	0.16	-1174.58
$D(\sim1)\ g_0(\sim bk+A+Y\times A)\sigma(\sim A)\Phi(\sim1)$	9	2369.43	0.73	0.14	-1174.73
$D(\sim A)\ g_0(\sim bk+A)\sigma(\sim1)\Phi(\sim1)$	7	2369.95	1.26	0.11	-1177.38
$D(\sim1)\ g_0(\sim bk+A)\sigma(\sim1)\Phi(\sim1)$	6	2370.31	1.62	0.09	-1178.71
$D(\sim1)\ g_0(\sim bk+A)\sigma(\sim A)\Phi(\sim1)$	7	2370.69	1.99	0.07	-1177.75
$D(\sim A)\ g_0(\sim bk+A+Y\times A)\sigma(\sim A)\Phi(\sim1)$	10	2370.78	2.09	0.07	-1174.18
$D(\sim1)\ g_0(\sim bk)\sigma(\sim A)\Phi(\sim1)$	6	2371.22	2.52	0.06	-1179.17
$D(\sim A)\ g_0(\sim bk+A)\sigma(\sim A)\Phi(\sim1)$	8	2371.46	2.76	0.05	-1176.96
$D(\sim A)\ g_0(\sim bk)\sigma(\sim A)\Phi(\sim1)$	7	2371.56	2.87	0.04	-1178.19
$D(\sim A)\ g_0(\sim bk)\sigma(\sim1)\Phi(\sim1)$	6	2374.06	5.36	0.01	-1180.59
$D(\sim1)\ g_0(\sim bk)\sigma(\sim1)\Phi(\sim1)$	5	2378.57	9.88	0.00	-1183.97
$D(\sim1)\ g_0(\sim bk+A+Y\times A)\sigma(\sim A)$	8	2379.61	10.91	0.00	-1181.03

Table B.1 (continued)

D(~A) g_0(~bk+A+Y×A)σ(~1)	8	2380.11	11.42	0.00	-1181.30
D(~1) g_0(~bk+A+Y×A)σ(~1)	7	2380.57	11.88	0.00	-1182.69
D(~A) g_0(~bk+A+Y×A)σ(~A)	9	2380.59	11.89	0.00	-1180.32
D(~1) g_0(~bk+A)σ(~A)	6	2381.07	12.37	0.00	-1184.09
D(~A) g_0(~bk+A)σ(~1)	6	2381.25	12.55	0.00	-1184.18
D(~A) g_0(~bk+A)σ(~A)	7	2381.45	12.75	0.00	-1183.13
D(~A) g_0(~bk)σ(~A)	6	2381.77	13.08	0.00	-1184.44
D(~1) g_0(~bk)σ(~A)	5	2381.88	13.19	0.00	-1185.63
D(~1) g_0(~bk+A)σ(~1)	5	2382.58	13.89	0.00	-1185.98
D(~A) g_0(~bk)σ(~1)	5	2388.74	20.05	0.00	-1189.06
D(~1) g_0(~bk)σ(~1)	4	2395.96	27.27	0.00	-1193.78
Females					
D(~1) g_0(~bk+A+Y×A)σ(~1)Φ(~1)	8	1918.27	0.00	0.27	-950.41
D(~1) g_0(~bk+A)σ(~1)Φ(~1)	6	1918.33	0.06	0.26	-952.75
D(~A) g_0(~bk+A)σ(~1)Φ(~1)	7	1920.27	2.00	0.10	-952.58
D(~A) g_0(~bk+A+Y×A)σ(~1)Φ(~1)	9	1920.38	2.10	0.09	-950.27
D(~1) g_0(~bk+A)σ(~A)Φ(~1)	7	1920.58	2.31	0.08	-952.73
D(~1) g_0(~bk+A+Y×A)σ(~A)Φ(~1)	9	1920.62	2.35	0.08	-950.39
D(~A) g_0(~bk+A)σ(~A)Φ(~1)	8	1922.42	4.15	0.03	-952.48
D(~A) g_0(~bk+A+Y×A)σ(~A)Φ(~1)	10	1922.63	4.36	0.03	-950.18
D(~1) g_0(~bk)σ(~A)Φ(~1)	6	1922.88	4.61	0.03	-955.02
D(~A) g_0(~bk)σ(~A)Φ(~1)	7	1925.12	6.85	0.01	-955.00

Table B.1 (continued)

D(~A) g_0(~bk)σ(~1)Φ(~1)	6	1928.64	10.37	0.00	-957.90
D(~1) g_0(~bk)σ(~1)Φ(~1)	5	1928.68	10.41	0.00	-959.05
D(~1) g_0(~bk+A)σ(~1)	5	1933.73	15.46	0.00	-961.57
D(~1) g_0(~bk+A+Y×A)σ(~1)	7	1933.84	15.57	0.00	-959.36
D(~1) g_0(~bk+A)σ(~A)	6	1935.63	17.36	0.00	-961.40
D(~A) g_0(~bk+A)σ(~1)	6	1935.64	17.36	0.00	-961.40
D(~1) g_0(~bk+A+Y×A)σ(~A)	8	1935.84	17.57	0.00	-959.20
D(~A) g_0(~bk+A+Y×A)σ(~1)	8	1935.91	17.64	0.00	-959.23
D(~A) g_0(~bk+A)σ(~A)	7	1937.77	19.50	0.00	-961.33
D(~A) g_0(~bk+A+Y×A)σ(~A)	9	1938.13	19.85	0.00	-959.14
D(~1) g_0(~bk)σ(~A)	5	1939.71	21.44	0.00	-964.56
D(~1) g_0(~bk)σ(~1)	4	1941.51	23.24	0.00	-966.56
D(~A) g_0(~bk)σ(~A)	6	1941.93	23.66	0.00	-964.55
D(~A) g_0(~bk)σ(~1)	5	1942.03	23.76	0.00	-965.72

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[a]: Number of model parameters

[b]: Akaike's Information Criterion corrected for small sample size

[c]: Relative difference between AIC_c of model and the highest ranked model

[d]: Model weight

[e]: log Likelihood.

References

Akçakaya, H. R. 2000. Population viability analyses with demographically and spatially structured models. Ecological Bulletins 48:23–38.

Allendork, F. W., and G. Luikart. 2007. Conservation and the genetics of populations. Blackwell, Malden, Massachusetts, USA.

Allison, P. D. 2010. Survival analysis using SAS: a practical guide. Second edition. SAS Institute, Cary, North Carolina, USA.

Alt, G. L. 1995. Black bear population establishment in southwestern Pennsylvania. Final report for Job 06233, Pennsylvania Game Commission, Harrisburg, USA.

Antao, T., A. Pérez-Figueroa, and G. Luikart. 2011. Early detection of population declines: high power of genetic monitoring using effective population size as estimators. Evolutionary Applications 4:144–154.

Appalachian Regional Commission. 2016. Subregions of the Appalachian Mountain Ecoregion based on United States Census Bureau cartographic boundaries. Appalachian Regional Commision, Washington, District of Columbia, USA.

Armstrong, D. P., I. Castro, and R. Griffiths. 2007. Using adaptive management to determine requirements of reintroduced populations: the case of the New Zealand hihi. Journal of Applied Ecology 44:953–962.

Armstrong, D. P., and P. J. Seddon. 2008. Directions in reintroduction biology. Trends in Ecology and Evolution 23:20–25.

Augustine, B. C., C. A. Tredick, and S. J. Bonner. 2014. Accounting for behavioral response to capture when estimating population size from hair snare studies with missing data. Methods in Ecology and Evolution 5:1154–1161.

Ausband, D. E., J. Young, B. Fannin, M. S. Mitchell, J. L. Stenglein, L. P. Waits, and J. A. Shivik. 2011. Hair of the dog: obtaining samples from coyotes and wolves noninvasively. Journal of Wildlife Management 35:105–111.

