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EXPLAINING AND MONITORING POPULATION PERFORMANCE IN GRIZZLY AND
AMERICAN BLACK BEARS

By

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Explaining and monitoring population performance in grizzly and American black bears.

ABSTRACT

Chairperson: Dr. Michael Mitchell

Understanding how environmental factors influence wildlife populations is at the heart of ecology and management. Populations and their habitats are, however, inherently dynamic, which requires monitoring responses to changes in the environment. Beyond quantifying population dynamics, understanding why populations respond as they do may allow improved predictions within and across populations, ideally leading to better management. Grizzly bears (*Ursus arctos*) and American black bears (*U. americanus*) have been researched in North America for decades, providing excellent opportunities to explore ecological questions involving inter- and intraspecific competition and responses to spatial and temporal variation in resources. The wealth of data collected on these species may be used to answer ecological questions and obtain reliable information for monitoring and management in a rapidly changing world.

Chapter 1: Why do grizzly and black bear densities vary in space and time? I used data from noninvasive genetic sampling of grizzly and black bears in northwestern Montana with spatially-explicit capture-recapture models to predict sex-specific density patterns for both species. In addition to intraspecific effects on density, I considered biotic and abiotic factors such as net primary productivity and habitat security.

Chapter 2: Why do detection probabilities of grizzly bears at bear rubs vary within and across populations? Research has shown detection to vary by sex and season, but also across populations. I used data from two large noninvasive genetic sampling studies to explore a suite of biotic and abiotic factors that are plausibly related to bear rubbing behavior. After creating predicted density surfaces for both species, I compared models including effects of density, terrain characteristics, and sampling effort in mark-recapture models to evaluate support for my hypotheses.

Chapter 3: Monitoring the performance of any wildlife population can be difficult, and the variety of research tools to do so can be overwhelming at times. To assist black bear managers across northeastern North America in identifying suitable tools, I assessed the tradeoffs of methods including traditional mark-recapture, spatially-explicit methods, and known fate models. For some methods, I also conducted simulations based on published data to provide insights into study design and expectations of model performance.

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Funding for the analysis of population monitoring options for black bears in the northeast was provided by the member agencies of the Northeast Black Bear Technical Committee (NEBBTC) through the Wildlife Management Institute. I am grateful for the valuable guidance and constructive feedback on all stages of this work from J. McDonald and J. Hurst and thank all other members of the NEBBTC for their contributions: P. Rego, J. Vashon, H. Spiker, L. Conlee, K. Craig, C. Dyke, A. Timmins, K. Burguess, S. Spencer, M. de Almeida, M. Obbard, M. Terner, R. Dibblee, S. Lefort, C. Brown, F. Hammond, J. Sajecki, and C. Carpenter. I thank K. Noyce and B. Scheick for sharing valuable data, S. Williamson of the Wildlife Management Institute for his help with contract management, and T. White for her administrative support throughout this project. This large undertaking was successful thanks to the hard work, insights, and patience of Drs. M. Sawaya, F. van Manen, and J. Clark, who have collectively and individually done tremendous things to advance my skills and knowledge and, more importantly, the conservation of bears around the globe. I am beyond grateful for the opportunity to work with them.

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Finally, I want to thank whatever the force was out there that introduced me to this path. I am beyond grateful for the opportunity to spend time in some of the most spectacular landscapes on earth, while working and living in the presence of such amazing animals.

Hopefully I can manage to give something back.

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CHAPTER 1 : DISSERTATION OVERVIEW AND INTRODUCTION

The distribution and abundance of a species reflects its relationship with its environment. As such, one of the most important questions in ecology is to understand how the processes that determine distribution and abundance function in time and space (Brown et al. 1995).

Populations and the landscapes that they inhabit, however, are rarely homogenous at scales relevant to conservation or management efforts. Fine-scale patterns may appear homogenous, yet extrapolate poorly to the population level. Conversely, coarse-scale patterns can mask the heterogeneity that exists at finer scales and that drives how populations perform. This heterogeneity makes linking spatial patterns to population processes such as survival and habitat selection a challenge (Wiens et al. 1993). Further, the specific spatial structuring of population performance can play an important role in its overall dynamics, ability to respond to landscape changes, and, therefore, viability (Wiegand et al. 2002). A better understanding of the mechanisms behind population performance may allow us to develop spatially-explicit monitoring methods, thereby improving our ability to predict detailed population responses to landscape changes and focus conservation efforts where they will have the greatest impacts.

All populations have inherent variation in how they respond to their environment in both space and time. At its heart, the overall variation in population performance is driven by individual-level variation in vital rates such as survival and reproductive output (Caswell 2006). Variation in vital rates can in turn be linked to heterogeneous resource availability and use in addition to other extrinsic factors such as human caused mortality. For example, McLoughlin et al. (2006) identified a relationship between spatial variation in lifetime reproductive success and resource selection in red deer (*Cervus elaphus*) in Scotland. Although rare, this study was able

to demonstrate how variation in habitat selection can explain differences in individual vital rates that can have population-level effects (McLoughlin et al. 2006).

Such variation in individual vital rates can manifest as measurable differences in abundance, population growth rates, and distribution at scales finer than the population level (Mills 2012). For organisms that interact at a local scale, populations do not respond to large-scale average conditions; instead it is these finer-scale processes that determine local, and thereby overall, population performance (Tilman and Lehman 1997, Wiegand et al. 2002). Moreover, variation will exist in how populations perform in the face of interactions among numerous dynamic factors including inter- and intraspecific competition and seasonal changes to resource availability (Tilman and Lehman 1997). As such, what is clearly needed is a better understanding of what determines spatial and temporal variation in population performance in order to answer questions of interest to conservation and management.

It is often difficult, however, to detect and monitor such sub-population-level processes and to place their role in population-level performance into context (Wiegand et al. 2002). In particular, monitoring changes in abundance and population growth rates, and ultimately linking changes to their environmental drivers, continue to challenge research biologists despite a sometimes overwhelming number of tools that seem to advance daily (Williams et al. 2002). Once a research objective has been well defined, identifying and optimizing sampling methods is a key step, but one that often fails to fully incorporate the ecology and behavior of the study species. This can be especially problematic for cryptic species such as grizzly and American black bears whose behaviors are difficult to study and may vary with age, sex, or other factors. With these challenges in mind, I present the following chapters:

Chapter 2: Why do grizzly and black bear densities vary in space and time within a given population? Specifically, how do these species influence the density patterns of the other? I used data from noninvasive genetic sampling of grizzly and black bears in northwestern Montana with spatially-explicit capture-recapture models to predict sex-specific density patterns for both species. In addition to intraspecific effects on density, I explored the effects of biotic and abiotic factors such as net primary productivity and habitat security on density patterns of these sympatric populations.

Chapter 3: Why do detection probabilities of grizzly bears at naturally occurring bear rubs vary within and across populations? Research has shown detection to vary by sex and season, but also across populations. I used data from two large noninvasive genetic sampling studies conducted in northwestern Montana and Banff National Park, Alberta, to explore a suite of biotic and abiotic factors that are plausibly related to bear rubbing behavior. Related to my primary hypothesis, the Montana study area had roughly twice the density of grizzly bears as Banff, and three times as many black bears. After creating predicted density surfaces for both species in each study area, I compared models including effects of density, terrain characteristics, and sampling effort in closed-population mark-recapture models to evaluate support for my hypotheses.

Chapter 4: Monitoring the performance of any wildlife population can be difficult, and the variety of research tools to do so can be overwhelming at times. To assist black bear managers across northeastern North America in identifying suitable tools, I assessed the tradeoffs of methods including traditional mark-recapture, spatially-explicit methods, and known fate models. For some methods, I also conducted simulations based on published data to provide insights into study design and expectations of model performance.

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CHAPTER 2 : EVIDENCE OF COMPETITION IN SHAPING SEASONAL DENSITY PATTERNS OF SYMPATRIC URSIDS

INTRODUCTION

The density of animals in a population is one of the metrics of population performance most relied upon for assessing and managing wildlife populations (Williams et al. 2002; Karanth et al. 2004; Fuller et al. 2016). Density reflects the sum of births, deaths, immigration, and emigration for a defined area at a specific period of time, with each rate being influenced by the suitability of the local environment to the species' requirements (Brown et al. 1995; Garshelis 2000). As such, understanding how density is related to the environment remains a fundamental pursuit in ecology, and may directly influence efforts to promote the long term viability of a species (Andrewartha & Birch 1986; Brown et al. 1995; Karanth et al. 2004).

Density of animals is expected to reflect the suitability of habitat for a given population, with higher densities being indicative of higher quality habitat, and vice versa (Brown et al. 1995; Bock & Jones 2004). Although there are multiple ways in which habitat can be assessed, including resource selection functions (Manly et al. 2007) and habitat suitability indices (Brooks 1997), linking environmental conditions to demographic measures like density should be a research priority (Garshelis 2000). More abundant resources, such as food, thermal and security cover, and mating opportunities, should result in larger numbers of individuals per unit area, other than situations of attractive sinks (Delibes et al. 2001). Empirical challenges, however, remain daunting as the data and analytical tools needed to identify relationships between environmental variation and density are generally lacking (Fahrig and Merriam 1994; Graves et al. 2011; Apps et al. 2016).

Within populations, spatial and temporal variation in the suitability and availability of resources is a primary driver of the fitness of members of a population (Brown 1984; Wiegand et al. 2002). This can result in substantial heterogeneity in density patterns within a population, which can be further influenced by changing needs related to the life history of individuals (Festa-Bianchet 1988; Pulliam et al. 1992). This intrapopulation variation is particularly difficult to explain given the typically coarse temporal and spatial scale of available data (Brown et al. 1995; Nielsen et al. 2010). Most studies have therefore used static indices of environmental factors at fixed spatial scales based on average movement rates or home range size (Brown et al. 1995; Wiegand et al. 1999), although exceptions are becoming more common (Ciarniello et al. 2007; Wiegand et al. 2008; Nielsen et al. 2010).

Beyond the intrinsic suitability of an area, the value of resources to individuals can be diminished through competition among members of one or more species, potentially creating differential impacts on species' population performance (Sih et al. 1985; Begon et al. 1996). Competition among individuals can take different forms, including interference competition where animals directly interact and compete for resources (Murphy et al. 1998; Steinmetz et al. 2013), or exploitative competition where multiple species attempt to use the same resources (Wiens 1993; Linnell & Strand 2000). Both of these forms of competition can occur within a species, between two or more species, or both (Connell 1983; Gurevitch et al. 2000). Thus, effects of competition can be real in the sense of reduced quantities of resources, or perceived in the sense that animals may simply avoid areas of higher densities of competitors (Abrahams 1986; Delibes et al. 2001).

Quantifying the effects of competition on natural populations, however, has proven to be difficult (Connell 1961; Palomares & Caro 1999; Miller et al. 2015). Although field and

laboratory experiments have suggested that the effect size of interspecific competition is often greater than that of intraspecific competition (Connell 1983), experimental manipulation of populations is rare. This is particularly true for terrestrial carnivores and species of conservation or management concern (Caro and Stoner 2003; Miller et al. 2015), often due to insufficient data or sensitivity of analytical methods across multiple species (Mowat et al. 2005; Mattson et al. 2005; Harrington et al. 2009).

To advance understanding of how animals perceive the quality of an area in the presence of competition, we examined the seasonal variation in density patterns of two species believed to exhibit both exploitative and interference competition on each other. Across nearly all of their range in continental North America, grizzly bears (grizzlies, *Ursus arctos*) are sympatric with American black bears (*U. americanus*) and have been for at least 13,000 years (Kurten & Anderson 1980; Schwartz et al. 2010). Having diverged >3.5 million years ago (Leonard et al. 2000), each species has evolved a suite of morphological and behavioral adaptations to better exploit specific resources (Herrero 1978). The front claws of grizzly bears, for example, are well adapted to excavating subterranean foods including rodents and tubers, whereas black bears have short claws that allow them to climb trees for security and to access tree-borne foods (Herrero 1978; Mattson et al. 2005). In many parts of their shared ranges, however, their diets show nearly complete overlap (Jacoby et al. 1999; Mattson et al. 2005), and their digestive efficiencies are essentially identical (Pritchard & Robbins 1990).

A common assumption is that grizzly bears will dominate direct competitions with black bears because adult grizzlies are typically larger and more aggressive than black bears. While there are empirical examples of this (Gunther et al. 2002; Mattson et al. 2005), recent studies have shown that there may be more exceptions to this assumption than expected, and the

deciding factors of interspecific interactions may have as much to do with motivation and perception of risk as with body size (Miller et al. 2015; Allen et al. 2016). Actual encounter rates, their outcome, and effects on emergent properties (Salt 1979) like population density have not been thoroughly evaluated for either species (Schwartz et al. 2010; Mattson et al. 2005).

Despite grizzly bears being expected to win direct contests with black bears, competition between these species is likely to favor black bears at a population level in areas lacking highly concentrated resources such as spawning salmon or garbage dumps (Craighead and Craighead 1971; Herrero 1978; Mattson et al. 2005). Where sympatric, black bears can exist at densities 10 times that of grizzly bears, and are more efficient at exploiting dispersed foods, such as small berry patches (Jonkel 1971; Mattson et al. 2005). The smaller, more intensively used home ranges of black bears should also allow them to respond to changes in resource availability more rapidly than grizzly bears (Aune 1994; Mattson et al. 2005). In northwestern Montana, USA, for example, foods preferred by bears are often patchy and widely dispersed, with both species relying heavily on berries and forbs (Aune 1994; Mattson et al. 2005; McLellan 2011). Along the Rocky Mountain Front in northern Montana, Aune (1994) found substantial overlap in grizzly and black bear home ranges, with only subtle differences in habitat use and food habits that were likely facilitated by temporal partitioning of shared resources. Similar diet and range overlap was found in the Apgar Mountains of Glacier National Park, Montana, with both bear species relying heavily on cowparsnip (*Heracleum lanatum*) at low elevation in early summer, huckleberries (*Vaccinium spp*) and serviceberries (*Amelanchier alnifolia*) in mid-summer, with similar use of insects, carrion, sedges, and other foods throughout the summer (Shaffer 1971). Again, temporal partitioning was believed to explain the high degree of overlap between grizzly

and black bear food habits, as has long been proposed (e.g., Wright 1910; Hornocker 1962; Jonkel 1971).