Bales, S. L., E. C. Hellgren, D. M. Leslie Jr., and J. Hemphill Jr. 2005. Dynamics of a recolonizing population of black bears in the Ouachita Mountains of Oklahoma. Wildlife Society Bulletin 33:1342–1351.

Balloux, F., and N. Lugon-Moulin. 2002. The estimation of population differentiation with microsatellite markers. Molecular Ecology 11:155–165.

Beck, B. B., L. G. Rapaport, M. R. S. Price, and A. C. Wilson. 1994. Reintroduction of captive-born animals. Pages 265–286 *in* P. J. S. Olney, G. M. Mace, and A. T. C. Feistner, editors. Creative conservation: interactive management of wild and captive animals. Chapman and Hall, London, England.

Beston, J. A. 2011. Variation in life history and demography of the American black bear. Journal of Wildlife Management 75:1588–1596.

Benson, J. F., and M. J. Chamberlain. 2007. Space use, survival, movements, and reproduction of reintroduced Louisiana black bears. Journal of Wildlife Management 71:2393–2403.

Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64:377–385.

Boulanger, J., B. N. McLellan, J. G. Woods, M. F. Proctor, and C. Strobeck. 2004. Sampling design and bias in DNA-based capture-mark-recapture population and density estimates of grizzly bears. Journal of Wildlife Management 68:457–469.

Braun, E. L. 1950. Deciduous forests of eastern North America. McGraw-Hill, New York, New York, USA.

Breitenmoser, U., C. Breitenmoser-Würsten, L. N. Carbyn, and S. M. Funk. 2001. Assessment of carnivore reintroductions. Pages 241–281 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore conservation – conservation biology 5. Cambridge University Press, Cambridge, United Kingdom.

Bridges, A. S. 2005. Population ecology of black bears in the Alleghany Mountains of Virginia. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, USA.

Bridges, A. S., M. R. Vaughn, and J. A. Fox. 2011. American black bear estrus and parturition in the Alleghany Mountains of Virginia. Ursus 22:1–8.

Brook, B. W. 2008. Demographics versus genetics in conservation biology. Pages 35–49 *in* S. P. Carroll and C. W. Fox, editors. Conservation biology – evolution in action. Oxford University Press, New York, USA.

Buchalczyk, T. 1980. The brown bear in Poland. International Conference on Bear Research and Management 4:229–232.

Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears – implications. Pages 75–98 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. John Wiley and Sons, New York, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical-theoretic approach. Second edition. Springer-Verlag, New York, USA.

Burnham, K. P., D. R. Anderson, and K. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–35.

Campbell, M. R. 1893. Geology of the Big Stone Gap coal field of Virginia and Kentucky. Survey Bulletin 111, United States Geological Survey, Washington, District of Columbia, USA.

Casella, G., and R. L. Berger. 2008. Statistical Inference. 2nd edition. Thomson Press, Haryana, India.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, Chichester, United Kingdom.

Chapron, G., P. Kaczensky, J. D. C. Linnell, M. von Arx, D. Huber, H. Andrén, J. V. López-Bao, M. Adamec, F. Álvares, O. Anders, L. Balčiauskas, V. Balys, P. Bedő, F. Bego, J. C. Blanco, U. Breitenmoser, H. Brøseth, L. Bufka, R. Bunikyte, P. Cicucci, A. Dutsov, T. Engleder, C. Fuxjäger, C. Groff, K. Holmala, B. Hoxha, Y. Iliopoulos, O. Ionescu, J. Jeremić, K. Jerina, G. Kluth, F. Knauer, I. Kojola, I. Kos, M. Krofel, J. Kubala, S. Kunovac, J. Kusak, M. Kutal, O. Liberg, A. Majić, P. Männil, R. Manz, E. Marboutin, F. Marucco, D. Melovski, K. Mersini, Y. Mertzanis, R. W. Mysłajek, S. Nowak, J. Odden, J. Ozolins, G. Palomero, M. Paunović, J. Persson, H. Potočnik, P-Y. Quenette, G. Rauer, I. Reinhardt, R. Rigg, A. Ryser, V. Salvatori, T. Skrbinšek, A. Stojanov, J. E. Swenson, L. Szemethy, A. Trajçe, E. Tsingarska-Sedefcheva, M. Váňa, R. Veeroja, P. Wabakken, M. Wölfl, F. Zimmermann, D. Zlatanova, and L. Boitani. 2014. Recovery of large carnivores in Europe’s modern human-dominated landscapes. Science 346:1517–1519.

Clark, J. D. 2009. Aspects and implications of bear reintroductions. Pages 126–145 *in* M. W. Hayward, and M. J. Somers, editors. Reintroduction of top-order predators. Blackwell, Hoboken, New Jersey, USA.

Clark, J. D., and R. Eastridge. 2006. Growth and sustainability of black bears at White River National Wildlife Refuge, Arkansas. Journal of Wildlife Management 70:1094–1101.

Clark, J. D., R. Eastridge, and M. J. Hooker. 2010. Effects of exploitation on black bear populations at White River National Wildlife Refuge. Journal of Wildlife Management 74:1448–1456.

Clark, J. D., D. Huber, and C. Servheen. 2002. Bear reintroductions: lessons and challenges. Ursus 13:335–345.

Clark, J. D., J. S. Laufenberg, M. Davidson, and J. L. Murrow. 2015. Connectivity among subpopulations of Louisiana black bears as estimated by a step selection function. Journal of Wildlife Management 79:1347–1360.

Clark, J. D., and M. R. Pelton. 1999. Management of a large carnivore: black bear. Pages 209–222 *in* J. D. Peine, editor. Ecosystem management for sustainability: principles and practices. CRC Press, Boca Raton, Florida, USA.

Clark, J. D., and K. G. Smith. 1994. A demographic comparison of two black bear populations in the Interior Highlands of Arkansas. Wildlife Society Bulletin 22:593–603.

Clevenger, A. P., and M. R. Pelton. 1990. Pre and post breakup movements and space use of black bear family groups in Cherokee National Forest, Tennessee. Bears: Their Biology and Management 8:289–295.

Collins, L. 1882. Historical sketches of Kentucky. Collins and Company, Covington, KY, USA.

Collins, C., and R. Kays. 2011. Causes of mortality in North American populations of large and medium-sized mammals. Animal Conservation 14:474–483.

Comly-Gericke, L. M., and M. R. Vaughn. 1997. Survival and reproduction of translocated Virginia black bears. Bears: Their Biology and Management 9:113–117.

Coster, S. S., A. I. Kovach, P. J. Pekins, A. B. Cooper, and A. Timmins. 2011. Genetic mark-recapture population estimation in black bears and issues of scale. Journal of Wildlife Management 75:1128–1136.

Cox, J. J., D. S. Maehr, and J. L. Larkin. 2002. The biogeography of faunal place names in the United States. Conservation Biology 16:1143–1150.

Czetwertynski, S. M., M. S. Boyce, and F. K. Schmiegelow. 2007. Effects of hunting on demographic parameters of American black bears. Ursus 18:1–18.

De Barba, M., L. P. Waits, E. O. Garton, P. Genovesi, E. Randi, A. Mustoni, and C. Groff. 2010. The power of genetic monitoring for studying demography, ecology and genetics of a reintroduced brown bear population. Molecular Ecology 19:3938–3951.

Devineau, O., T. M. Shenk, G. C. White, P. F. Doherty Jr., P. M. Lukacs, and R. H. Kahn. 2010. Evaluating the Canada lynx reintroduction programme in Colorado: patterns in mortality. Journal of Applied Ecology 47:524–531.