Due to the highly seasonal nature of high quality foods in temperate, mountainous areas, both grizzly and black bears rely on hibernation as a strategy to survive long periods of time when food resources are especially scarce (Herrero 1978; Hilderbrand et al. 2000). To acquire sufficient energy reserves for hibernation, both species exhibit hyperphagia beginning in late summer as berries in particular become abundant, with daily caloric intake increasing 3-4 fold (Nelson et al. 1983). The significance of seasonal peaks in food availability, and the adaptations that bears have evolved to deal with them, is a critical but often overlooked component of assessing habitat quality for bears (Belant et al. 2006; Wiegand et al. 2008).

Recognizing the dietary and physiological similarities of grizzly and black bears, we chose to test the hypothesis that interspecific competition influences the population performance of bears in a large area known to support populations of both species at high densities (Kendall et al. 2008; Stetz et al. 2014). We further hypothesized that seasonal variation in resource availability will be important to how bears perceive habitat quality (Wiegand et al. 2008), and seasonal density patterns will change accordingly. From our hypotheses, we predicted that patches of resources used by both species will be sufficiently reduced to produce an asymmetrical effect on the density patterns of grizzly and black bears at an intra-population level (Mattson et al. 2005). We also predicted that the effects of interspecific competition on density patterns will vary seasonally due to changes in both resource availability and the changing behavioral and nutritional needs of bears (Nelson et al. 1983).

We also considered potential effects of sexual segregation, where females use lower quality areas to avoid interactions with males, on seasonal density patterns of both bear species

(Clutton-Brock 1987). Wielgus and Bunnell (1995) tested three hypotheses of sexual segregation in grizzly bears in two populations that were sympatric with black bears. They found inconclusive evidence for the no-avoidance hypotheses, where females do not avoid males, or the food hypothesis, where females avoid areas occupied by males that may compete for food or even cannibalize subordinate bears as a food source (Wielgus and Bunnell 1995). There was, however, support for the sex hypothesis of segregation in one population, with only adult females avoiding areas with potentially infanticidal males (Wielgus and Bunnell 1995). Similarly, Czetwertynski et al. (2007) found no support for the food hypothesis and limited support for the sex hypothesis of habitat segregation for populations of black bears in east-central Alberta. From these hypotheses, we predicted that, if present, sexual segregation would be most pronounced during the mating season for both bear species, with males displacing females from areas of more suitable habitat.

To test our hypotheses, we used data from two large noninvasive genetic sampling (NGS) studies in conjunction with spatially-explicit capture-recapture (SECR) models (Efford 2004; Borchers & Efford 2008; Royle et al. 2013). The basic SECR model combines a state model that describes the distribution of activity centers across the sampled area with an observation model that relates the probability of detecting an animal at a given site to the distance of that site to the center of an animal's home range (Borchers & Efford 2008). Advances in SECR now allow the use of spatial covariates to relate the variation in density to environmental conditions (Efford & Fewster 2013; Royle et al. 2013), including landscape factors that change over the course of a study, without requiring a predetermined spatial resolution of analyses (e.g., average home range). Although relatively new, SECR has been used to estimate density and provide valuable insights into how animals respond to their environment for many taxa, including skinks

(*Oligosoma infrapunctatum*; Efford and Fewster 2013), common genets (*Genetta genetta*; Sarmiento et al. 2014), and American black bears (Royle et al. 2013), and may provide a novel approach to test hypotheses about complex processes including intra and interspecific competition.

Noninvasive genetic sampling methods are among the most used and useful means to sample wildlife populations to estimate demographic values such as survival and abundance (Waits & Paetkau 2005), and are particularly well-suited for use with SECR modeling. Nearly any biological material can be used to obtain genotypes for use with capture-recapture models, with hair samples being used extensively in bear research and monitoring globally. There are several recognized advantages of NGS over other population sampling methods including less restriction to the spatial extent of sampling, permanent genetic identifiers to track detection histories, limited disturbances to study animals that may otherwise induce behavioral responses to sampling, and typically no limit to the number of individuals that can be detected at a given site, unlike with live captures (Waits & Paetkau 2005; Boulanger et al. 2008). When used in capture-recapture models, NGS methods have been shown to be particularly reliable when multiple sources of detections are used (Boulanger et al. 2008) and when applied at spatial scales that are large relative to the biology of the species being sampled (Stetz et al. 2014). When used with SECR models, large NGS datasets may provide valuable opportunities to test ecological hypotheses as well as inform conservation and management of wildlife populations.

STUDY AREA

Our ca. 7,350 km² study area included all lands within 10km of GNP, truncated at the U.S.–Canada border (Fig. 2-1), which provided a larger range of land cover, uses, and management regimes than found within just GNP. The area was considered to be a relatively intact natural

system, with a nearly complete assemblage of native species, including what are believed to be healthy grizzly and black bear populations (Kendall et al. 2008; Stetz et al. 2014). Fifty-six percent of the study area was within GNP, which was largely roadless and managed as wilderness, yet received >2 million visitors in 2004 (84% during June-September). Outside of GNP, lands were managed for multiple uses, including hunting, numerous non-consumptive recreational activities, and low-density residential development. There were no recognized barriers to bear movement between any parts of the study area (Kendall et al. 2009). All areas adjacent to GNP had spring and fall black bear hunting seasons except Waterton Lakes National Park, Alberta. Hunting of grizzly bears was limited to portions of British Columbia, outside of where sampling occurred.

Elevation ranged from approximately 900 m to 3,190 m above sea level. High elevations received more precipitation and contained more exposed rock and permanent snow and ice fields than did valleys. Average annual precipitation, much of which was deposited as snow in winter, was 63 cm. The study area spanned the Continental Divide, which effected local climate and vegetation composition. Areas west of the Divide generally received more precipitation and had more densely forested areas with less grasslands than the drier areas east of the Divide. Human development is also greater on the west side of the Divide, although there were no areas of concentrated development within the sampled area.

METHODS

Field Methods

We used two noninvasive methods concurrently to sample the grizzly and black bear populations in our study area: baited hair traps and unbaited bear rubs (Fig. 2-1), neither of which required handling of any animals. Hair traps consisted of a single strand of barbed wire stretched 50 cm

above ground around 3–6 trees to form a corral, at the center of which we poured 3L of a liquid lure on a pile forest debris (Woods et al. 1999; Kendall et al. 2009). We established one hair trap per 7x7-km cell for 14 days, after which all hair samples were collected and the trap was moved >1 km to decrease the potential for a waning response to the non-rewarding lure (Kendall et al. 2008). Hair trapping began 15 June and ran for four 14-day sessions, ending 18 August 2004. During 15 June–7 September 2004, we also repeatedly surveyed a network of 1,366 naturally occurring bear rubs found along maintained trails and other obvious animal travel routes. We identified bear rubs by evidence of rubbing activity such as snagged hair and smoothed tree bark; we did not use lure with bear rubs to either attract bears or elicit a rubbing response (Kendall et al. 1992; Stetz et al. 2010). We affixed several 30-cm strands of barbed wire to each uniquely numbered bear rub to improve sample quality and minimize mixing of hairs from more than one bear. As with previous analyses (Kendall et al. 2009; Stetz et al. 2014), hair samples were assigned to the two-week sampling occasion in which they were collected.

For both methods, we defined a sample as all hairs found on one set of barbs, although we also collected hairs left by bears rolling in the lure pile. All samples were placed in paper envelopes pre-labeled with a uniquely numbered bar code, and stored on silica desiccating agent until analyzed. Locations of all hair traps and bear rubs, which we refer to generically as detectors, were recorded with handheld Garmin 12 GPS units. Sample numbers and site coordinates were electronically entered into a relational database in order to minimize data entry errors (Kendall et al. 2009).

Genetic analyses

All genetic analyses were performed by Wildlife Genetics International (Nelson, BC, Canada) following the protocols of Woods et al. (1999), Paetkau (2003), and Kendall et al. (2009) to

ensure adequate marker power and to minimize genotyping errors. We determined the species, individual identity, and gender of animals that visited our sampling sites by analyzing nuclear DNA extracted from hair follicles collected in the field. We used 7 microsatellite loci to identify individual grizzly bears from all hair samples with ≥ 1 guard hair follicle or ≥ 5 underfur hairs. Due to the large number of putative or known (via a species-specific genetic test) black bear samples, we instituted a subsampling routine that used the location of each sample relative to others at a given sampling site along with partial genotypes obtained during earlier analyses (Stetz et al. 2014). We used 6 microsatellite loci total to identify individual black bears, plus the amelogenin marker (Ennis and Gallagher 1994; Pilgrim et al. 2005) to identify sex of individuals of both species. Our conservative estimate of multilocus genotyping error rate was < 0.001 for either species, with the probability of 2 full-siblings sharing the same genotype (P_{SIB}) < 0.0018 for either species (Kendall et al. 2009; Stetz et al. 2014). Details of our sample sizes, subsampling routine, marker power, and error rates for grizzly and black bear analyses can be found in Kendall et al. (2009) and Stetz et al. (2014), respectively.

Modeling density

We developed a suite of *a priori* SECR models (Borchers & Efford 2008; Efford & Fewster 2013) using DNA-based encounter histories to explore how biotic and abiotic landscape characteristics are related to density patterns of grizzly and black bears in our study area. SECR models estimate the density of animal activity centers, D , in a user-defined area that is large enough that animals residing beyond it have a negligible chance of being detected (Borchers & Efford 2008). We therefore defined an area extending 15km beyond all sampling points based on the buffer size suggested by functions in the *secr* package in R (Efford 2011), which we used

for all analyses. From this 15,204 km² area, we removed areas of rock, persistent snow and ice, and lakes >1 ha, which we considered “non-habitat” for either bear species (Stetz et al. 2014).

We were also interested in how seasonal changes to landscape characteristics, including density patterns of the sympatric species, may explain variation in density relative to important periods in the life history of bears. Similar to Mace et al. (1996) we defined the period through 15 July as spring, which contains the peak of the breeding season for both species of bears (Jonkel and McCowan 1971; Mace and Waller 1997). Based on changes in which foods bears prefer (Mace and Jonkel 1983; Zeger et al. 1993), we defined the subsequent month as early summer, and the final month as late summer, during which time bears’ diets consist largely of fleshy fruits (Mace and Jonkel 1986; Raine and Kansas 1989). We therefore parsed our detection data into three approximately one-month periods for each species and sex for use in SECR analyses.

For each of these time periods, we developed spatial covariates that we hypothesized could influence density of black and grizzly bears. We considered two biotic habitat variables, landcover class and the enhanced vegetation index (EVI; Huete et al. 2002), which, alone or in combination with other variables, pertain to availability of bear foods (Zedrosser et al. 2011). We derived both biotic variables from 2004 MODIS 500m datasets (Pettorelli et al. 2014; Nemani & Running 1997). The EVI has been shown to have good sensitivity to monitoring temporal and spatial variation in photosynthetic output across a range of conditions, including mountainous regions that show strong seasonal productivity patterns (Villamuelas et al. 2015). The EVI has also been shown to outperform other remotely sensed vegetation indices in areas of high biomass, and to be more robust to contamination from exposed soils or atmospheric conditions such as smoke from wildfires (Huete et al. 2002; Pettorelli et al. 2014). We

hypothesized three ways in which EVI could reflect the quality of resources available to bears. First, EVI values could reflect the energetic value of emergent foods such as grasses and sedges, particularly during spring (Posse & Cingolani 2004). Second, there may be a lag between the height of photosynthetic activity of plants and the production of berries and other late-summer foods (Holden et al. 2012). Third, the cumulative amount of photosynthetic activity may reflect the energy content of numerous food species including ants (Bentley 1976) and grasses and shrubs (Gamon et al. 1995). We therefore calculated the average EVI value for each 500m pixel from the two 16-day scenes that most closely aligned with each one-month modeling season (Fig 2-1) as a covariate in SECR analyses. Due to potential lag effects, we also considered models with EVI values from each season to explain subsequent seasons' density patterns. Finally, to compare cumulative EVI to within-season values, we created a variable that was the sum of the average values across time periods.

Land cover type can influence how animals use an area, and thereby population density, through variable productivity and accessibility of preferred foods, thermoregulation, and escape cover, among other reasons (Clark et al. 1993; Ciarniello et al. 2007; Carter et al. 2010). Further, how animals use a given cover type may change seasonally according to life history traits (Nielsen et al. 2010). We therefore classified each 500m pixel in our study area as consisting of one of six landcover classes: forest, shrublands, grasslands, permanent wetlands, urban, and croplands. We chose these classes because they have been shown (Waller & Mace 1997; Apps et al. 2016) or hypothesized (Jonkel 1971; Ciarniello et al. 2007) as being important factors in the density of grizzly and black bear populations. We also included abiotic factors that have been hypothesized as important predictors of bear density, including terrain roughness, elevation, and habitat security, for modeling variation in density (Fig. 2-1) (Apps et al. 2006;

Graves et al. 2011). For elevation, we resampled a 30m DEM to 250m pixels using bilinear interpolation, which retained sufficient resolution to capture topographic variation in the vicinity of detectors. As an index of terrain roughness, we used the relative topographic position, which may reflect soil and hydrological profiles that influence biological diversity and productivity (Jenness 2002). We calculated this index using the resampled 250m DEM, both of which we standardized for use in SECR models. Finally, areas that provide greater security for wildlife species are generally expected to support higher animal densities due to lower anthropogenic disturbance and mortalities (Woodroffe & Ginsberg 1998). For an index of habitat security, we assigned national or provincial parks or protected areas to have the highest security; other federal, state, provincial, and tribal lands to have medium security; and private lands to have the lowest security, similar to Mace et al. (1996) and Graves et al. (2011) (Fig. 2-1).

To test hypotheses related to how density of sympatric species and conspecifics influence bear density patterns, we first developed suites of models using the covariates above to create predicted density surfaces for each species, sex, and season combination. This first modeling stage did not include densities of sympatric species or conspecifics as covariates. We ranked model support at this stage using AICc, and used model averaging based on AICc weights to account for model selection uncertainty (Burnham & Anderson 2001). We then created additional SECR models including these density surfaces as explanatory, spatially-explicit covariates. We also considered total density of each species, and species combined, as covariates in our models. We did not use predicted density covariates in subsequent models of the data used to build the initial models. We then ranked model support for each complete suite of models using AICc.

In addition to modeling density, the observation sub-model of SECR models the process of detecting animals by explicitly considering animal movements in relation to the characteristics and distribution of detectors. Two parameters comprise the observation submodel: g_0 is the probability of detecting a given animal at its activity center, and σ is the spatial scale parameter describing how detection probability declines with increasing distance between the activity center and each detector. For all SECR models, we used a binomial observation model with a halfnormal detection function to relate the probability of detection to distance from the predicted home range center, which is unobserved and assumed stationary. We modeled hair traps and bear rubs as different types of proximity detectors (Efford et al. 2004), and used non-binary usage coding to directly account for variation in sampling effort (Efford et al. 2013; Stetz et al. 2014). As with density, we modeled the observation process separately for each species, sex, and season, and considered time (t) effects on detection.