Diggle, P. J., and P. J. Ribeiro Jr. 2007. Model-based geostatistics. Springer-Verlag, New York, USA.

Dixon, J. D., M. K. Oli, M. C. Wooten, T. H. Eason, J. W. McCown, and M. W. Cunningham. 2007. Genetic consequences of habitat fragmentation and loss: the case of the Florida black bear (*Ursus americanus floridanus*). Conservation Genetics 8:455–464.

Do, C., R. S. Waples, D. Peel, G. M. Macbeth, B. J. Tillett, and J. R. Ovenden. 2014. $\mathrm{N_E}$ESTIMATOR v2: re-implementation of software for the estimation of contemporary effective population size (N_E) from genetic data. Molecular Ecology Resources 14:209–214.

Dobey, S., D. V. Masters, B. K. Scheick, J. D. Clark, M. R. Pelton, and M. E. Sunquist. 2005. Ecology of Florida black bears in the Okefenokee-Osceola Ecosystem. Wildlife Monographs 158.

Earnhardt, J. M. 1999. Reintroduction programmes: genetic trade-offs for populations. Animal Conservation 2(4):279–286.

Eastridge, R. 2000. Experimental repatriation of black bear to the Big South Fork area of Kentucky and Tennessee. Thesis, University of Tennessee, Knoxville, USA.

Eastridge, R., and J. D. Clark. 2001. Evaluation of two soft-release techniques to reintroduce black bears. Wildlife Society Bulletin 29:1163–1174.

Edwards, A. S. 2002. Status of the black bear in southwestern Alabama. Thesis, University of Tennessee, Knoxville, USA.

Efford, M. G. 2015. secr: spatially explicit capture-recapture models. R package version 2.9-4.

Efford, M. G., D. L. Borchers, and A. E. Byrom. 2009. Density estimation by spatially explicit capture-recapture: likelihood-based methods. Pages 255–269 *in* D. L.

Thomson, E. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer-Verlag, New York, USA.

Efford, M. G., D. K. Dawson, and C. S. Robbins. 2004. DENSITY: software for analysing capture-recapture data from passive detector arrays. Animal Biodiversity and Conservation 27:217–228.

Efford, M. G., and R. M. Fewster. 2012. Estimating population size by spatially explicit capture-recapture. Oikos 122:918–928.

Efford, M. G., and G. Mowat. 2014. Compensatory heterogeneity in spatially explicit capture-recapture data. Ecology 95:1341–1348.

Eiler, J. H., W. G. Wathen, and M. R. Pelton. 1989. Reproduction in black bears in the southern Appalachian mountains. Journal of Wildlife Management 53:353–360.

Ennis, S., and T. F. Gallagher. 1994. PCR-based sex determination assay in cattle based on the bovine amelogenin locus. Animal Genetics 25:425–427.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Excoffier, L. 2001. Analysis of population subdivision. Pages 271–307 *in* D. J. Balding, M. Bishop, and C. Cannings, editors. Handbook of statistical genetics. John Wiley & Sons, New York, USA.

Excoffier, L., M. Foll, and R. J. Petit. 2009. Genetic consequences of range expansions. Annual Reviews of Ecology, Evolution, and Systematics 40:481–501.

Fabbri, E., R. Caniglia, J. Kusak, A. Galov, T. Gomerčić, H. Arbanasić, D. Huber, and E. Randi. 2014. Genetic structure of expanding wolf (*Canis lupus*) populations in Italy and Croatia, and the early steps of the recolonization of the Eastern Alps. Mammalian Biology – Zeitschrift fur Saugetierkunde 79:138–148.

Fies, M. L., D. D. Martin, and G. T. Blank Jr. 1987. Movements and rates of return of translocated black bears in Virginia. Bears: Their Biology and Management 7:369–372.

Frankham, R. 2005. Genetics and extinction. Biological Conservation 126:131–140.

Frankham, R. 2009*a*. Effective population size/adult population size ratios in wildlife: a review. Genetical Research 66:95–107.

Frankham, R. 2009*b*. Genetic considerations in reintroduction programmes for top-order, terrestrial predators. Pages 371–387 *in* M. W. Hayward and M. J. Somers, editors. Reintroduction of top-order predators. Blackwell, Hoboken, New Jersey, USA.

Frankham, R. 2015. Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. Molecular Ecology 24:2610–2618.

Frankham, R., J. Ballou, and D. Briscoe. 2003. Introduction to conservation genetics. Cambridge University Press, New York, USA.

Frary, V. J., J. Duchamp, D. S. Maehr, and J. L. Larkin. 2011. Density and distribution of a recolonizing front of the American black bear (*Ursus americanus*). Wildlife Biology 17:404–416.

Gotelli, N. J. 2008. A primer of Ecology. Fourth edition. Sinauer Associates, Sunderland, Massachussets, USA.

Grambsch, P., and T. M. Therneau. 1994. Proportional hazards tests and diagnostics based on weighted residuals. Biometrika 81:515–526.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science 245:477–480.

Groombridge, J. J., C. Raisin, R. Bristol, and D. S. Richardson. 2012. Genetic consequences of reintroductions and insights from population history. Pages 395–440 *in* J. G. Ewen, D. P. Armstrong, K. A. Parker, and P. J. Seddon, editors. Reintroduction biology: integrating science and management. Wiley-Blackwell, Oxford, United Kingdom.

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

Güthlin, D., F. Knauer, T. Kneib, H. Küchenhoff, P. Kaczensky, G. Rauer, M. Jonozovič, A. Mustoni, and K. Jerina. 2011. Estimating habitat suitability and potential population size for brown bears in the Eastern Alps. Biological Conservation 144:1733–1741.

Hall, E. R. 1981. The mammals of North America. Second edition. John Wiley and Sons, New York, New York, USA.

Hagen, S. B., A. Kopatz, J. Aspi, I. Kojola, and H. G. Eiken. 2015. Evidence of rapid change in genetic structure and diversity during range expansion in a recovering large terrestrial carnivore. Proceedings of the Royal Society B 282:20150092.

Harris, H. B. 2011. The return of the black bear to eastern Kentucky: conflict and tolerance between people and wildlife. Dissertation, University of Kentucky, Lexington, USA.

Harris, R. B., C. C. Schwartz, R. D. Mace, and M. A. Haroldson. 2011. Study design and sampling intensity for demographic analyses of bear populations. Ursus 22:14–36.

Hartl, D. L. 2000. A primer of population genetics. Third edition. Sinauer Associates, Sunderland, Massechussetts, USA.

Hast, J. T. 2010. Genetic diversity, structure, and recolonization patterns of Kentucky black bears. Thesis, University of Kentucky, Lexington, USA.

Hayward, M. W., and M. J. Somers. 2009. Reintroduction of top-order predators: using science to restore one of the drivers of biodiversity. Pages 1–9 *in* M. W. Hayward, and M. J. Somers, editors. Reintroduction of top-order predators. Blackwell, Hoboken, New Jersey, USA.

Hedrick, P. W. 1999. Perspective: highly variable loci and their interpretation in evolution and conservation. Evolution 53:313–318.

Heisey, D. M., and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in the presence of competing risks. Journal of Wildlife Management 70:1544–1555.

Hellgren, E. C., and D. S. Maehr. 1992. Habitat fragmentation and black bears in the eastern United States. Proceedings of the Eastern Workshop on Black Bear Management and Research 11:154–166.

Hendricks, S. A., P. R. S. Clee, R. J. Harrigan, J. P. Pollinger, A. H. Freedman, R. Callas, P. J. Figura, and R. K. Wayne. 2016. Re-defining historical geographic range in species with sparse records: implications for the Mexican wolf reintroduction program. Biological Conservation 194:48–57.

Hill, J. D. 1976. Climate of Kentucky. Agriculture Experiment Station Progress Report, University of Kentucky, Lexington, USA.

Hill, W. G. 1981. Estimation of effective population size from data on linkage disequilibrium. Genetics Research 38:209–216.

Hinton, J. W., M. J. Chamberlain, and D. R. Rabon Jr. 2013. Red wolf (*Canis rufus*) recovery: a review with suggestions for future research. Animals 3:722–744.

Hoehn, M., B. Gruber, S. D. Sarre, R. Lange, and K. Henle. 2012. Can genetic estimators provide robust estimates of the effective number of breeders in small populations? PLoS ONE 7:e48464.

Hooker, M. J., J. S. Laufenberg, A. K. Ashley, J. T. Sylvest, and M. J. Chamberlain. 2015. Abundance and density estimation of the American black bear population in central Georgia. Ursus 26:107–115.

Howe, E. J., M. E. Obbard, and J. A. Schaefer. 2007. Extirpation risk of an isolated black bear population under different management scenarios. Journal of Wildlife Management 71:603–612.

Huggins, R. M. 1989. On the statistical analysis of capture experiments. Biometrika 76:133–140.

Humm, J., J. W. McCown, B. K. Scheick, and J. D. Clark. 2015. Black bear population size an density in Osceola and Ocala/St.Johns study areas, Florida. Annual Report to Florida Fish and Wildlife Conservation Commission, University of Tennessee, Knoxville, USA.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577–586.

International Union for Conservation of Nature (IUCN). 2013. Guidelines for reintroductions and other conservation translocations, Version 1. IUCN Species Survival Commission, Gland, Switzerland.

Jakobsson, M., M. D. Edge, and N. A. Rosenberg. The relationsihp between F_{ST} and the frequency of the most frequent allele. Genetics 193:515–528.

Jaimeson., I. G. 2010. Founder effects, inbreeding, and loss of genetic diversity in four avian reintroduction programs. Conservation Biology 25:115–123.

Jensen, R. 2009. The effects of roads and space use on movements of black bears in eastern Kentucky. Thesis, University of Kentucky, Lexington, USA.

Jerina, K., and M. Adamič. 2008. Fifty years of brown bear population expansion: effects of sex-biased dispersal on rate of expansion and population structure. Journal of Mammalogy 89:1491–1501.

Jin, S., L. Yang, P. Danielson, C. Homer, J. Fry, and G. Xian. 2013. A comprehensive change detection method for updating the National Land Cover Database to circa 2011. Remote Sensing of Environment 132:159–175.

Johnson, D. L. 1977. Inbreeding in populations with overlapping generations. Genetics 87:581–591.

Johnson, K. G., and M. R. Pelton. 1980. Prebaiting and snaring techniques for black bears. Wildlife Society Bulletin 8:46–54.

Jones, R. L. 2005. Plant life of Kentucky: an illustrated guide to the vascular flora. University of Kentucky Press, Lexington, USA.

Kaeuffer, R., D. W. Coltman, J.-L. Chapuis, D. Pointer, and D. Reale. 2007. Unexpected heterozygosity in an island mouflon population founded by a single pair of individuals. Proceedings of the Royal Society of Biological Sciences 274:527–533.

Karamanlidis, A. A., M. de Gabriel Hernando, L. Krambokoukis, and O. Gimenez. 2015. Evidence of a large carnivore population recovery: counting bears in Greece. Journal for Nature Conservation 27:10–17.

Kasbohm, J. W., D. A. Miller, and M. R. Vaughn. 1994. Taxonomy of black bears in the southeastern United States. Second Annual Report to the United States Fish and Wildlife Service, Virginia Polytechnical and State University, Blacksburg, USA.

Keenan, K., P. McGinnity, T. F. Cross, W. W. Crozier, and P. A. Prodohl. 2013. diveRsity: an R package for the estimation and exploration of population genetics parameters and their associated errors. Methods in Ecology and Evolution 4:782–788.

Kekkonen, J., M. Wikstrom, and J. E. Brommer. 2012. Heterozygosity in an isolated population of large mammal founded by four individuals is predicted by an individual-based genetic model. PLoS ONE 7:e43482.

Kempthorne, O. 1957. An introduction to genetic statistics. Iowa State University Press, Ames, USA.

Kentucky Department of Fish & Wildlife Resources (KDFWR). 2009. Kentucky hunting and trapping guide: July 2009–February 2010. Kentucky Department of Fish & Wildlife Resources, Frankfort, USA.

_____. 2013. Kentucky hunting and trapping guide: July 2013–February 2014. Kentucky Department of Fish & Wildlife Resources, Frankfort, USA.

_____. 2015. Kentucky hunting and trapping guide: July 2015–February 2016. Kentucky Department of Fish & Wildlife Resources, Frankfort, USA.

_____. 2016. Bear harvest telecheck results. Kentucky Department of Fish & Wildlife Resources. <https://app.fw.ky.gov/webtelecheckresults/tcbearresults.aspx>. Accessed 22 Feb 2016.

Kim, Y-K., Y-J. Hong, M-S. Min, K. S. Kim, Y-J. Kim, I. Voloshina, A. Myslenkov, G. J. D. Smith, N. D. Cuong, H. H. Tho, S-H. Han, D-H. Yang, C-B. Kim, and H. Lee. 2011. Genetic status of Asiatic black bear (*Ursus thibetanus*) reintroduced into South Korea based on mitochondrial DNA and microsatellite loci analysis. Journal of Heredity 102:165–174.

Kindall, J. L., L. I. Muller, J. D. Clark, J. L. Lupardus, and J. L. Murrow. 2011. Population viability analysis to identify management priorities for reintroduced elk in the Cumberland Mountains, Tennessee. Journal of Wildlife Management 75:1745–1752.

King, T., C. Chamberlain, and A. Courage. 2013. Assessing reintroduction success in long-lived primates through population viability analysis: western lowland gorillas *Gorilla gorilla gorilla* in Central Africa. Oryx 48:294–303.

Kirkland, G. L., and J. N. Layne. 1989. Advances in the study of *Peromyscus* (Rodentia). Texas Tech University Press, Lubbock, USA.

Kleber, J. E. 1992. The Kentucky encyclopedia. Third edition. The University Press of Kentucky, Lexington, USA.

Kreeger, T. J., and J. M. Arnemo. 2007. Handbook of wildlife chemical immobilization. Third edition. Laramie, Wyoming, USA.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

Lande, R., S. Engen, and B. Sæther. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, New York, USA.

LaRue, M. A., and C. K. Nielsen. 2016. Population viability of recolonizing cougars in midwestern North America. Ecological Modelling 321:121–129.

LaRue, M. A., C. K. Nielsen, M. Dowling, K. Miller, B. Wilson, H. Shaw, and C. R. Anderson. 2012. Cougars are recolonizing the midwest: analysis of cougar confirmations during 1990–2008. Journal of Wildlife Management 76:1364–1369.

Laufenberg, J. S. 2010. Effect of subsampling genotyped hair samples on model averaging to estimate black bear population abundance and density. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Laufenberg, J. S., and J. D. Clark. 2014. Population viability and connectivity of the Louisiana black bear (*Ursus americanus luteolus*). United States Geological Survey Open-File Report 2014–1228, Reston, Virginia, USA.

Laufenberg, J. S., J. D. Clark, M. J. Hooker, C. L. Lowe, K. C. O'Connell-Goode, J. C. Troxler, M. M. Davidson, M. J. Chamberlain, and R. B. Chandler. 2016. Demographic rates and population viability of black bears in Louisiana. Wildlife Monographs, *In Press.*

Laufenberg, J. S., F. T. van Manen, and J. D. Clark. 2013. Effects of sampling conditions on DNA-based estimates of American black bear abundance. Journal of Wildlife Management 77:1010–1020.