The detection process can also be modeled using spatial covariates, including those that change over time, to relate variation in detection to landscape features. To improve overall model performance, we therefore included biotic and abiotic covariates that we hypothesized could explain detection of grizzly and black bears. Beyond potentially improving model fit, the use of covariates relaxes the assumption of circular home ranges (Royle et al. 2013), although simulations suggest that SECR models are robust to such violations even without the use of covariates (Stenhouse et al. 2015).

We used ArcGIS (v. 10.2; ESRI) to derive spatial covariate values and assign them to detectors, and we added covariates to the habitat mask using functions in the *secr* package (Efford 2012). Computational limitations precluded using all-combinations model selection methods such as stepwise AIC (Yamashita et al. 2007). Within each full suite, we considered

models with an AICc value within 2 units of the top model to be supported by the data (Symonds & Moussalli 2011). We also visually inspected parameter estimates and standard errors for signs of models failing to run successfully (O'Brien & Kinnaird 2011). We present complete SECR model selection results in Appendix A.

RESULTS

Hair collection and genetic analyses

During 15 June-18 August, 2004, we established one hair trap in each of 150 7x7 km cells during four 14-day sessions (Fig. 2-1). We collected 5,645 bear hair samples from 550 hair traps, of which 1,193 and 1,890 were classified as grizzly and black bear, respectively. From these, we identified 248 individual grizzly bears (147 F, 101 M), and 468 black bears (249 F, 219 M). We also collected 3,493 hair samples from 4,860 surveys of 1,366 bear rubs during 15 June-7 September, 2004. Of these, 833 and 956 were classified as grizzly and black bear, respectively. From these, we identified 154 individual grizzly bears (66 F, 88 M), and 223 black bears (89 F, 134 M). In total, we identified 309 individual grizzly bears (170 F, 139 M), and 597 black bears (303 F, 294 M). We assigned all grizzly (Table 2-1) and black bear (Table 2-2) detections into one of six 14-day occasions, which we then parsed into our three seasons. Details of detection and recapture frequencies are reported in Table 2-3.

Bear density

Our most supported models of female grizzly bear density for the spring season contained a single covariate, the predicted total density of black bears during the same time period (Table 2-4; Fig. 2-3), which was negative and significant (i.e., the 95% confidence interval did not include zero; Tables 2-4, 2-5). Top models for early summer female grizzly bear density included predicted density of male grizzlies with an additive effect of spring EVI, which were also both

negative and significant (Tables 2-4, 2-5). Similar to spring model results, total predicted density of black bears was the only supported covariate for late summer, which was negative but not significant (Table 2-5).

Top models for male grizzly bears in spring contained only the predicted density of female grizzlies during the same time period (Table 2-4; Fig. 2-3), which was positive and significant (Table 2-5). Top models for early summer contained total predicted bear density with an additive effect of terrain roughness, both of which were negative but only total predicted density was significant. Similarly, top late summer models included only total predicted density of bears, which was negative and nearly significant.

Female and male black bears had the same top model during spring, with total predicted density of grizzly bears being the sole supported covariate (Table 2-4; Fig. 2-4), which was negative and significant for both sexes (Table 2-6). Largely in contrast with grizzlies, top density models for both sexes of black bears in early and late summer did not include any covariates of predicted bear density. Top models for early summer density of female black bears included a positive relationship with spring EVI and a negative relationship with terrain roughness, both of which were significant. Late summer models contained the same covariates as early summer, although the positive relationship between EVI and density was no longer significant; a significant negative relationship with terrain roughness remained (Table 2-6).

Similar to female black bears, top density models for male black bears had positive and significant relationships with spring EVI in both early and late summer (Table 2-6; Fig. 2-4). Density in early summer was also significantly higher in areas we defined as low habitat security, and lowest in areas of moderate security, although this relationship was not significant.

Spring EVI was the only supported covariate for late summer density of male black bears (Table 2-3).

The detection components of supported SECR models varied considerably both within and across species and seasons, with the exception that detection probabilities were always higher with hair trap data than bear rubs (Appendix A). Generally, detection probabilities were highest for grizzly bears in areas of higher EVI and elevation, and tended to increase over time. A relationship between density of conspecifics or sympatric species and detection was partially supported, with most seasons showing a positive relationship for both sexes (Table 2-7). Female grizzly bears in early summer had a small negative relationship with total bear density, although the effect was not significant. The spatial scale parameter, sigma, for grizzly bears was generally smaller in areas of higher EVI and higher density of bears (Table 2-7), although few covariates had any support based on AICc. Estimated home range sizes calculated from sigma values (Noss et al. 2012) were 331 km² (95% CI: 278-396 km²) for female and 535 km² (95% CI: 476-600 km²) for male grizzly bears. Estimates were similar to those made from radiocollared bears in a nearby study, with female home ranges averaging 216 km² (95% CI: 62-668 km²) and males averaging 720 km² (95% CI: 449-1179 km²; Mace and Waller 1996).

We found less consistency with explaining detection of black bears. Detection probabilities were generally higher in areas we defined as providing greater security, although this relationship was reversed in late summer for male black bears (Table 2-8). Forests, shrublands, and areas with lower total predicted density of bears also had a negative relationship with detection rates. The spatial scale parameter for black bears had a negative relationship to home ranges with a larger proportion of forest and grasslands, and a positive relationship to areas of higher total predicted bear density, EVI, and greater security (Table 2-8). Elevation had a

positive relationship with sigma, although it was not significant (Table 2-8). Estimated home range size for female black bears was 74 km² (95% CI: 72-76 km²), which is consistent with Mattson et al. (2005) who reported a range of 24-137 km² for populations sympatric with grizzly bears. Estimated home range size for male black bears was 415 km² (95% CI: 401-429 km²), which was intermediate between more forested areas west of the Continental Divide (62 km²; Chilton-Radandt 2006) and the more open Rocky Mountain Front (1405 km²; Stevens and Gibeau 2005).

DISCUSSION

Our results are consistent with the hypothesis that competition among ecologically similar species influences how animals perceive the suitability of their environment, which can manifest as reduced local densities of even a larger, more aggressive competitor. Evidence of this was strongest with female grizzly bears, which exhibited reduced densities in areas of higher black bear densities in two of three seasons. Further, we observed potential effects of competition on density patterns for both sexes of both species in at least one season each. In nearly every case where density was related to the sympatric species' density, the relationship was negative, significant, and was the only supported factor.

We found partial support for the hypothesis that seasonal variation in resource availability influences how bears perceive habitat quality, as areas of higher primary productivity contained higher local densities of black bears in most seasons. For both sexes of black bears, spring EVI was predictive of both early and late summer density, consistent with our hypothesis that photosynthetic activity in the spring would result in more abundant bear foods such as huckleberries later in the year. Conversely, we found little evidence of a relationship between primary productivity and grizzly bear density. In fact, the only time EVI was found to be

predictive for grizzly bear density was a negative relationship between females in early summer and spring EVI, contrary to our predictions. This finding may be explained by considering the strongly positive relationship between EVI and black bear density in both early and late summer. We hypothesize that EVI may have acted as a proxy for black bear density in our model, as the relationships were similar. Further, our next best model for density of female grizzly bears during this season contained total bear density as the only factor, although support was limited (Appendix A).

Collectively, our results provide limited support for the hypothesis that more topographically complex areas support more abundant and diverse foods, at least with respect to the density of bears in such areas. Specifically, terrain roughness was important in predicting female black bear density in early and late summer, although the direction of the relationship changed between seasons. We hypothesize that this may reflect the use of flatter valley bottoms when grasses and emergent foods are abundant, with a transition to more topographically complex areas in late summer as berries ripen, similar to the findings of Apps et al. (2006) in a nearby population.

Surprisingly, we found no support for relationships between density patterns of either species and landcover type or elevation, both of which have been found elsewhere (Mowat et al. 2005; Apps et al. 2006). We do not propose that bears respond indifferently to different landcover types, nor that these relationships are temporally invariable, and we expect that they may help explain variation in bear density in some populations. As with previous studies, we recognize that our landcover categories may not adequately capture how bears perceive their environment and may miss potentially valuable resources such as army cutworm moths (*Euxoa auxiliaris*) or understory vegetation (Apps et al. 2006). Conversely, elevation is a generic factor

not directly linked to specific biological processes, even though it may be correlated with seasonal density of bears. Our results suggest that the other factors we considered, particularly effects of competition and primary productivity, were in fact better suited to explain variation in density than factors used in previous analyses.

We also found very little support for our hypothesis that habitat security influences densities of bears in this area. In the only case where a significant relationship existed, the effect was opposite of our predictions, with areas assigned to the lowest security having the highest density of male black bears in early summer. This suggests that, during the seasons we investigated, bears' perception of security has less influence on their space use than the other factors we considered, although other indices of security may produce different results. Finally, we found that areas expected to provide the least security (private lands) were predicted to have higher densities of male black bears than the highest security areas (parks), with the lowest density predicted for intermediate security areas, which included national forest and tribal lands. Although regulated black bear hunts occurred before and after our sampling, we hypothesize that our results could reflect the fact that the majority of anthropogenic disturbance and mortality occurred on these multiple-use lands, with lower levels of mortality occurring on private lands and protected areas. This suggestion reinforces the complex relationship between many carnivore populations, whether hunted or not, and concepts of habitat security (Mitchell & Hebblewhite 2012).

The relationship we observed between male and female grizzly bear densities in spring and early summer is consistent with bear behaviors reflecting sexual segregation during their breeding season. Male grizzly density in spring had a significant positive relationship with female grizzly density, the only positive relationship between densities that we observed. Based

on this and the significantly negative relationship that female grizzly density had with male density in the following season, we can hypothesize that females were still responding to pursuant males and avoiding areas that may pose greater risk to dependent offspring from infanticidal males (Steyaert et al. 2012). That female grizzly bears had negative relationships with either conspecific or sympatric species densities in every season suggests that they are more sensitive to competition than other classes of bears.

We found that black bear density, whether alone or as part of total bear density, was important in predicting the density of both sexes of grizzlies in most seasons. Although we also found that black bear density had a negative relationship with grizzly density during spring, black bears showed a markedly different pattern in later seasons, with higher EVI being positively related to density of both sexes for early and late summer. Had we observed a negative relationship between densities of both species across all seasons, it could be possible that each species was showing preference for different resources or that one species was excluding the other. Instead, we found that the effect on density patterns was more efficiently described by a single value (i.e., density of the sympatric species) than the potentially complex interactions of multiple environmental factors. That black and grizzly bears showed such differences during summer supports the notion that our analyses were able to identify plausible relationships between density patterns of both species and the conditions that we hypothesized to be important.

A common challenge in efforts to explain variation in animal density is that there are often limited data on measures of population performance like density, and the tools to analyze those data lack the power to identify relationships with environmental conditions. As with traditional capture-recapture methods (Boulanger et al. 2008), the concurrent use of multiple

types of detection data is a particularly powerful approach that has been shown to improve the quality of SECR analyses (Sollmann et al. 2013; Stetz et al. 2014; Kendall et al. 2016), and should be considered whenever possible.

Few analytical methods have evolved more rapidly than SECR models, having advanced from simple estimates of population density (Efford 2004) to providing inference into animal space use (Royle et al. 2013) and population growth rates (Whittington & Sawaya 2015) in just a matter of years. Similar to our study, Royle et al. (2013) used NGS detection data of American black bears in New York, USA, to evaluate resource selection during a two-month period. Genetic analyses of hair samples collected at 103 sites identified 33 individual bears, with 14 recapture events. From these data, the authors concluded that bear density and elevation had a positive association, and that SECR models can reliably explain space use even without the use of telemetry data (Royle et al. 2013).

In our study, we used NGS data from 550 hair traps and 1,366 bear rubs, which yielded a total of 1,699 detections with 510 recaptures of over 900 bears. The computational demands of running SECR models with large datasets required that we use a high performance computing cluster with 22 nodes, each with 16 cores and up to 128 GB of memory, with a peak performance of 13 teraflops (<http://hpc.mtech.edu/>). Nonetheless, we were unable to successfully run every *a priori* model. Although our results reflect well over 50,000 hours of run time and over 1,200 models, we recognize that our analyses reflect just one realization of the complex ecological processes that we are attempting to explain. Rapid advances in data collection methods, analytical methods, and computing power will continue to allow more complex ecological questions to be addressed. We propose that using large-scale detection data in a SECR framework may provide opportunities to test hypotheses that, although long-held in ecology,

have seen little attention in practice, including the potential effects on density and space use that competition between sympatric species may exert.

Understanding how ecologically similar species partition resources is vitally important to linking concepts of habitat quality with population performance (Amarasekare 2003). Although a fundamental component in niche theory (Chase & Leibold 2003), interspecific competition has rarely been considered in habitat studies, with the focus remaining on behavior-based resource selection (Garshelis 2000; Morris 2003). Further, most empirical studies that have considered effects of competition have used species distribution models that provide little insight into demographic consequences of competition (Belant et al. 2006; Sozio & Mortelliti 2016). Our results suggest that competition among black and grizzly bears plays a significant role in how these species perceive habitat quality, with measurable effects on the performance of both populations that changed seasonally. This supports the call to include effects of competition in research to test ecological theory and in applied research to inform conservation (Fisher et al. 2013).

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TABLES

Table 2-1. Summary of grizzly bear detection data, by sex and sampling method, used in spatially-explicit capture-recapture analyses of grizzly and black bear density. Sample collection occurred in northwestern Montana, between 15 June-7 September, 2004.

	Season ^a					
	Spring		Early summer		Late summer	
Hair trap effort ^b	1918	1946	1904	1932	-	-
Bear rub effort ^c	5433	12026	13459	16657	26055	19563
Hair trap						
No. unique males	35	33	19	46	-	-
No. male detections	40	37	19	49	-	-
No. unique females	39	30	60	64	-	-
No. female detections	42	34	62	71	-	-
Bear rub						
No. unique males	20	35	33	24	35	14
No. male detections	58	93	54	46	51	23
No. unique females	0	10	11	16	28	18
No. female detections	0	10	13	18	35	24

Total						
No. unique males	50	57	49	68	35	13
No. male detections	98	130	73	95	50	22
No. recaptures ^d		140		72		29
No. unique females	39	39	69	74	28	18
No. female detections	42	44	75	89	34	23
No. recaptures		13		44		14

^a Each season consists of two 14-day sampling occasions. Hair traps were active for spring and early summer only.