Lee, D. J., and M. R. Vaughn. 2004. Black bear family breakup in western Virginia. Northeastern Naturalist 11:111–122.

Long, R. A., P. MacKay, W. Zielinksi, and J. C. Ray. 2008. Noninvasive survey methods for carnivores. Island Press, Washington D.C., USA.

Louis, E. J., and E. R. Dempster. 1987. An exact test for Hardy-Weinberg and multiple alleles. Biometrics 43:805–811.

Luikart, G., N. Ryman, D. A. Tallmon, M. K. Schwartz, and F. W. Allendorf. 2010. Estimation of census and effective population sizes: the increasing usefulness of DNA-based approaches. Conservation Genetics 11:355–373.

Maehr, D. S. 1984. Distribution of black bears in eastern North America. Eastern Workshop on Black Bear Research and Management 7:74.

Marucco, F., L. Boitani, D. Pletscher, and M. Schwartz. 2011. Bridging the gaps between non-invasive genetic sampling and population parameter estimation. European Journal of Wildlife Research 57:1–13.

McLean, P. K., and M. R. Pelton. 1994. Estimates of population density and growth of black bears in the Smoky Mountains. Pages 253–261 *in* J. Claar and P. Schullery, editors. Bears: Their Biology and Management. Proceedings of the 9th International Conference. International Association for Bear Research and Management, Missoula, Montana, USA.

McLoughlin, P. D., M. K. Taylor, D. H. Cluff, R. J. Gau, R. Mulders, R. L. Case, and F. Messier. 2003. Population viability of barren-ground grizzly bears in Nunavut and the Northwest Territories. Arctic 56:185–190.

Meirmans, P. G. 2006. Using the AMOVA framework to estimate a standardized genetic differentiation measure. Evolution 60:2399–2402.

Miller, S. D. 1990. Population management of bears in North America. Bears: Their Biology and Management 8:357–373.

Miller, T. E. X., and B. D. Inouye. 2013. Sex and stochasticity affect range expasion of experimental invasions. Ecology Letters 16:354–361.

Miller, K. A., N. J. Nelson, H. G. Smith, and J. A. Moore. 2009. How do reproductive skew and founder group size affect genetic diversity in reintroduced populations? Molecular Ecology 18:3792–3802.

Mills, L. S. 2012. Conservation of wildlife populations: demography, genetics, and management. John Wiley and Sons, West Sussex, United Kingdom.

Mills, L. S., and F. W. Allendorf. 1996. The one-migrant-per-generation rule in conservation and management. Conservation Biology 10:1509–1518.

Milner, J. M, E. B. Nilsen, and H. P. Andreassen. 2007. Demogrpahic side effects of selective hunting in ungulates and carnivores. Conservation Biology 21:36–47.

Mowat, G., and C. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. Journal of Wildlife Management 64:183–193.

Mumma, M. A., C. Zieminski, T. K. Fuller, S. P. Mahoney, and L. P. Waits. 2015. Evaluating noninvasive genetic sampling techniques to estimate large carnivore abundance. Molecular Ecology Resources DOI: 10.1111/1755-0998.12390.

Murphy, S. M. 2011. Status of a reintroduced black bear population in the Big South Fork area of Kentucky. Thesis, University of Kentucky, Lexington, USA.

Murphy, S. M., J. J. Cox, B. C. Augustine, J. T. Hast, J. M. Guthrie, J. Plaxico, and J. Wright. 2016. Recolonization characteristics of a reintroduced black bear population based on noninvasive genetic spatial capture-recapture methods. Journal of Wildlife Management, *In Press*.

Murphy, S. M., J. J. Cox, J. D. Clark, B. C. Augustine, J. T. Hast, D. Gibbs, M. Strunk, and S. Dobey. 2015. Rapid growth and genetic diversity retention in an isolated reintroduced black bear population in the central Appalachians. Journal of Wildlife Management 79:807–818.

Murray, D. L., D. W. Smith, E. E. Bangs, C. Mack, J. K. Oakleaf, J. Fontaine, D. Boyd, M. Jiminez, C. Niemeyer, T. J. Meier, D. Stahler, J. Holyan, and V. J. Asher. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biological Conservation 143:2514–2524.

Murrow, J. L., J. D. Clark, S. Flanagan, and C. Thatcher. 2013. A tool for estimating effects of land-use changes on Louisiana black bear habitat. Final Report to United States Fish and Wildlife Service, Ecological Services, Lafayette, Louisiana, USA.

National Park Service. 2005. Big South Fork final general management plan and environmental impact statement. National Park Service, Big South Fork National River and Recreation Area, Oneida, Tennessee, USA.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583–590.

Nei, M., T. Maruyama, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. Evolution 29:1–10.

Nichols, J. D., and D. P. Armstrong. 2012. Monitoring for reintroductions. Pages 223–255 *in* J. G. Ewen, D. P. Armstrong, K. A. Parker, and P. J. Seddon, editors. Reintroduction biology: integrating science and management. Wiley-Blackwell, Chichester, United Kingdom.

Noyce, K. 2011. Summary of state/provincial status reports. Pages 14–20 *in* C. Olfenbuttel and G. Warburton, editors. Proceedings of The 20th Eastern Black Bear Workshop, Hendersonville, North Carolina, USA.

Nunney, L. 1993. The influence of mating system and overlapping generations on effective population size. Evolution 47:1329–1341.

Nunney, L., and D. R. Elam. 1994. Estimating the effective population size of conserved populations. Conservation Biology 8:175–184.

Nyman, T., M. Valtonen, J. Aspi, M. Ruokonen, M. Kunnasranta, and J. U. Palo. 2014. Demographic histories and genetic diversities of Fennoscandian marine and landlocked ringed seal subspecies. Ecology and Evolution 4:3420–3434.

O’Connell-Goode, K. C., C. L. Lowe, and J. D. Clark. 2014. Effects of a flooding event on a threatened black bear population in Louisiana. Animal Conservation 17:476–485.

Onorato, D. P., E. C. Hellgren, R. A. Van Den Bussche, D. L. Doan-Crider, and J. R. Skiles Jr. 2007. Genetic structure of American black bears in the desert southwest of North America: conservation implications for recolonization. Conservation Genetics 8:565–576.

Ordiz, A., R. Bischof, and J. E. Swenson. 2013. Saving large carnivores, but losing the apex predator? Biological Conservation 168:128–133.

Ordiz, A., C. Milleret, J. Kindberg, J. Månsson, P. Wabakken, J. E. Swenson, and H. Sand. 2015. Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. Ecosphere 6:1–14.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:3–135.

Ovenden, J., D. Peel, R. Street, A. Courtney, S. Hoyle, S. Peel, and H. Podlich. 2007. The genetic effective and adult census size of an Australian population of tiger prawns (*Penaeus esculentus*). Molecular Ecology 16:127–138.

Paetkau, D. 2003. An emprical exploration of data quality in DNA-based population inventories. Molecular Ecology 12:1375–1387.

Paetkau, D., and C. Strobeck. 1994. Microsatellite analysis of genetic variation in black bear populations. Molecular Ecology 3:489–495.

Palstra, F. P., and D. J. Fraser. 2012. Effective/census population size ratio estimation: a compendium and appraisal. Ecology and Evolution 2:2357–2365.

Peakall, R. and P. E. Smouse. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research - an update. Bioinformatics 28:2537–2539.

Pelton, M. R. 1989. The impacts of oak mast on black bears in the southern Appalachians. Pages 7–11 *in* C. E. McGee, editor. Proceedings of the Southern Appalachian Mast Management Workshop. University of Tennessee, Knoxville, USA.