^b The total number of days that hair traps were available to detect bears per two-week sampling occasion.

^c The number of days since the previous survey of a given bear rub summed across all bear rubs surveyed in a given occasion.

^d The total number of recaptures within a given session regardless of detector type.

Table 2-2. Summary of black bear detection data, by sex and sampling method, used in spatially-explicit capture-recapture models. Sampling occurred in northwestern Montana, 2004.

	Season ^a					
	Early summer		Early summer		Early summer	
	1918	1946	1904	1932	-	-
Hair trap effort ^b						
Bear rub effort ^c	5433	12026	13459	16657	26055	19563
Hair trap						
No. unique males	92	74	41	40	-	-
No. male detections	98	78	41	40	-	-
No. unique females	95	82	54	47	-	-
No. female detections	95	85	57	48	-	-
Bear rub						
No. unique males	10	42	36	39	30	27
No. male detections	20	65	47	44	34	27
No. unique females	3	15	24	14	26	31
No. female detections	4	17	30	17	33	44

Total						
No. unique males	96	111	73	77	30	27
No. male detections	118	143	88	84	34	27
No. recaptures ^d	80	36	5			
No. unique females	97	96	75	60	26	31
No. female detections	99	102	87	65	33	44
No. recaptures	27	27	23			

^a Each season consists of two 14-day sampling occasions. Hair traps were active for spring and early summer only.

^b The total number of days that hair traps were available to detect bears per two-week sampling occasion.

^c The number of days since the previous survey of a given bear rub summed across all bear rubs surveyed in a given occasion.

^d The total number of recaptures within a given session regardless of detector type.

Table 2-3. Distribution of the combined number of detections of individual grizzly bears (*Ursus arctos*) and American black bears (*U. americanus*) by sex and season at hair traps and bear rubs in Montana, USA, 2004. Also shown is the observed and expected number of individual bears detected for the most supported model. The expected number was calculated as $E(n) = \int p.(X)D(X)dX$, with $p.(X)$ is the probability a given individual was detected at least once and $D(X)$ is the expected density at X for the most supported model.

Species	Sex	Season	Distribution of number of detections						No. individuals	
			1	2	3	4	≥ 5	Total	Observed	Expected
Grizzly	F	Spring	61	11	1	0	0	86	73	73.12
		Early Summer	85	28	5	2	0	164	120	118.55
		Late Summer	30	12	1	0	0	57	43	42.96
	M	Spring	47	15	9	6	11	228	88	87.92
		Early Summer	66	17	6	0	7	168	96	96
		Late Summer	31	5	4	0	3	72	43	42.95
Black	F	Spring	150	22	1	1	0	201	174	174.13
		Early Summer	107	12	4	1	1	152	125	124.94
		Late Summer	41	6	4	3	0	77	54	53.99
	M	Spring	135	35	6	3	2	261	181	181.74
		Early Summer	109	19	5	1	1	172	135	135.04
		Late Summer	52	3	1	0	0	61	56	56

Table 2-4. The most supported SECR model, based on AICc, for seasonal density of grizzly bears (*Ursus arctos*) and American black bears (*U. americanus*) in northwestern Montana, USA, 2004. Number of estimated parameters (K), model deviance, AICc, and model weight (w_i) are shown. Complete model results can be found in Appendix A.

Species	Sex	Season	<i>D</i>	<i>K</i>	Deviance	<i>AICc</i>	w_i
Grizzly	F	Spring	Black bear density in spring	10	518.88	542.43	0.14
		Early summer	Male grizzly bear density in early summer + Spring EVI ^a	10	1087.08	1109.10	0.54
		Late summer	Black bear density in late summer	9	539.08	562.54	0.108
	M	Spring	Female grizzly bear density in spring	9	1853.23	1873.54	0.26
		Early summer	Total bear density in early summer + terrain roughness	12	1485.28	1513.39	0.48
		Late summer	Total bear density in early summer	6	778.34	792.67	0.07
Black	F	Spring	Grizzly bear density in spring	12	932.38	958.32	0.37
		Early summer	Spring EVI + terrain roughness	8	926.44	943.67	0.44
		Late summer	Spring EVI + terrain roughness	6	721.18	734.97	0.08
	M	Spring	Grizzly bear density in spring	9	1692.06	1711.11	0.61

Early summer	Spring EVI + Habitat security	19	1257.68	1302.28	0.32
Late summer	Spring EVI	4	579.92	588.70	0.08

^a EVI: enhanced vegetation index (Huete et al. 2002)

Table 2-5. Model averaged estimates, standard errors, and 95% confidence intervals from the most supported full likelihood spatially-explicit capture-recapture density models for grizzly bears (*Ursus arctos*) in northwestern Montana, 2004, by sex and season. Each season represents two 14-day sampling occasions.

Species	Sex	Season	Density submodel parameters	β	SE	LCL	UCL
Grizzly	F	Spring	Baseline density ^a	1.072	0.449	0.488	2.359
			Total black bear density in spring	-0.092	0.024	-0.139	-0.045
		Early summer	Baseline density	1.273	0.397	0.700	2.313
			Male grizzly bear density in early summer	-1.545	0.380	-2.289	-0.800
			Spring EVI	-0.508	0.104	-0.711	-0.305
		Late summer	Baseline density	2.396	1.010	1.085	5.295
	Total black bear density in late summer		-0.013	0.037	-0.086	0.059	
	M	Spring	Baseline density	0.960	0.317	0.511	1.805
			Female grizzly bear density in spring	0.189	0.082	0.028	0.350
		Early summer	Baseline density	0.036	0.052	0.005	0.287
			Total bear density in early summer terrain roughness	-0.202	0.070	-0.341	-0.064
		Late	Baseline density	1.277	0.815	-0.321	2.875
Baseline density			0.148	0.183	0.022	0.981	

summer

Total bear density in early summer	-0.127	0.067	-0.255	0.007
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^a Density is reported in bears per 100km² at the base level of covariates.

Table 2-6. Model averaged estimates, standard errors, and 95% confidence intervals from the most supported full likelihood spatially-explicit capture-recapture density models for American black bears (*Ursus americanus*) in northwestern Montana, 2004, by sex and season. Each season represents two 14-day sampling occasions.

Species	Sex	Season	Density submodel parameters	β	SE	LCL	UCL
Black	F	Spring	Baseline density	11.795	2.158	8.265	16.832
			Total grizzly bear density in spring	-0.180	0.078	-0.333	-0.028
		Early summer	Baseline density	14.304	3.148	9.339	21.908
			Spring EVI	0.969	0.251	0.477	1.460
			terrain roughness	-0.700	0.279	-1.246	-0.154
		Late summer	Baseline density	3.324	1.509	1.423	7.766
	Spring EVI		0.077	0.079	-0.079	0.233	
	terrain roughness		1.115	0.514	0.108	2.122	
	M	Spring	Baseline density	7.409	0.789	6.017	9.124
			Total grizzly bear density in spring	-0.502	0.155	-0.807	-0.198
		Early summer	Baseline density	11.918	3.518	6.763	21.002
			Spring EVI	0.937	0.301	0.348	1.527
			Low security	1.417	0.484	0.468	2.366
			Medium security	-0.139	0.423	-0.969	0.690
Late summer		Baseline density	20.603	9.795	8.505	49.906	
		Spring EVI	1.089	0.425	0.257	1.921	

^a Density is reported in bears per 100km² at the base level of covariates.

Table 2-7. Parameter estimates and 95% confidence intervals from the most supported full likelihood spatially-explicit capture-recapture detection sub-models for grizzly bears (*Ursus arctos*) in northwestern Montana, 2004, by sex and season. g_0 is the estimated detection probability at the home range center; σ is the spatial scale parameter relating detection probability to distance from the home range center in meters. Each season represents two 14-day sampling occasions.

Sex	Season	Detection parameter (g_0)	β	LCL	UCL	Detection parameter (σ)	β	LCL	UCL
F	Spring	Baseline	0.015	0.001	0.038	Baseline	1674.475	1269.683	2208.318
		Spring EVI	1.159	0.321	1.998	Spring EVI	-0.552	-0.945	-0.158
	Early summer	Baseline	0.012	0.007	0.018	Baseline	4374.224	3775.689	5067.640
		Total bear density in early summer	-0.009	-0.029	0.012				
	Late summer	Baseline	0.000	0.000	0.001	Baseline	1970.784	1439.701	2697.774
		Total black bear density in late summer	0.045	-0.008	0.098	Total black bear density in late summer	0.022	0.001	0.042
M	Spring	Baseline	0.019	0.010	0.027	Baseline	3321.965	2779.124	3970.837
		Male grizzly density in spring	0.689	0.227	1.152	Male grizzly density in spring	-0.346	-0.512	-0.180
	Early summer	Baseline	0.003	0.002	0.005	Baseline	4409.197	3882.796	5006.963
						Forest	-0.379	-0.657	-0.101
						Grassland	-0.131	-0.419	0.158
						Shrub	-4.475	-4.475	-4.475
	Late summer	Baseline	0.001	0.001	0.002	Baseline	5027.973	4158.661	6079.002
		Total EVI	0.273	0.109	0.436				

Female grizzly density in late summer	0.372	-0.339	1.082
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Table 2-8. Parameter estimates and 95% confidence intervals from the most supported full likelihood spatially-explicit capture-recapture detection sub-models for American black bears (*Ursus americanus*) in northwestern Montana, 2004, by sex and season. g_0 is the estimated detection probability at the home range center; sigma (σ) is the spatial scale parameter relating detection probability to distance from the home range center in meters. Each season represents two 14-day sampling occasions.

Sex	Season	Detection parameter (g_0)	β	LCL	UCL	Detection parameter (σ)	β	LCL	UCL	
F	Spring	Baseline	0.027	0.009	0.045	Baseline	1845.934	1396.988	2439.156	
		Forest	-1.336	-2.248	-0.425	Forest	-1.336	-2.248	-0.425	
		Grassland	-1.479	-2.513	-0.445	Grassland	-1.479	-2.513	-0.445	
		Shrub	0.083	-1.071	1.237	Shrub	0.083	-1.071	1.237	
	Early summer	Baseline	0.097	0.027	0.167	Baseline	1017.287	835.850	1238.109	
		Total bear density in early summer	-0.080	-0.124	-0.036	Total bear density in early summer	0.029	0.014	0.044	
	Late summer	Baseline	0.003	0.001	0.005	Baseline	1266.230	1012.507	1583.532	
		Total bear density in late summer	0.013	-0.029	0.055					
		Terrain roughness	-0.196	-0.568	0.175					
	M	Spring	Baseline	0.013	0.009	0.017	Baseline	3959.068	3531.434	4438.486
			Spring EVI	-0.288	-0.784	0.206	Spring EVI	0.307	0.095	0.518
			Total bear density in spring	0.014	-0.009	0.037				
Security (low)			-1.410	-2.804	-0.016					
Security (medium)			-0.599	-0.944	-0.254					
Early summer		Baseline	0.001	0.000	0.001	Baseline	4413.681	3239.445	6013.555	
		Security (low)	-0.538	-3.761	2.298	Security (low)	-0.163	-1.477	1.152	
		Security (medium)	-1.953	-2.949	-0.957	Security (medium)	1.043	0.644	1.442	

					Elevation	0.757	-0.004	1.517
Late summer	Baseline	0.001	0.000	0.001	Baseline	1999.196	1310.663	3049.437
	Total bear density in early summer	0.019	-0.021	0.058				
	Security (low)	2.389	0.939	3.840				
	Security (medium)	0.340	-0.400	1.080				

FIGURES

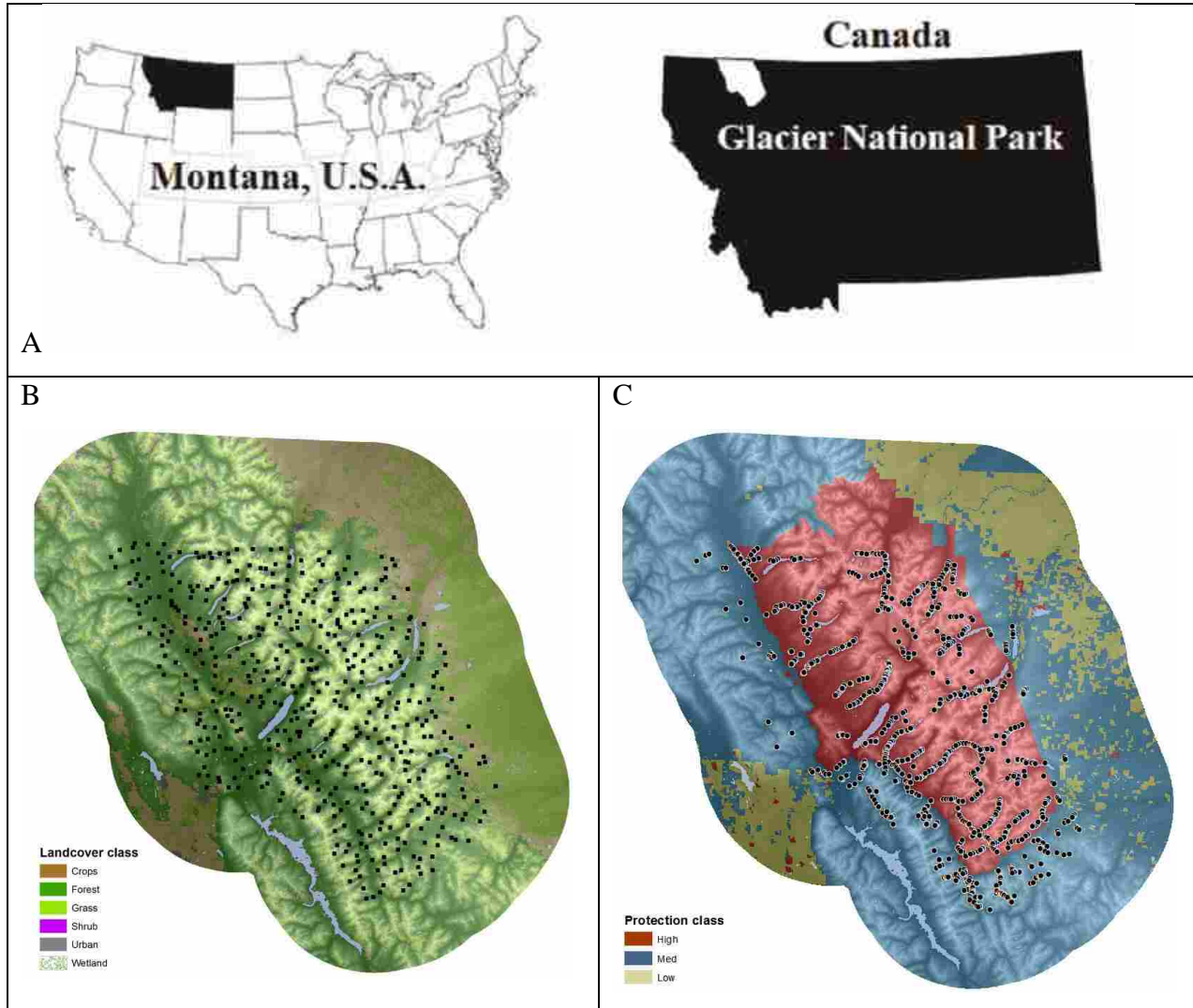


Figure 2-1. (A) Location of study area in northwestern Montana. Locations of (B) 550 hair traps in relation to landcover class derived from 2004 MODIS imagery, and (C) 1,366 surveyed bear rubs in relation to level of security for bears. Hair collection occurred in 2004 from 15 June – 18 August for hair traps and 15 June - 7 September for bear rubs.