Pelton, M. R. 1996. The importance of old growth to carnivores in eastern deciduous forests. Pages 65–75 *in* M. B. Davis, editor. Eastern old-growth forests: prospects for rediscovery and recovery. Island Press, Washington, D. C., USA.

Pelton, M. R. 2001. American black bear. Pages 224–233 *in* J. G. Dickson, editor. Wildlife of southern forests: habitat and management. Hancock House, Blaine, Washington, USA.

Pelton, M. R., and F. T. van Manen. 1997. Status of black bears in the southeastern United States. International Symposium on the Trade of Bear Parts 2:31–44.

Penteriani, V., M. d. M. Delgado, F. Pinchera, J. Naves, A. Fernández-Gil, I. Kojola, S. Härkönen, H. Norberg, J. Frank, J. M. Fedriani, V. Sahlén, O-G. Støen, J. E. Swenson, P. Wabakken, M. Pellegrini, S. Herrero, and J. V. López-Bao. 2016. Human behaviour can trigger large carnivore attacks in developed countries. Scientific Reports 6:20552.

Peters, W., M. Hebblewhite, M. Cavedon, L. Pedrotti, A. Mustoni, F. Zibordi, C. Groff, M. Zanin, and F. Cagnacci. 2015. Resource selection and connectivity reveal conservation challenges for reintroduced brown bears in the Italian Alps. Biological Conservation 186:123–133.

Plaxico, J., and S. Bonney. 2001. Kentucky status report. Pages 16–18 *in* C. V. Waters, editor. Proceedings of the 16th Eastern Black Bear Workshop, Clemson, South Carolina, USA.

Pledger, S. 2000. Unified maximum likelihood estimates for closed capture-recapture models using mixtures. Biometrics 56:434–442.

Population Reference Bureau. 2014. 2014 world population data sheet. Population Reference Bureau, Washington, D. C., USA.

Puckett, E. E., T. V. Kristensen, C. M. Wilton, S. B. Lyda, K. V. Noyce, P. M. Holahan, D. M. Leslie, J. Berringer, J. L. Belant, D. White, and L. S. Eggert. 2014. Influence of drift and admixture on population structure of American black bears (*Ursus americanus*) in the Central Interior Highlands, USA, 50 years after translocation. Molecular Ecology 23:2414–2427.

Putter, H., L. de Wreede, and M. Fiocco. 2015. Package ‘mstate’. R package version 0.2.7.

Pyare, S., S. Cain, D. Moody, C. Schwartz, and J. Berger. 2004. Carnivore re-colonisation: reality, possibility and a non-equilibrium century for grizzly bears in the Southern Yellowstone Ecosystem. Animal Conservation 7:1–7.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raymond, M., and F. Rousset. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Ribeiro Jr., P. J., and P. J. Diggle. 2001. geoR: a package for geostatistical analysis. R-NEWS Vol. 1, No. 2, ISSN 1609–3631.

Ripley, B. 2016. Package ‘nnet’. R package version 7.3-12.

Ripple, W. J., J. A. Estes, R. L. Bescheta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letmic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D.

Wallach, and A. J. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. Science 343:151–162.

Robert, A., B. Colas, I. Guigon, C. Kerbiriou, J-B. Mihoub, M. Saint-Jalme, and F. Sarrazin. 2015. Defining reintroduction success using IUCN criteria for threatened species: a demographic assessment. Animal Conservation 18:397–406.

Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2010. Grizzly bear movements relative to roads: application of step selection functions. Ecography 33:1113–1122.

Rogers, L. L. 1987. Factors influencing dispersal in the black bear. Pages 75–84 *in* B. D. Chepko-Sade and Z. T. Halpin, editors. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Illinois, USA.

Rondinini, C., and P. Visconti. 2015. Scenarios of large mammal loss in Europe for the 21st century. Conservation Biology 29:1028–1036.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2014. Spatial capture-recapture. Academic Press, Waltham, Massachusetts, USA.

Royle, J. A., R. B. Chandler, C. C. Sun, and A. K. Fuller. 2013. Integrating resource selection information with spatial capture-recapture. Methods in Ecology and Evolution 4:520–530.

Rueda-Cediel, P., K. E. Anderson, T. J. Regan, J. Franklin, and H. M. Regan. 2015. Combined influences of model choice, data quality, and data quantity when estimating population trends. PLoS ONE 10:e0132255.

Ryan, C. W. 2009. Population ecology, residents' attitudes, hunter success, economic impact, modeling management options and retention time of Telazol of West Virginia black bears. Dissertation, West Virginia University, Morgantown, USA.

Ryan, C. W., J. C. Pack, W. K. Igo, and A. B. Billings. 2007. Influence of mast production on black bear non-hunting mortalities in West Virginia. Ursus 18:46–53.

Ryan, C. W., J. C. Pack, W. K. Igo, J. C. Rieffenberger, and A. B. Billings. 2004. Influence of mast production on big game harvests in West Virginia. Wildlife Society Bulletin 32:786–794.

Safley, J. M. 1970. Vegetation of the Big South Fork, Cumberland River, Kentucky and Tennessee. Thesis, University of Tennessee, Knoxville, USA.

Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. Journal of Animal Ecology 80:244–258.

Sarrazin, F. 2007. Introductory remarks: a demographic frame for reintroduction. Ecoscience 14:iii–v.

Sarrazin, F., and R. Barbault. 1996. Reintroduction: challenges and lessons for basic ecology. Trends in Ecology and Evolution 11:474–478.

Sawaya, M. A., T. K. Ruth, S. Creel, J. J. Rotella, J. B. Stetz, H. B. Quigley, and S. T. Kalinowski. 2011. Evaluation of noninvasive genetic sampling methods for cougars in Yellowstone National Park. Journal of Wildlife Management 75:612–622.

Scheick, B. K., and W. McCown. 2014. Geographic distribution of American black bears in North America. Ursus 25:24–33.

Schenk, A., and K. M. Kovacs. 1995. Multiple mating between black bears revealed by DNA fingerprinting. Animal Behaviour 50:1483–1490.

Schmeller, D. S., and J. Merilä. 2007. Demographic and genetic estimates of effective population and breeding size in the amphibian *Rana temporaria*. Conservation Biology 21:142–151.

Seddon, P. J. 1999. Persistence without intervention: assessing success in wildlife reintroductions. Trends in Ecology and Evolution 11:474–478.

Seddon, P. J. 2015. Using the IUCN Red List criteria to assess reintroduction success. Animal Conservation 18:407–408.

Seddon, P. J., D. P. Armstrong, and R. E. Maloney. 2007. Developing the science of reintroduction biology. Conservation Biology 21:303–312.

Seddon, P. J., P. S. Soorae, and F. Launay. 2005. Taxonomic bias in reintroduction projects. Animal Conservation 8:51–58.

Seignobosc, M., L. Hemerik, and H. P. Koelewijn. 2011. A demo-genetic analysis of a small reintroduced carnivore population: the otter (*Lutra lutra*) in the Netherlands. International Journal of Ecology 2011:1–11.

Servheen, C. S. Herrero, and B. Peyton. 1999. Bears: status survey and conservation action plan. IUCN Species Survival Commission Bear Specialist Group, Gland, Switzerland.

Servheen, C., W. F. Kasworm, and T. J. Their. 1995. Transplanting grizzly bears (*Ursus arctos horribilis*) as a management tool – results from the Cabinet Mountains, Montana, USA. Biological Conservation 71:261–268.

Settlage, K. E., F. T. van Manen, J. D. Clark, and T. L. King. 2008. Challenges of DNA-based mark–recapture studies of American black bears. Journal of Wildlife Management 72:1035–1042.

Shaw, J., and B. E. Wofford. 2003. Woody plants of Big South Fork National River and Recreation Area, Tennessee and Kentucky, and floristic comparison of selected southern Appalachian woody floras. Castanea 68:119–134.