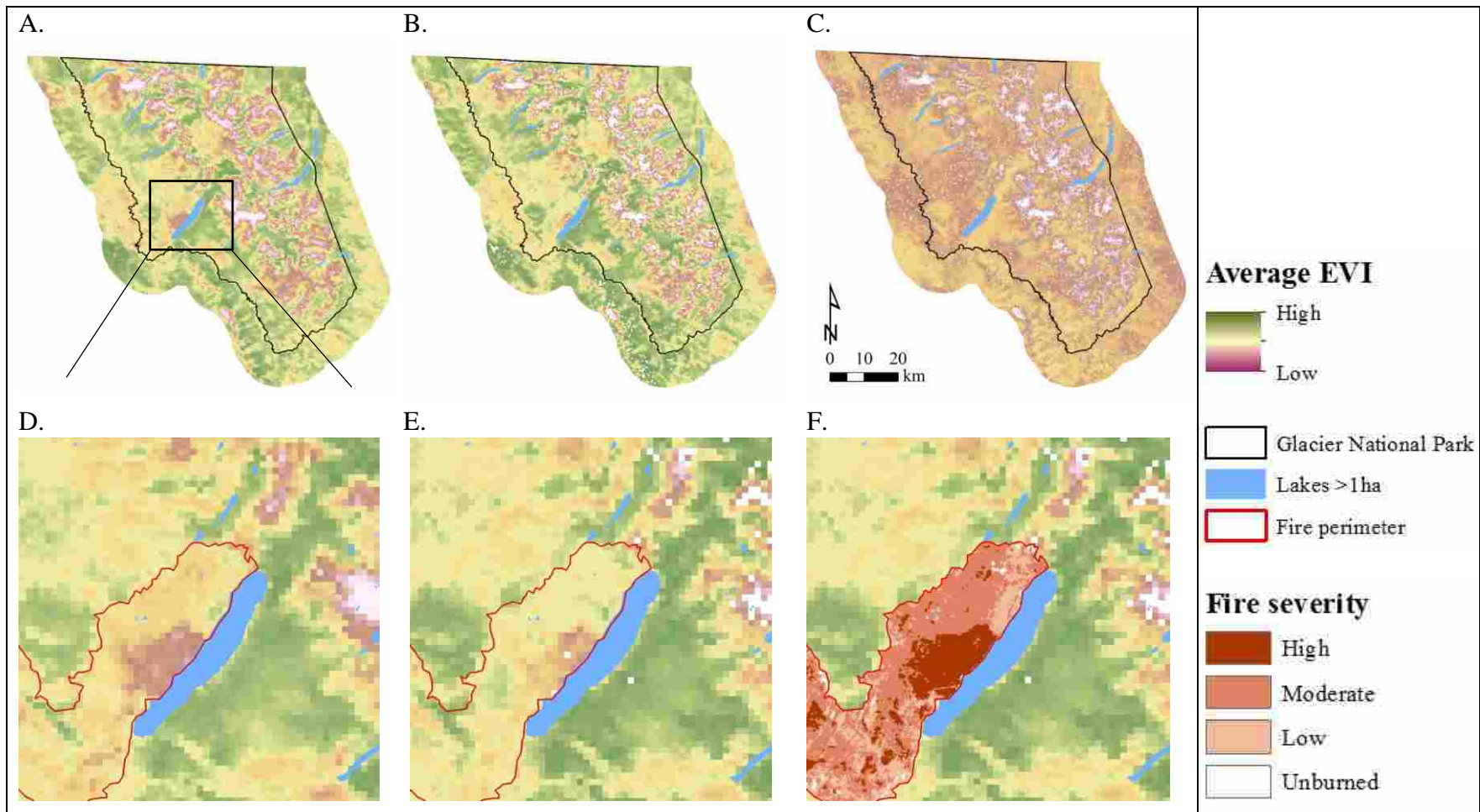


Figure 2-2. (A-C) Maps showing changes in average 500m EVI values for each one-month period, beginning 15 June 2004, with Glacier National Park (GNP) outlined in black for reference. (D-E) Average EVI for spring and early summer 2004, relative to the 2003 Robert fire, with fire severity shown in (F).

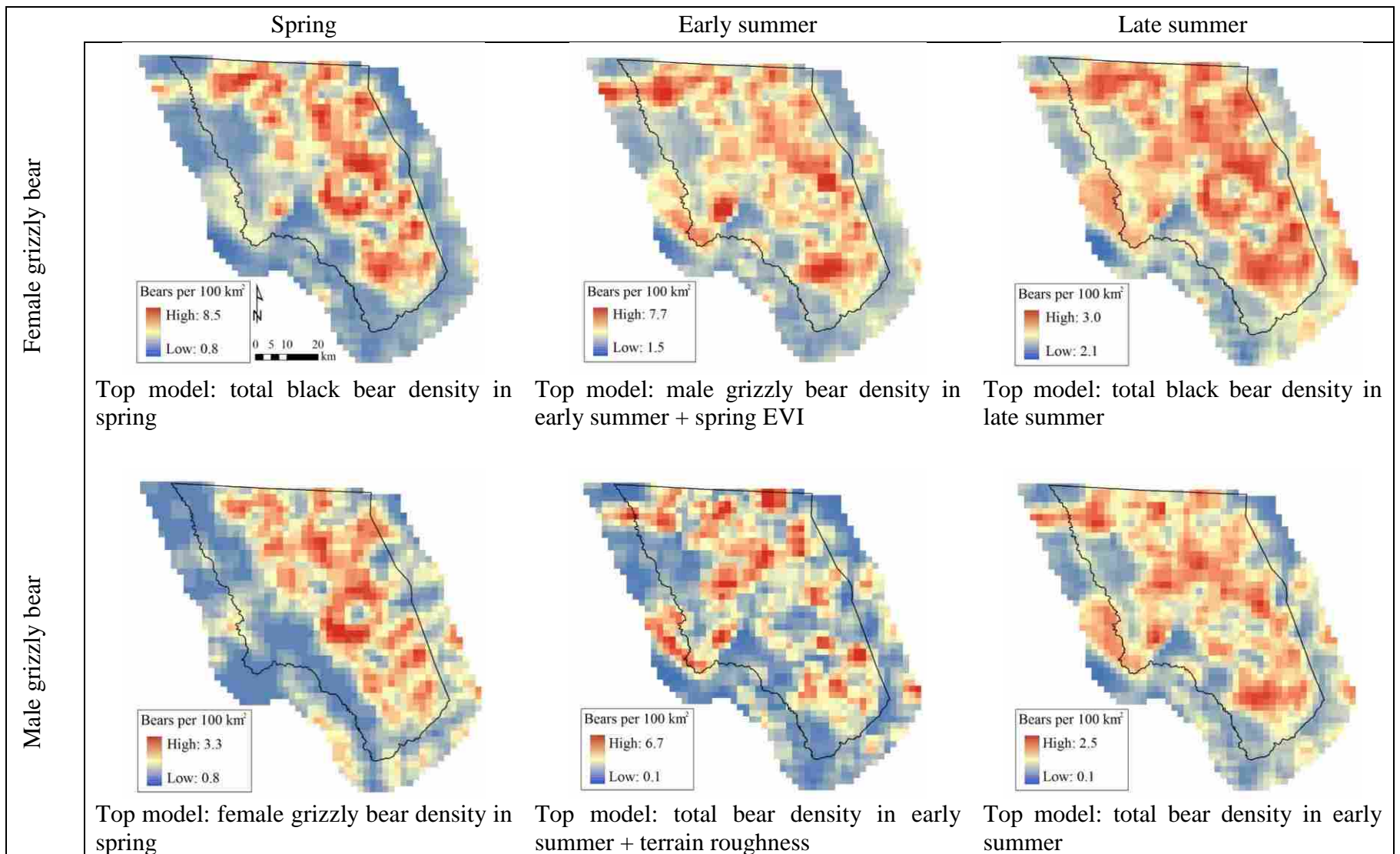


Figure 2-3. Predicted density of grizzly bears by sex and season using the most supported SECR model based on AICc values. We conducted sampling during June-September, 2004, on all lands in Montana within 10 km of Glacier National Park, which is shown in black outline. EVI is the enhanced vegetation index.

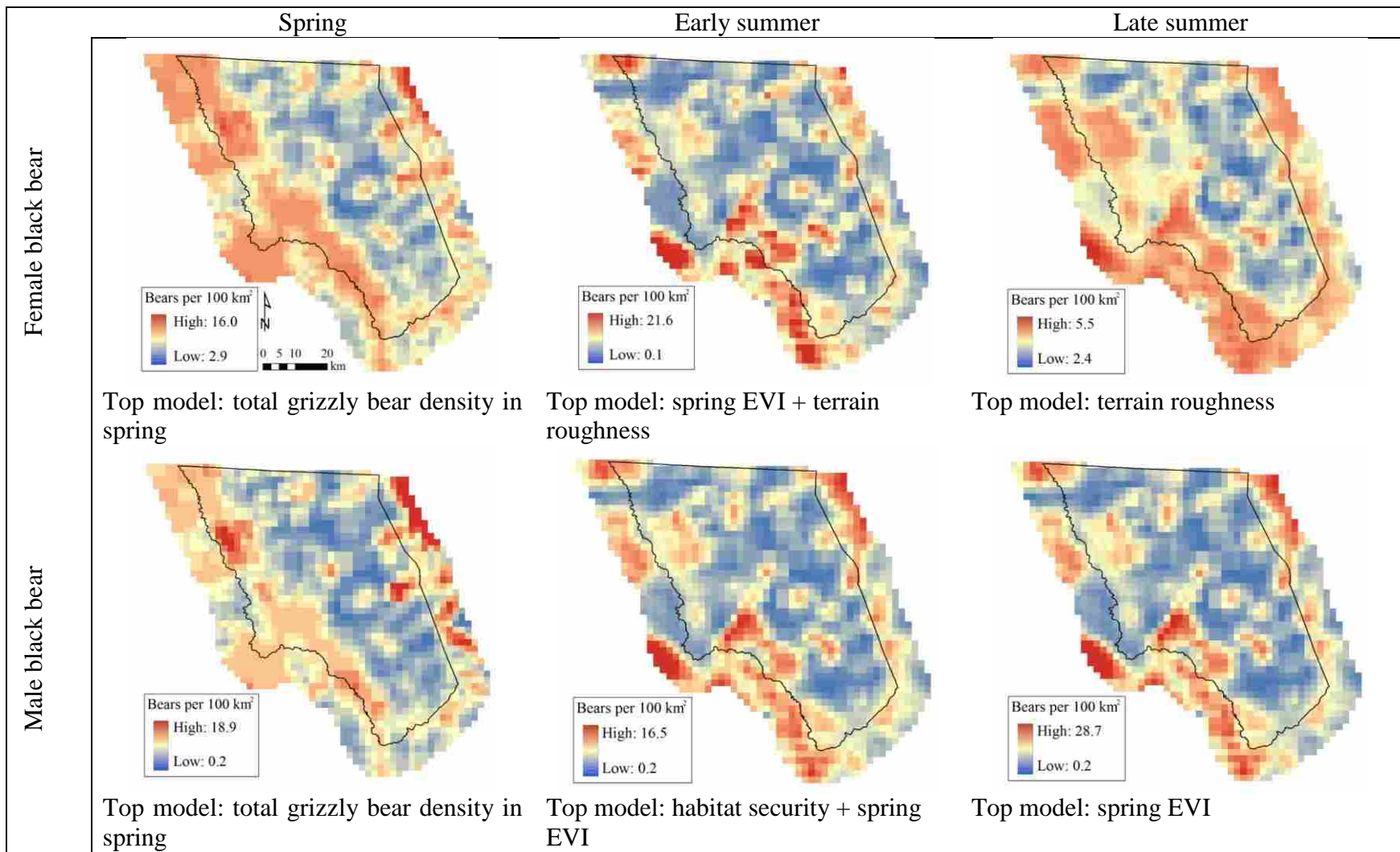


Figure 2-4. Predicted density of black bears by sex and season from the most supported SECR model based on AICc values. We conducted sampling during June-September, 2004, on all lands in Montana within 10 km of Glacier National Park, which is shown in black outline. EVI is the enhanced vegetation index.

APPENDIX A. SUPPLEMENTAL MATERIALS

Table 2-S 1. Model selection results from spatially-explicit capture-recapture models grizzly bears (*Ursus arctos*) and American black bears (*U. americanus*) in northwestern Montana, USA, 2004.

Definitions: K: number of estimated parameters; logLik: log-likelihood; AICc: Akaike Information Criterion value adjusted for small sample size; dAICc: difference of AICc value between given model and the top model; AICcwt: AICc model weight; time: model run time in seconds. D: density; g0: probability of detection at the home range center; sigma: spatial scale parameter. Session: species, sex, season (1=spring, 2=early summer, 3=late summer); example: BB M3 = black bear, male, late summer. Model notation: rtp: relative terrain position (terrain complexity); elev: standardized elevation; elevcat: categorical elevation; TYPE: type of detector; categorical hair trap or bear rub; t: time; security: categorical index of habitat security; landcover: categorical landcover type; evi: enhanced vegetation index, Julian date of first scene, Julian date of last scene (example: evi177257 = sum of EVI values during Julian days 177-257); predicted density surfaces (prdD): species+sex+season (example: bbf3prdD = black bear female, 3rd season [late summer]).