Simmons, M. 1997. Virginia's bear population. Star-News. 3 September 1997; section StarWatch.

Skalski, J. R., K. E. Ryding, and J. J. Millspaugh. 2005. Wildlife demography: analysis of sex, age, and count data. Elsevier Academic Press, Burlington, Massechussets, USA.

Slatkin, M., and N. H. Barton. 1989. A comparison of three indirect methods for estimating average levels of gene flow. Evolution 43:1349–1368.

Smalley, G. W. 1986. Classification and evaluation of forest sites in the Northern Cumberland Plateau. United States Department of Agriculture Forest Service General Technical Report SO-60, Winchester, Kentucky, USA.

Smith, K. G., and J. D. Clark. 1994. Black bears in Arkansas: characteristics of a successful translocation. Journal of Mammalogy 75:309–320.

Smith, J. B., C. K. Nielsen, and E. C. Hellgren. 2015. Suitable habitat for recolonizing large carnivores in the midwestern USA. Oryx DOI: 10.1017/S0030605314001227.

Smith, D. W., Peterson, R. O., and D. B. Houston. 2003. Yellowstone after wolves. Bioscience 53:330–340.

Sollmann, R., B. Gardner, and J. L. Belant. 2012. How does spatial study design influence density estimates from spatial capture-recapture models? PLoS ONE 7:e34575.

Sun, C. C., A. K. Fuller, and J. A. Royle. 2014. Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. PLoS ONE 9:e88025.

Sundqvist, L., M. Zackrisson, and D. Kleinhans. 2013. Directional genetic differentiation and asymmetric migration. arXiv:1304.0118v2 (q-bio.PE).

Sutherland, C., A. K. Fuller, and J. A. Royle. 2015. Modeling non-Euclidean movement and landscape connectivity in highly structured ecological networks. Methods in Ecology and Evolution 6:169–177.

Swaisgood, R. R. 2010. The conservation-welfare nexus in reintroduction programmes: a role for sensory ecology. Animal Welfare 19:125–137.

Swanton, J. R. 1979. The Indians of the southeastern United States. Smithsonian Institution Press, Washington, D. C., USA.

Swenson, J. E., F. Sandegren, and A. Söderberg. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. Journal of Animal Ecology 67:819–826.

Taberlet, P., and G. Luikart. 1999. Non-invasive genetic sampling and individual identification. Biological Journal of the Linnean Society 68:41–55.

Tallmon, D. A., E. Bellemain, J. Swenson, and P. Taberlet. 2004. Genetic monitoring of Scandinavian brown bear effective population size and immigration. Journal of Wildlife Management 68:960–965.

Taylor, D. F. 1971. A radio-telemetry study of the black bear (*Euarctos americanus*) with notes on its history and present status in Louisiana. Thesis, Louisiana State University, Baton Rouge, USA.

Taylor, M. K., J. Laake, D. H. Cluff, M. Ramsay, and F. Messier. 2002. Managing the risk of hunting for the Viscount Melville Sound polar bear population. Ursus 13:185–202.

Taylor, M. K., J. Laake, P. D. McLoughlin, H. D. Cluff, and F. Messier. 2006. Demographic parameters and harvest-explicit population viability analysis for polar bears in M'Clintock Channel, Nunavut, Canada. Journal of Wildlife Management 70:1667–1673.

Taylor, M. K., M. Obbard, B. Pond, M. Kuc, and D. Abraham. 2003. A guide to using RISKMAN stochastic and deterministic population modeling RISK MANagement decision tool for harvested and unharvested populations, Version 1.9. Government of Nunavut, Iqaluit, Nunavit Territory, Canada.

Tennessee Wildlife Resources Agency (TWRA). 2015. Tennessee hunting & trapping guide 2015–2016. Tennessee Wildlife Resources Agency, Nashville, USA.

_____. 2016. Harvest report. Tennessee Wildlife Resources Agency. <https://jc.activeoutdoorsolutions.com/TNHFInternetHarvest/app/mainHarvestReport.do>. Accessed 22 Feb 2016.

Thatcher, C. A., F. T. van Manen, and J. D. Clark. 2006. Identifying suitable sites for Florida panther reintroduction. Journal of Wildlife Management 70:752–763.

Therneau, T. M. 2015. Package 'survival'. R package version 2.38-3.

Therneau, T. M., and P. Grambsch. 2000. Modeling survival data: extending the Cox model. Springer-Verlag, New York, USA.

Thornbury, W. D. 1965. Regional geomorphology of the United States. John Wiley and Sons, New York, New York, USA.

Townsend, P. A., D. P. Helmers, C. C. Kingdon, B. E. McNeil, K. M. de Beurs, and K. N. Eshleman. 2009. Changes in the extent of surface mining and reclamation in the central Appalachians detected using a 1976–2006 Landsat time series. Remote Sensing of Environment 113:62–72.

Triant, D. A., R. M. Pace, and M. Stine. 2004. Abundance, genetic diversity and conservation of Louisiana black bears (*Ursus americanus luteolus*) as detected through noninvasive sampling. Conservation Genetics 5:647–659.

Unger, D. E. 2007. Population dynamics, resource selection, and landscape conservation of a recolonizing black bear population. Dissertation, University of Kentucky, Lexington, USA.

Unger, D. E., J. J. Cox, H. B. Harris, J. L. Larkin, B. Augustine, S. Dobey, J. M. Guthrie, J. T. Hast, R. Jensen, S. Murphy, J. Plaxico, D. S. Maehr. 2013. History and current status of the black bear in Kentucky. Northeastern Naturalist 20:289–308.

Unger, D. E., S. Fei, and D. S. Maehr. 2008. Ecological niche factor analysis to determine habitat suitability of a recolonizing carnivore. Pages 237–250 *in* P. Bettinger, K. Merry, S. Fei, J. Drake, N. Nibbelink, and J. Hepinstall, editors. Proceedings of the 6th Southern Forestry and Natural Resources GIS Conference, University of Georgia, Athens, USA.

United States Census Bureau. 2010. Census 2010 data for the state of Kentucky. United States Census Bureau, Washington D.C., USA.

United States Fish and Wildlife Service (USFWS). 2016. Endangered and threatened wildlife and plants; removing the Greater Yellowstone Ecosystem population of grizzly bears from the Federal List of Endangered and Threatened Wildlife; 81 FR 13173. USFWS, Grizzly Bear Recovery Office, Missoula, Montana, USA.

_____2015. Draft post-delisting monitoring plan for the Louisiana black bear (*Ursus americanus luteolus*). USFWS, Ecological Services, Lafayette, Louisiana, USA.

United States Forest Service. 2009. About us. Daniel Boone National Forest. <http://www.fs.fed.us/r8/boone/aboutus/>. Accessed 14 Sep 2011.

van Manen, F. T., and M. R. Pelton. 1997. Procedures to enhance the success of a black bear reintroduction program. Ninth International Conference on Bear Research and Management 9:67–78.

Vaughn, M. R. 2002. Oak trees, acorns, and bears. Pages 224–240 *in* W. J. McShea and W. M. Healy, editors. Oak forest ecosystems: ecology and management for wildlife. Johns Hopkins University Press, Baltimore, Maryland, USA.

Virginia Department of Game & Inland Fisheries (VDGIF). 2008. VDGIF bear relocation report 2008. Virignia Department of Game & Inland Fisheries, Henrico, USA.

_____. 2002. Virginia black bear management plan 2002–2011. Virginia Department of Game & Inland Fisheries, Henrico, USA.

_____. 2012. Virginia black bear management plan 2012–2021. Virginia Department of Game & Inland Fisheries, Henrico, USA.

_____. 2016. Virginia black bear harvest by county. Virginia Department of Game & Inland Fisheries. <http://www.dgif.virginia.gov/wildlife/bear/harvest/>. Accessed 12 Jan 2016.

Votsi, N-E. P., M. S. Zomeni, and J. D. Pantis. 2016. Evaluating the effectiveness of Natura 2000 Network for wolf conservation: a case-study in Greece. Environmental Management 57: 257–270.

Waits, L. P., and D. Paetkau. 2005. Noninvasive genetic sampling tools for wildlife biologists: a review of applications and recommendations for accurate data collection. Journal of Wildlife Management 69:1419–1433.

Waples, R. S. 2005. Genetic estimates of contemporary effective population size: to what time periods do the estimates apply? Molecular Ecology 14:3335–3352.

Waples, R. S., T. Antao, and G. Luikart. 2014. Effects of overlapping generations on linkage disequilibrium estimates of effective population size. Genetics 197:769–780.

Waples, R. S., and D. J. Teel. 1990. Conservation genetics of pacific salmon: temporal changes in allele frequency. Conservation Biology 4:144–156.

Wathen, G. 2001. Tennessee status report. Pages 79–84 *in* C. V. Waters, editor. Proceedings of the 16th Eastern Black Bear Workshop, Clemson, South Carolina, USA.

Wathen, W. G., G. F. McCracken, and M. R. Pelton. 1985. Genetic variation in black bears from the Great Smoky Mountains National Park. Journal of Mammalogy 66:564–567.

Wear, B. J., R. Eastridge, and J. D. Clark. 2005. Factors affecting settling, survival, and viability of black bears reintroduced to Felsenthal National Wildlife Refuge, Arkansas. Wildlife Society Bulletin 33:1363–1374.

Weir, B. S., and C. C. Cockerham. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38:1358–1370.

Weise, F. J., K. J. Stratford, and R. J. van Vuuren. 2014. Financial costs of large carnivore translocations – accounting for conservation. PLoS ONE 9:e105042.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.

Wielgus, R. B., D. E. Morrison, H. S. Cooley, and B. Maletzke. 2013. Effects of male trophy hunting on female carnivore population growth and persistence. Biological Conservation 167:69–75.

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

Williams, C. K., G. Ericsson, and T. A. Heberlein. 2002. A quantitative summary of attitudes toward wolves and their reintroduction (1972–2000). Wildlife Society Bulletin 2:575–584.

Wilton, C. M., J. L. Belant, and J. Beringer. 2014. Distribution of American black bear occurrences and human-bear incidents in Missouri. Ursus 25:53–60.

Wilton, C. M., E. E. Puckett, J. Beringer, B. Gardner, L. S. Eggert, and J. L. Belant. 2014. Trap array configuration influences estimates and precision of black bear density and abundance. PLoS ONE 9:e111257.

Wolfe, M. L., D. N. Koons, D. C. Stoner, P. Terletzky, E. M. Gese, D. M. Choate, and L. M. Aubry. 2015. Is anthropogenic cougar mortality compensated by changes in natural mortality in Utah? Insight from long-term studies. Biological Conservation 182:187–196.

Woods, A. J., J. M. Omernik, W. H. Martin, G. J. Pond, W. M. Andrews, S. M. Call, J. A. Comstock, and D. D. Taylor. 2002. Ecoregions of Kentucky. United States Geological Survey, Reston, Virginia, USA.

Woods, J. G., D. Paetkau, D. Lewis, B. N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27:616–627.

Wright, S. 1931. Evolution in Mendelian populations. Genetics 16:91–159.

Wright, S. 1938. Size of a population and breeding structure in relation to evolution. Science 87:430–431.

Wright, S. 1951. The genetical structure of populations. Annals of Eugenics 15:323–354.

Zar, J. H. 2010. Biostatistical analysis. Fifth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zedrosser, A., O.-G. Støen, S. Sæbø, and J. E. Swenson. 2007. Should I stay or should I go? Natal dispersal in the brown bear. Animal Behavior 74:369–376.

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Curriculum Vitae

Born:	Big Stone Gap, Virginia
Citizenship:	United States of America

EDUCATION

2011	**Master of Science**. Forestry, University of Kentucky Thesis: Status of a Reintroduced Black Bear Population in the Big South Fork Area of Kentucky
2009	**Bachelor of Science**. Forestry, University of Kentucky Project: Space Use and Food Habits of Florida Black Bears

PROFESSIONAL POSITIONS

2013–Present	**Large Carnivore Biologist** Louisiana Department of Wildlife & Fisheries
2010–Present	**Research Assistant/Graduate Student** University of Kentucky, Department of Forestry/Department of Animal and Food Sciences
2009–2010	**Lead Research Technician** University of Kentucky, Department of Forestry
2009	**Research Technician** Colorado Parks and Wildlife
2008	**Research Technician** University of Kentucky, Department of Forestry
2008	**Lead Research Technician** University of Kentucky, Department of Biology
2008	**Lead Research Technician** Archbold Biological Station/University of Kentucky, Department of Forestry

PROFESSIONAL PUBLICATIONS

Murphy, S.M., Cox, J.J., Augustine, B.C., Hast, J.T., Guthrie, J.M., Plaxico, J., and J. Wright. (2016). "Recolonization characteristics of a reintroduced black bear population based on noninvasive genetic spatial capture-recapture methods." *Journal of Wildlife Management,* In Press.

Murphy, S.M., Cox, J.J., Clark, J.D., Augustine, B.C., Hast, J.T., Gibbs, D., Strunk, M., and S. Dobey. (2015). "Rapid growth and genetic diversity retention in an isolated reintroduced black bear population in the central Appalachians." *Journal of Wildlife Management,* 79:807–818.

Murphy, S.M., and M. Davidson. (2015). "Genetic characteristics of the Tensas River Basin subpopulation of Louisiana black bears." Technical Report to United States Fish and Wildlife Service, Louisiana Department of Wildlife & Fisheries, Lafayette, Louisiana, USA.

Murphy, S.M. (2015). "Hunting safely in bear country." *Louisiana Wildlife Insider* 1:6–7.

Davidson, M., **Murphy, S.M.**, Ribbeck, K., Kimmel, F., and J. Duguay. (2015). "Louisiana black bear management plan." Louisiana Department of Wildlife and Fisheries, Baton Rouge, USA.

Unger, D.E.,Cox, J.J., Harris, H.B., Larkin, J.L., Augustine, B.C., Dobey, S., Gutherie, J.M., Hast, J.T., Jensen, R., **Murphy, S.M.,** Plaxico, J., and D.S. Maehr. (2013). "History and current status of the black bear in Kentucky." *Northeastern Naturalist* 20:289–308.

REPRESENTATIVE ABSTRACTS

Murphy, S.M., and M. Davidson. (2015). "Using the winter soft-release translocation method for human-bear conflict abatement." The 22nd Eastern Black Bear Workshop, Louisville, Mississippi, USA.

Siracusa, C., **Murphy, S.M.**, and M. Davidson. (2015). "Efficacy of agency-funded community bear-proofing programs: a case study in Louisiana." The 22nd Eastern Black Bear Workshop, Louisville, Mississippi, USA.

PROFESSIONAL AWARDS

2012	The Kentucky Chapter of The Wildlife Society Annual Meeting, Golden Pond, KY, Best Poster Award
2011	The 18th Annual Wildlife Society Conference, Kona, HI, Best Student Poster Award

2011	Graduate Student Award for Excellence in Research, Academics, and Leadership, University of Kentucky, Lexington, KY

PERSONAL

2003–2007	Letterman, University of Kentucky Football Music City Bowl Champions: 2006, 2007
2006–2007	Academic All-Conference, Southeastern Athletic Conference (SEC)