Session	Model	K	logLik	AICc	dAICc	AICcwt	time
GB F1	D~bbt1prdD g0~TYPE + evi177193trap sigma~evi177193trap	7	-263.835	542.43	0.00	0.13	104875
GB F1	D~bbt1prdD g0~TYPE:t sigma~1	8	-262.611	543.47	0.08	0.13	36945
GB F1	D~bbt1prdD g0~TYPE + ttl1prdDtrap sigma~ttl1prdDtrap	7	-264.529	544.78	1.39	0.07	41823
GB F1	D~bbt1prdD g0~TYPE sigma~1	5	-267.229	545.35	1.96	0.05	6776
GB F1	D~bbt1prdD g0~TYPE:t sigma~ttl1prdDtrap	9	-262.259	545.38	1.98	0.05	58697
GB F1	D~bbt1prdD g0~TYPE + bbT1prdDtrap sigma~bbT1prdDtrap	7	-264.845	545.41	2.02	0.05	79394
GB F1	D~bbt1prdD + gbmlprdD g0~TYPE:t sigma~1	9	-262.577	546.01	2.62	0.04	19657
GB F1	D~bbt1prdD g0~TYPE:t + evi177193trap sigma~1	9	-262.591	546.04	2.65	0.04	664260
GB F1	D~bbt1prdD g0~TYPE + gbM1prdDtrap sigma~gbM1prdDtrap	7	-265.432	546.59	3.20	0.03	15270
GB F1	D~bbt1prdD g0~TYPE + rtp sigma~1	6	-266.706	546.69	3.29	0.03	4443
GB F1	D~bbt1prdD g0~TYPE sigma~ttl1prdDtrap	6	-266.864	547.00	3.61	0.02	13373
GB F1	D~bbt1prdD g0~TYPE + bbT1prdDtrap sigma~1	6	-266.876	547.02	3.63	0.02	38156
GB F1	D~bbt1prdD g0~TYPE + gbM1prdDtrap sigma~1	6	-266.999	547.27	3.88	0.02	11098
GB F1	D~bbt1prdD g0~TYPE:t + evi177193trap sigma~evi177193trap	10	-261.925	547.40	4.01	0.02	86042
GB F1	D~bbt1prdD g0~TYPE + evi177193trap sigma~1	6	-267.094	547.46	4.07	0.02	74811
GB F1	D~bbt1prdD g0~TYPE + t sigma~1	6	-267.118	547.51	4.12	0.02	8808
GB F1	D~bbt1prdD + evi177193 g0~TYPE sigma~1	6	-267.173	547.62	4.23	0.02	9405
GB F1	D~bbt1prdD + gbmlprdD g0~TYPE sigma~1	6	-267.186	547.64	4.25	0.02	2978
GB F1	D~bbt1prdD g0~TYPE + ttl1prdDtrap sigma~1	6	-267.200	547.67	4.28	0.02	10364

Session	Model	K	logLik	AICc	dAICc	AICcwt	time
GB F2	D~evi177193+gbm2prdD g0~TYPE+elevcat sigma~1	1	-543.542	1109.10	0.00	0.54	239332
GB F2	D~evi177193+gbm2prdD g0~TYPE+elevcat sigma~gbM2prdDtrap	11	-543.159	1110.76	1.66	0.23	175311
GB F2	D~evi177193+gbm2prdD g0~TYPE+ttl2prdDtrap+elevcat sigma~1	11	-543.395	1111.23	2.13	0.18	975016
GB F3	D~bbt3prdD g0~elevcat sigma~bbT3prdDtrap	9	-269.543	562.54	0.00	0.11	236213
GB F3	D~ttl3prdD g0~elevcat sigma~bbT3prdDtrap	9	-269.561	562.58	0.04	0.11	401384
GB F3	D~gbm3prdD g0~elevcat sigma~bbT3prdDtrap	9	-269.588	562.63	0.09	0.10	323679
GB F3	D~rtp g0~elevcat sigma~bbT3prdDtrap	9	-269.596	562.65	0.11	0.10	301981
GB F3	D~bbt3prdD g0~elevcat sigma~ttl3prdDtrap	9	-269.745	562.95	0.40	0.09	150784
GB F3	D~ttl3prdD g0~elevcat sigma~ttl3prdDtrap	9	-269.757	562.97	0.43	0.09	303233
GB F3	D~bbt3prdD g0~elevcat sigma~1	8	-271.676	563.59	1.05	0.06	15946
GB F3	D~bbt3prdD g0~elevcat+bbT3prdDtrap sigma~1	9	-270.246	563.95	1.41	0.05	125857
GB F3	D~ttl3prdD g0~elevcat sigma~1	8	-272.002	564.24	1.70	0.05	36033
GB F3	D~bbt3prdD+elev g0~elevcat sigma~1	9	-270.692	564.84	2.30	0.03	34355
GB F3	D~bbt3prdD g0~elevcat sigma~1	12	-265.660	565.72	3.18	0.02	53373
GB F3	D~bbt3prdD g0~elevcat+bbT3prdDtrap sigma~bbT3prdDtrap	10	-269.457	565.79	3.25	0.02	176193
GB F3	D~bbt3prdD+evi177193 g0~elevcat sigma~bbT3prdDtrap	10	-269.507	565.89	3.35	0.02	376805
GB F3	D~bbt3prdD+gbm3prdD g0~elevcat sigma~bbT3prdDtrap	10	-269.518	565.91	3.37	0.02	135138
GB F3	D~bbt3prdD+gbm3prdD g0~elevcat sigma~bbT3prdDtrap	10	-269.550	565.97	3.43	0.02	135265
GB F3	D~bbt3prdD g0~elevcat sigma~gbF3prdDtrap	9	-271.397	566.25	3.71	0.02	27927
GB F3	D~bbt3prdD g0~t+elevcat sigma~bbT3prdDtrap	10	-269.729	566.33	3.79	0.02	643602
GB F3	D~bbt3prdD g0~elevcat+gbF3prdDtrap sigma~1	9	-271.603	566.66	4.12	0.01	27902
GB F3	D~bbt3prdD g0~elevcat+gbM3prdDtrap sigma~1	9	-271.675	566.81	4.26	0.01	10205
GB F3	D~bbt3prdD+rtp g0~elevcat sigma~1	9	-271.676	566.81	4.27	0.01	10954
GB F3	D~bbt3prdD g0~elevcat sigma~1	8	-273.629	567.49	4.95	0.01	16217
GB M1	D~gbf1prdD g0~TYPE+gbM1prdDtrap+security sigma~gbM1prdDtrap	9	-926.614	1873.54	0.00	0.26	63206
GB M1	D~gbf1prdD+bbt1prdD+elev g0~TYPE+bbT1prdDtrap+security sigma~bbT1prdDtrap	11	-925.157	1875.79	2.25	0.09	340482
GB M1	D~gbf1prdD+bbt1prdD+elev g0~TYPE+gbM1prdDtrap sigma~gbM1prdDtrap	9	-927.861	1876.03	2.49	0.08	72820
GB M1	D~gbf1prdD g0~TYPE+gbF1prdDtrap+security sigma~gbM1prdDtrap	9	-928.016	1876.34	2.80	0.06	210076
GB M1	D~gbf1prdD+bbt1prdD+elev g0~TYPE+bbT1prdDtrap sigma~bbT1prdDtrap+security	11	-925.483	1876.44	2.90	0.06	459122
GB M1	D~gbf1prdD+bbt1prdD+elev g0~TYPE+gbM1prdDtrap+security sigma~bbT1prdDtrap	11	-925.643	1876.76	3.22	0.05	278357
GB M1	D~gbf1prdD+bbt1prdD+elev g0~TYPE+bbT1prdDtrap sigma~bbT1prdDtrap	9	-928.330	1876.97	3.43	0.05	90009

Session	Model	K	logLik	AICc	dAICc	AICcwt	time
GB M1	D~gbf1prdD g0~TYPE+gbM1prdDtrap+security sigma~ttl1prdDtrap	9	-928.679	1877.67	4.13	0.03	269677
GB M1	D~gbf1prdD+bbm1prdD+elev g0~TYPE+bbT1prdDtrap+security sigma~bbT1prdDtrap	11	-926.112	1877.70	4.16	0.03	380303
GB M1	D~gbf1prdD+bbt1prdD+elev+rtp g0~TYPE+bbT1prdDtrap+security sigma~bbT1prdDtrap	12	-924.781	1877.72	4.19	0.03	736071
GB M1	D~gbf1prdD+bbt1prdD+elev g0~TYPE+bbT1prdDtrap+gbF1prdDtrap sigma~bbT1prdDtrap	10	-927.538	1877.93	4.40	0.03	196492
GB M1	D~gbf1prdD+bbt1prdD+elev g0~TYPE+gbM1prdDtrap sigma~bbT1prdDtrap	9	-928.860	1878.03	4.49	0.03	122014
GB M1	D~ttl1prdD g0~TYPE+bbT1prdDtrap+security sigma~bbT1prdDtrap	9	-928.924	1878.16	4.62	0.03	371259
GB M2	D~ttl2prdD+rtp g0~TYPE:t sigma~landcover	12	-742.816	1513.39	0.00	0.48	329886
GB M2	D~ttl2prdD g0~TYPE:t sigma~landcover	11	-744.432	1514.01	0.62	0.35	369175
GB M3	D~ttl2prdD g0~t+evi177257trap sigma~1	6	-389.168	792.67	0.00	0.07	21812
GB M3	D~ttl2prdD g0~t+evi177257trap sigma~evi177257trap+rtp	8	-386.492	793.22	0.55	0.05	96032
GB M3	D~ttl2prdD g0~evi177257trap sigma~evi177257trap+rtp	7	-388.023	793.25	0.58	0.05	24973
GB M3	D~ttl2prdD g0~evi177257trap sigma~evi177257trap	6	-389.459	793.25	0.58	0.05	13320
GB M3	D~ttl2prdD+rtp g0~evi177257trap sigma~1	6	-389.499	793.33	0.66	0.05	55931
GB M3	D~ttl2prdD g0~evi177257trap+rtp sigma~1	6	-389.565	793.46	0.79	0.05	34424
GB M3	D~bbm3prdD g0~evi177257trap sigma~1	5	-390.928	793.48	0.81	0.04	11281
GB M3	D~ttl3prdD g0~evi177257trap sigma~1	5	-391.022	793.67	1.00	0.04	25406
GB M3	D~bbt3prdD g0~evi177257trap sigma~1	5	-391.156	793.93	1.26	0.04	10787
GB M3	D~ttl2prdD g0~evi177257trap+gbF3prdDtrap sigma~1	6	-389.920	794.17	1.50	0.03	14444
GB M3	D~ttl2prdD g0~evi177257trap sigma~rtp	6	-390.003	794.34	1.67	0.03	19997
GB M3	D~bbt3prdD+rtp g0~evi177257trap sigma~1	6	-390.046	794.43	1.76	0.03	10496
GB M3	D~ttl2prdD g0~evi177257trap sigma~gbM3prdDtrap	6	-390.100	794.53	1.87	0.03	15441
GB M3	D~bbt3prdD+elev+rtp g0~evi177257trap sigma~1	7	-388.672	794.54	1.88	0.03	25105
GB M3	D~elev+ttl2prdD g0~evi177257trap sigma~1	6	-390.258	794.85	2.18	0.02	33306
GB M3	D~ttl2prdD g0~evi177257trap+ttl3prdDtrap sigma~1	6	-390.299	794.93	2.26	0.02	591707
GB M3	D~ttl2prdD+rtp+elev g0~evi177257trap sigma~1	7	-388.870	794.94	2.27	0.02	65044
GB M3	D~ttl2prdD g0~evi177257trap sigma~ttl3prdDtrap	6	-390.367	795.07	2.40	0.02	93692
GB M3	D~ttl2prdD g0~evi177257trap sigma~security	7	-388.957	795.11	2.45	0.02	16095
GB M3	D~evi177225+ttl2prdD g0~evi177257trap sigma~1	6	-390.438	795.21	2.54	0.02	48941
GB M3	D~ttl2prdD g0~evi177257trap sigma~bbT3prdDtrap	6	-390.444	795.22	2.55	0.02	93904
GB M3	D~evi209225+ttl2prdD g0~evi177257trap sigma~1	6	-390.452	795.24	2.57	0.02	44545
GB M3	D~ttl2prdD g0~security+evi177257trap sigma~1	7	-389.058	795.32	2.65	0.02	31626
GB M3	D~evi209225+bbt3prdD g0~evi177257trap sigma~1	6	-390.502	795.34	2.67	0.02	110562

Session	Model	K	logLik	AICc	dAICc	AICcwt	time
GB M3	D~ttl2prdD g0~evi177257trap+gbM3prdDtrap sigma~1	6	-390.545	795.42	2.76	0.02	55423
GB M3	D~ttl2prdD g0~t+evi177257trap sigma~evi177257trap+gbF3prdDtrap	8	-387.631	795.50	2.83	0.02	98156
GB M3	D~evi209225+ttl2prdD g0~evi177257trap sigma~1	6	-390.663	795.66	2.99	0.02	146870
GB M3	D~bbt3prdD+elev g0~evi177257trap sigma~1	6	-390.693	795.72	3.05	0.01	7207
GB M3	D~evi177257 g0~evi177257trap sigma~1	5	-392.154	795.93	3.26	0.01	10697
GB M3	D~bbf3prdD g0~evi177257trap sigma~1	5	-392.167	795.96	3.29	0.01	9008
GB M3	D~ttl2prdD g0~t+evi177257trap+rtp sigma~evi177257trap+rtp	9	-386.251	795.96	3.29	0.01	66764
GB M3	D~gbf2prdD g0~evi177257trap sigma~1	5	-392.407	796.44	3.77	0.01	62999
GB M3	D~gbf3prdD+evi177225 g0~evi177257trap sigma~1	6	-391.117	796.57	3.90	0.01	17400
GB M3	D~gbm2prdD g0~evi177257trap sigma~1	5	-392.517	796.66	3.99	0.01	102271
GB M3	D~evi209225+gbf3prdD g0~evi177257trap sigma~1	6	-391.236	796.81	4.14	0.01	124333
GB M3	D~gbf3prdD+evi177257 g0~evi177257trap sigma~1	6	-391.410	797.15	4.49	0.01	16783
GB M3	D~gbf3prdD g0~evi177257trap sigma~1	5	-392.795	797.21	4.54	0.01	11046
GB M3	D~ttl2prdD+security g0~evi177257trap sigma~1	7	-390.099	797.40	4.73	0.01	35238
GB M3	D~elev g0~evi177257trap sigma~1	5	-392.929	797.48	4.81	0.01	19230
BB F1	D~gbl1prdD g0~TYPE+landcover+ttl1prdDtrap sigma~landcover	12	-466.192	958.32	0.00	0.37	274705
BB F1	D~gbl1prdD g0~TYPE+landcover sigma~landcover	11	-467.716	959.06	0.74	0.25	30616
BB F1	D~gbl1prdD g0~TYPE+landcover+ttl1prdDtrap sigma~landcover+ttl1prdDtrap	13	-466.081	960.44	2.12	0.13	165532
BB F1	D~gbl1prdD g0~TYPE+landcover sigma~landcover	15	-464.666	962.37	4.05	0.05	135349
BB F1	D~gbl1prdD g0~TYPE+landcover+ttl1prdDtrap sigma~landcover	16	-463.721	962.91	4.59	0.04	1E+06
BB F2	D~evi177193+rtp g0~TYPE+ttl2prdDtrap sigma~ttl2prdDtrap	8	-463.216	943.67	0.00	0.44	366112
BB F2	D~evi177193+rtp g0~TYPE+ttl2prdDtrap sigma~bbF2prdDtrap	8	-463.548	944.34	0.66	0.31	601566
BB F2	D~evi177193+rtp g0~TYPE+bbF2prdDtrap sigma~bbF2prdDtrap	8	-464.398	946.04	2.36	0.13	98649
BB F3	D~evi177225+rtp g0~t sigma~1	6	-360.590	734.97	0.00	0.08	10744
BB F3	D~rtp g0~t sigma~1	5	-361.156	733.56	1.41	0.04	3873
BB F3	D~rtp g0~t+rtp sigma~1	6	-360.609	735.00	1.44	0.04	11355
BB F3	D~rtp+evi177257 g0~t sigma~1	6	-360.654	735.09	1.53	0.04	9901
BB F3	D~rtp g0~t sigma~gbM3prdDtrap	6	-360.868	735.52	1.96	0.03	6429
BB F3	D~rtp+ttl3prdD g0~t sigma~1	6	-360.873	735.53	1.97	0.03	18728
BB F3	D~bbt2prdD+rtp g0~t sigma~1	6	-360.971	735.73	2.17	0.03	4916
BB F3	D~rtp g0~t+bbM3prdDtrap sigma~1	6	-360.979	735.75	2.18	0.03	33065
BB F3	D~rtp g0~t+ttl3prdDtrap sigma~1	6	-360.980	735.75	2.19	0.03	295163
BB F3	D~rtp g0~t+evi177257trap sigma~1	6	-360.983	735.75	2.19	0.03	197788
BB F3	D~rtp g0~t sigma~bbT3prdDtrap	6	-361.101	735.99	2.43	0.02	33895

Session	Model	K	logLik	AICc	dAICc	AICcwt	time
BB F3	D~rtp g0~t sigma~bbM3prdDtrap	6	-361.103	735.99	2.43	0.02	46034
BB F3	D~rtp g0~t sigma~ttl3prdDtrap	6	-361.114	736.02	2.45	0.02	216549
BB F3	D~ttl1prdD g0~t sigma~1	5	-362.403	736.06	2.50	0.02	20854
BB F3	D~rtp g0~t sigma~rtp	6	-361.144	736.08	2.51	0.02	12406
BB F3	D~rtp g0~t sigma~evi177257trap	6	-361.156	736.10	2.54	0.02	20135
BB F3	D~rtp g0~rtp sigma~rtp	6	-361.327	736.44	2.88	0.02	19351
BB F3	D~rtp g0~rtp sigma~rtp	6	-361.327	736.44	2.88	0.02	4543
BB F3	D~evi177225+rtp g0~1 sigma~t	6	-361.332	736.45	2.89	0.02	5621
BB F3	D~rtp g0~t:rtp sigma~1	6	-361.398	736.58	3.02	0.02	13915
BB F3	D~rtp g0~t:gbT3prdDtrap sigma~1	6	-361.511	736.81	3.25	0.02	7550
BB F3	D~rtp g0~rtp sigma~1	5	-362.873	737.00	3.43	0.01	3752
BB F3	D~evi177225+rtp g0~1 sigma~1	5	-362.875	737.00	3.44	0.01	4340
BB F3	D~gbt2prdD+rtp g0~1 sigma~1	5	-362.893	737.04	3.47	0.01	11052
BB F3	D~evi177225+rtp g0~t sigma~t	7	-360.329	737.09	3.53	0.01	4547
BB F3	D~evi177225 g0~t sigma~1	5	-363.000	737.25	3.69	0.01	2748
BB F3	D~rtp g0~t+rtp+ttl3prdDtrap sigma~1	7	-360.408	737.25	3.69	0.01	126847
BB F3	D~rtp g0~t+rtp+bbM3prdDtrap sigma~1	7	-360.407	737.25	3.69	0.01	330460
BB F3	D~rtp g0~t+rtp+evi177257trap sigma~1	7	-360.442	737.32	3.76	0.01	108257
BB F3	D~rtp g0~t+security sigma~1	7	-360.442	737.32	3.76	0.01	9006
BB F3	D~evi177225+rtp+ttl2prdD g0~t sigma~1	7	-360.457	737.35	3.79	0.01	17845
BB F3	D~rtp g0~t+elevcat sigma~1	9	-357.660	737.41	3.85	0.01	63632
BB F3	D~evi177257 g0~t sigma~1	5	-363.087	737.42	3.86	0.01	20781
BB F3	D~rtp g0~t sigma~security	7	-360.496	737.43	3.87	0.01	8373
BB F3	D~gbt2prdD g0~t sigma~1	5	-363.102	737.46	3.89	0.01	8759
BB F3	D~gbt2prdD g0~t sigma~1	5	-363.102	737.46	3.89	0.01	9914
BB F3	D~rtp g0~t+bbM3prdDtrap sigma~gbM3prdDtrap	7	-360.555	737.55	3.98	0.01	80029
BB F3	D~bbf2prdD g0~t sigma~1	5	-363.181	737.61	4.05	0.01	5730
BB F3	D~ttl3prdD g0~t sigma~1	5	-363.230	737.71	4.15	0.01	12762
BB F3	D~bbt2prdD g0~t sigma~1	5	-363.268	737.79	4.23	0.01	6139
BB F3	D~rtp g0~gbT3prdDtrap sigma~1	5	-363.309	737.87	4.31	0.01	8720
BB F3	D~rtp g0~bbM3prdDtrap sigma~1	5	-363.324	737.90	4.34	0.01	15073
BB F3	D~ttl2prdD g0~t sigma~1	5	-363.327	737.91	4.34	0.01	8619
BB F3	D~rtp+elev g0~1 sigma~1	5	-363.463	738.18	4.61	0.01	4486
BB F3	D~rtp g0~evi177257trap sigma~1	5	-363.485	738.22	4.66	0.01	8276
BB F3	D~elev g0~t sigma~1	5	-363.511	738.27	4.71	0.01	11398

Session	Model	K	logLik	AICc	dAICc	AICcwt	time
BB F3	D~rtp g0~t+ttl3prdDtrap+evi177257trap sigma~1	7	-360.925	738.29	4.72	0.01	244085
BB F3	D~rtp g0~t+ttl3prdDtrap sigma~ttl3prdDtrap	7	-360.927	738.29	4.73	0.01	64454
BB F3	D~rtp g0~t:bbF3prdDtrap sigma~1	6	-362.267	738.32	4.76	0.01	9672
BB F3	D~gbt3prdD g0~t sigma~1	5	-363.554	738.36	4.80	0.01	5415
BB F3	D~security+rtp g0~t sigma~1	7	-361.034	738.50	4.94	0.01	19815
BB F3	D~rtp g0~t sigma~ttl2prdDtrap	9	-358.215	738.52	4.96	0.01	58785
BB M1	D~gbt1prdD g0~TYPE+security+evi177193trap sigma~evi177193trap	9	-846.026	1711.11	0.00	0.60	524791
BB M1	D~elev g0~TYPE+security+evi177193trap sigma~evi177193trap	9	-847.487	1714.03	2.92	0.14	259372
BB M1	D~elev g0~TYPE+security+evi177193trap+ttl1prdDtrap sigma~evi177193trap	10	-846.611	1714.52	3.41	0.11	339759
BB M1	D~elev g0~TYPE+security+evi177193trap sigma~evi177193trap+ttl1prdDtrap	10	-847.057	1715.41	4.30	0.07	430579
BB M2	D~evi177193+security g0~TYPE+security+elevcat sigma~security+elevcat	19	-628.833	1302.28	0.00	0.33	2E+06
BB M2	D~evi177193 g0~TYPE+security+elevcat sigma~security+elevcat	17	-632.025	1303.28	1.01	0.20	806088
BB M2	D~evi177193+elev g0~TYPE+security+elevcat sigma~security+elevcat	18	-630.722	1303.34	1.06	0.19	581078
BB M2	D~evi177193+ttl2prdD g0~TYPE+security+elevcat sigma~security+elevcat	18	-631.980	1305.86	3.58	0.05	2E+06
BB M2	D~evi177193+bbf2prdD g0~TYPE+security+elevcat sigma~security+elevcat	18	-632.001	1305.90	3.62	0.05	641166
BB M2	D~evi177193+elev+bbf2prdD g0~TYPE+security+elevcat sigma~security+elevcat	19	-630.669	1305.95	3.67	0.05	273380
BB M2	D~bbf2prdD g0~TYPE+security+elevcat sigma~security+elevcat	17	-633.435	1306.10	3.82	0.05	562270
BB M3	D~evi177193 g0~1 sigma~1	6	-287.717	589.15	0.00	0.08	8964
BB M3	D~bbf3prdD+security g0~1 sigma~1	4	-290.381	589.55	0.40	0.07	6034
BB M3	D~bbf3prdD g0~ttl2prdDtrap sigma~1	5	-289.520	590.24	1.09	0.05	61962
BB M3	D~bbf3prdD+rtp g0~1 sigma~1	5	-289.533	590.27	1.12	0.05	9166
BB M3	D~bbf3prdD+evi177257 g0~1 sigma~1	5	-289.567	590.34	1.19	0.04	19174
BB M3	D~bbf3prdD+elev g0~1 sigma~1	5	-289.667	590.54	1.39	0.04	12176
BB M3	D~evi177257+security g0~1 sigma~1	6	-288.582	590.88	1.73	0.03	28728
BB M3	D~bbf3prdD+evi177193 g0~1 sigma~1	5	-289.861	590.92	1.77	0.03	14181
BB M3	D~bbf3prdD g0~t sigma~1	5	-289.887	590.97	1.82	0.03	9228
BB M3	D~bbf3prdD g0~rtp sigma~1	5	-289.951	591.10	1.95	0.03	4986
BB M3	D~bbf3prdD g0~1 sigma~bbF3prdDtrap	5	-289.955	591.11	1.96	0.03	7268
BB M3	D~bbf3prdD g0~1 sigma~security	6	-288.776	591.27	2.12	0.03	6813

Session	Model	K	logLik	AICc	dAICc	AICcwt	time
BB M3	D~bbf3prdD+evi177193+security g0~1 sigma~1	7	-287.549	591.43	2.28	0.03	18104
BB M3	D~gbt3prdD+bbf3prdD+security g0~1 sigma~1	7	-287.580	591.49	2.34	0.03	24573
BB M3	D~bbf3prdD g0~evi241257trap sigma~ttl2prdDtrap	6	-288.969	591.65	2.50	0.02	76785
BB M3	D~bbf3prdD g0~security sigma~1	6	-289.089	591.89	2.74	0.02	12066
BB M3	D~bbf2prdD g0~1 sigma~1	4	-291.580	591.95	2.80	0.02	5523
BB M3	D~bbf3prdD+security g0~bbM3prdDtrap sigma~ttl2prdDtrap	8	-286.462	591.99	2.84	0.02	304735
BB M3	D~evi177257+security+rtp g0~1 sigma~1	7	-287.930	592.19	3.04	0.02	18760
BB M3	D~ttl2prdD+evi177257+security g0~1 sigma~1	7	-287.942	592.22	3.07	0.02	10620
BB M3	D~evi177257 g0~1 sigma~1	4	-291.914	592.61	3.46	0.01	10257
BB M3	D~ttl3prdD+security g0~1 sigma~1	6	-289.504	592.72	3.57	0.01	27915
BB M3	D~evi177257+rtp g0~1 sigma~1	5	-290.789	592.78	3.63	0.01	11723
BB M3	D~ttl2prdD g0~1 sigma~1	4	-292.039	592.86	3.71	0.01	9844
BB M3	D~bbt2prdD g0~1 sigma~1	4	-292.063	592.91	3.76	0.01	8813
BB M3	D~gbt3prdD+bbf3prdD g0~evi241257trap sigma~1	6	-289.600	592.91	3.76	0.01	4187
BB M3	D~gbt3prdD+bbf3prdD g0~1 sigma~evi177257trap	6	-289.620	592.96	3.81	0.01	49758
BB M3	D~gbt3prdD+bbf3prdD g0~gbT3prdDtrap sigma~1	6	-289.631	592.98	3.83	0.01	66811
BB M3	D~gbt3prdD+bbf3prdD g0~1 sigma~evi241257trap	6	-289.663	593.04	3.89	0.01	10904
BB M3	D~gbt3prdD+bbf3prdD g0~1 sigma~t	6	-289.697	593.11	3.96	0.01	69858
BB M3	D~gbt3prdD+bbf3prdD g0~t sigma~1	6	-289.700	593.11	3.96	0.01	12398
BB M3	D~bbf3prdD g0~bbT3prdDtrap+gbT3prdDtrap sigma~1	6	-289.729	593.17	4.02	0.01	10276
BB M3	D~gbt3prdD+bbf3prdD g0~bbM3prdDtrap sigma~1	6	-289.759	593.23	4.08	0.01	25771
BB M3	D~bbf3prdD g0~t:evi241257trap sigma~1	6	-289.762	593.24	4.09	0.01	27521
BB M3	D~gbt3prdD+bbf3prdD g0~evi177257trap sigma~1	6	-289.766	593.25	4.10	0.01	60160
BB M3	D~gbt3prdD+bbf3prdD g0~evi177225trap sigma~1	6	-289.766	593.25	4.10	0.01	8782
BB M3	D~ttl3prdD+rtp+security g0~1 sigma~1	7	-288.632	593.60	4.45	0.01	7507
BB M3	D~bbf3prdD g0~bbF3prdDtrap sigma~bbF3prdDtrap	6	-289.954	593.62	4.47	0.01	13868
BB M3	D~bbm2prdD g0~1 sigma~1	4	-292.520	593.82	4.67	0.01	11450
BB M3	D~bbf3prdD g0~bbM3prdDtrap+security sigma~ttl2prdDtrap	8	-287.380	593.82	4.67	0.01	14513
BB M3	D~gbt3prdD+bbf3prdD g0~security sigma~1	7	-288.833	594.00	4.85	0.01	3176

CHAPTER 3 : EXPLAINING VARIATION IN DETECTION PROBABILITIES OF GRIZZLY BEARS AT NATURALLY OCCURRING BEAR RUBS.

INTRODUCTION

Monitoring population dynamics is a priority for agencies responsible for managing wildlife populations, particularly for conservation-reliant species (Scott et al. 2010). Monitoring programs should ideally both inform managers on the status and trends of populations as well as improve understanding of how environmental change and management actions influence those dynamics (Nichols & Williams 2006). Reliable estimates of population parameters such as density and population growth rate are, however, often difficult to acquire, particularly within short enough time frames to identify and address threats before they become irreversible. Further, monitoring programs need to be affordable, flexible, and preferably impose limited disturbance to the animals being studied. Beyond the potential social and ethical values attached to reducing disturbance, doing so may reduce behavioral responses of animals that can lead to biased demographic parameter estimates (Boulanger et al. 2004; Cattet et al. 2008).

Advances in sampling methods have greatly expanded the tools available for population monitoring, particularly noninvasive methods that require little if any disturbance to animals. Remote cameras, for example, have been used to estimate density in many populations, including tigers (*Panthera tigris*) and other species with coat patterns that allow individual identification (Karanth et al. 2004; Noss et al. 2012). Camera detection data can also be used to monitor changes in occupancy, even of species without individually identifiable markers, such as grizzly bears (*Ursus arctos*), which are difficult to study given they tend to exist at low densities, in remote areas, and are capable of moving large distances (Steenweg et al. 2016).

Noninvasive genetic sampling (NGS) provides similar benefits to remote cameras with the added power to identify cryptic individual animals and track their detections over space and time (Waits & Paetkau 2005). Such detection data are well-suited for use in traditional and spatially-explicit capture-recapture (SECR) methods, and have been used in dozens of studies to produce estimates of density and population growth rate, as well as species' distributions and genetic status (e.g., Kendall et al. 2009; Sawaya et al. 2012). The efficacy of NGS has made it possible to design study areas many times larger than animals' home ranges, which further reduces biases related to edge effects (Boulanger & McLellan 2001) or focusing on areas of high quality habitat that may bias estimates in smaller study areas that (Smallwood & Schonewald 1998; Yoccoz et al. 2001).

Perhaps for more than any other taxonomic group, NGS methods have been used to assess and monitor populations of grizzly and black bears (*U. americanus*) across North America. For grizzly bears, most studies have used baited sites placed pseudo-systematically in grid cells ranging from 25-100 km², based on the expected home range size of female bears, to ensure adequate detection rates (Boulanger et al. 2004). Bears are attracted to the sites by the prospect of obtaining food (i.e., carrion), although many studies have used non-rewarding lures to minimize behavioral responses (Boulanger et al. 2002). The density and overall number of sites, quantity and nature of lure, and whether sites are moved between sessions are all design factors that can influence detection probabilities, and thereby reliability of parameter estimates, of bears (Boulanger et al. 2004; Wilton et al. 2016). Further, any number of uncontrollable factors such as rain that can wash away lure, annual or seasonal variability in natural foods (McCall et al. 2013), or large scale disturbances like wildfires can add to the inherent heterogeneity in detection rates at these sites.

Because of these and other factors, heterogeneity in detection probabilities remains a fundamental challenge in estimating demographic parameters using capture-recapture (CR) methods (Schwarz & Seber 1999; Boulanger et al. 2004), which can result in severe biases if not properly modeled (Hines and Nichols 2001; Link 2003). Several statistical approaches to mitigate effects of detection heterogeneity have been developed, including the use of individual covariates (Huggins 1991), mixture models that partition animals into ≥ 2 groups that have relatively homogenous detection rates (Pledger 2000), and random effects that allow each individual's detection probability to differ from the population mean (Gimenez & Choquet 2010). Effective use of such extensions, however, requires meeting additional assumptions, such as having covariate values for every sampled individual, having a large number of sampling occasions, and all animals having a non-zero detection probability (Boulanger et al. 2008).

In addition to advances in the CR models themselves, the use of detection data from >1 sampling method has been shown to be particularly effective at reducing bias and improving precision of demographic parameter estimates with both traditional (Boulanger et al. 2008; Sawaya et al. 2012) and spatial CR methods (Stetz et al. 2014; Kendall et al. 2016; Morehouse & Boyce 2016). Secondary sampling methods can be more efficient than increasing sampling intensity with a single method, and can reduce the effects of heterogeneity by exposing more animals to detection (Dreher et al. 2007; Kendall et al. 2009), even if a segment of the population has low or zero probability of detection in one of the methods (Boulanger et al. 2008). Several such secondary sampling methods have been used with bear NGS studies, including detections at highway crossing structures (Sawaya et al. 2012), animals known to be on the study area through live capture or harvest (Dreher et al. 2007), or detected through hair samples collected at bear rubs (Karamanlidis et al. 2007; Kendall et al. 2008; Stetz et al. 2010).

Throughout the ranges of both grizzly and black bears, rubbing on trees, powerpoles, and other structures is an ubiquitous behavior, the foundation of which is poorly understood (Burst & Pelton 1983; Green et al. 2003; Karamanlidis et al. 2007). Regardless of the motivation for rubbing, several large-scale CR studies have used genetic samples collected at bear rubs to increase the number of bear detections and thereby improve the precision of demographic parameter estimates. For example, Kendall et al. (2009) combined detections at bear rubs with those at baited sites to improve the precision of the first population-wide estimate of abundance for grizzly bears in the Northern Continental Divide Ecosystem (NCDE) of Montana. Despite being a secondary sampling method, 155 male and 120 female grizzly bears were detected at bear rubs, representing an estimated 53% and 26% of their respective total abundance (Kendall et al. 2009). Taking advantage of the known ages of bears handled during other research and management actions, Kendall et al. (2009) concluded that bears of all sex-age classes were detected at bear rubs. Like other sampling methods, however, detection rates were not uniform across classes, nor can age be determined from genetic samples (Kendall et al. 2009). Simulations using similar data found that CR analyses that combined detection data from multiple sampling methods to be robust to this and other forms of detection heterogeneity (Boulanger et al. 2008).

Recognizing the potential for bear rubs to generate a large number of bear detections, Stetz et al. (2010) used simulations to evaluate the power of bear rub surveys to estimate population growth rates for the grizzly bear population in the NCDE. Based on empirical detection rates and using robust-design Pradel (1996) models, they determined that detection events from bear rubs alone could detect a 3% annual decline in abundance within 6 years with 80% power (Stetz et al. 2010). Other scenarios such as increasing or fluctuating abundance,

however, required additional years' data to achieve the desired power assuming the same detection rates.

In the first empirical study to use bear rub detection data to estimate population growth rates, Sawaya et al. (2012) repeatedly surveyed >300 bear rubs in the Bow Valley of Banff National Park (BNP) during 2006 to 2008. They analyzed their detection data with robust-design Huggins-Pradel open population models in program MARK (White et al. 2001) that use detections from multiple sampling occasions within each year to estimate demographic parameters both within and across years (Kendall and Nichols 1995). In addition to abundance estimates, Sawaya et al. (2012) obtained precise estimates of apparent survival and population growth rates, which suggested that grizzly abundance was declining in this area. In contrast to Kendall et al. (2009), annual detection probabilities for male and female grizzly bears were identical, and substantially higher (86%), although there were similar seasonal changes in detection rates in both studies. Such high detection probabilities led the authors to conclude that bear rub surveys alone can produce reliable estimates of multiple population parameters of value to management, in short time periods, without the need to handle bears or use more intensive sampling efforts such as hair traps (Sawaya et al. 2012). The difference in results between these studies, despite very similar sampling and analytical methods, highlights how little is known about the underlying processes related to detection rates of bears at bear rubs. And although previous research has attempted to explain the behavioral motivation of bear rubbing behavior (Clapham et al. 2012), results have been far from conclusive and do not relate directly to explaining detection probabilities.

To inform study design and improve understanding of detection probabilities of grizzly bears at bear rubs, we used data from two NGS studies (Kendall et al. 2009; Sawaya et al. 2012)

to model detection as a function of factors related to bear biology and sampling intensity. We hypothesized that bear density plays a primary role in the detection process based on our observation that bears in the lower density population of BNP had higher detection probabilities than bears in the higher density areas of Montana. Among the possible explanations for this relationship is potential behavioral differences between bears in populations of different densities, for example, bears in higher density areas potentially being less inclined to use maintained trails or to engage in rubbing. Alternatively, different detection rates could reflect differences in home range sizes, which have been found to be negatively related to density in some populations (Kjellender et al. 2004; Bjornlie et al. 2014). The larger home ranges and associated larger movements of lower density populations may enable bears to encounter more bear rubs, thereby increasing detection opportunities (Pollock et al. 1990; Wilton et al. 2016). We also hypothesized that landscape factors related to bear movement or habitat preferences may influence detection, such as increased use of trail systems in areas of higher terrain complexity or dense forest cover, as bears use trails to move between resource patches (Herrero et al. 1986; Green and Mattson 2003). Increased use of trails would result in bears encountering more bear rubs and thus likely having greater detection rates. We further hypothesized that bears may be more inclined to use trails in areas that they perceive to contain fewer risks, which may also change seasonally in response to changing human uses on the landscape, as has been observed in other populations (Woodruffe 2000; Coltrane and Sinnott 2015). The level of trail use by female bears in particular may also be related to sexual segregation, where females are expected to avoid areas occupied by adult males that may be cannibalistic or infanticidal (Clutton-Brock 1987; Wielgus and Bunnell 1995). Based on this theory and empirical observations, we hypothesized that detection probabilities of females would be lowest during the

mating season when adult males are moving large distances searching for mating opportunities. As risk of males displaying infanticidal behavior declines after the mating season, we predict increasing female use of trails, leading to higher detection probabilities. Finally, we hypothesized that the effect of sampling effort on detection can be better explained at the individual home range level than as a time covariate as is commonly used in bear mark-recapture modeling (e.g., Kendall et al. 2009). Although these factors likely influence detection of both males and females, we expect differences in their effect size and how they interact over the course of sampling seasons.

To test our hypotheses, we used two approaches to model detection probability with Huggins (1991) models in program MARK (White et al. 2001), which allow the use of individual, group, and time-varying covariates. We first combined encounter histories from both studies, which that allowed us to directly evaluate support for our hypotheses across populations. We then developed independent model sets for each study area to take advantage of the longer sampling season in the Banff study area, and to compare with results from the joint study area analysis.

STUDY AREA

The ca. 6,600 km² Glacier National Park (GNP) study area included all lands within 10 km of GNP, truncated at the U.S.–Canada border (Fig. 3-1), which provided a larger range of land cover, uses, and management regimes than found within just GNP. Sixty-seven percent of the study area was within GNP, which was largely roadless and managed as wilderness, yet received >2 million visitors in 2004 (84% during June-September). Outside of GNP, lands were managed for multiple uses, including hunting, numerous non-consumptive recreational activities, and low-density residential development. The study area contained no recognized barriers to bear

movement, and was considered to be a relatively intact natural system with a nearly complete assemblage of native species (Kendall et al. 2009). All areas adjacent to GNP had spring and fall black bear hunting seasons except Waterton Lakes National Park, Alberta; grizzly bears were not legally hunted during our study.

Elevation ranged from approximately 900 m to 3,190 m above sea level. Higher elevations received more precipitation and contained the majority of exposed rock and permanent snow and ice fields. Average annual precipitation was 63 cm, the majority of which was deposited as snow in winter. The study area was bisected north to south by the Continental Divide, which had dramatic effects on local climate and vegetation composition. Areas west of the Divide generally received more precipitation and had more forested areas with less grasslands than the drier areas east of the Divide. Human activities and development were greater on the west side of the Divide, although no heavily developed areas existed within the study area itself.

The ca. 3,900 km² study area in Banff National Park included approximately 56% of BNP, concentrated in the southeastern part of the park (Fig. 3-2). In contrast to our GNP study area, BNP contains a town with approximately 8,000 residents, a major transportation corridor with both the Trans-Canada Highway and a railroad line, and is only 120 km from a major human population center (Calgary, AB). To reduce wildlife-vehicle collisions and improve animal movement across this corridor, a series of wildlife crossing structures with extensive fencing to encourage their use have been built (Sawaya et al. 2012). The BNP study area also contained nearly all species that were present prior to European settlement and was considered to be relatively intact outside the developments associated with the Bow Valley transportation corridor.

Although the BNP study area was located entirely east of the Continental Divide, weather patterns were still strongly affected by it, with more snow typically accumulating in the western parts of the park. Annual precipitation averaged 47 cm, the majority of which falls as rain during summer months. Elevation ranged from 1,350 m to 3,450 m above sea level, with higher elevation receiving more snowfall. The heavily glaciated features produced broadly similar vegetative conditions to GNP with lower elevations being dominated by forests and upper elevations consisting more of exposed rock, snow, and ice. Bears in both study areas rely heavily on berries to obtain sufficient fat reserves for hibernation, with huckleberries being dominant in GNP and buffaloberry (*Shepherdia canadensis*) in BNP (Martinka 1976; Hamer and Herrero 1987).

Both GNP and BNP contained extensive networks of hiking trails that provided access to most lands within both study areas. In BNP there are over 1,000 km of trails, with over 1,100 km in GNP. Areas to the west and south of GNP on state and national forests also contained maintained trails for the full extent of our sampling area, although we relied on more opportunistic identification of survey routes, such as powerpole lines, on tribal lands to the east of GNP. An important difference between our study areas was the considerably higher density of grizzly bears in GNP ($> 30/1000 \text{ km}^2$; Kendall et al. 2008) than BNP ($15/1000 \text{ km}^2$; Whittington and Sawaya 2015). Pronounced differences in black bear density were also present, with $114/1000 \text{ km}^2$ in GNP (Stetz et al. 2014) and $37/1000 \text{ km}^2$ in BNP (Sawaya et al. 2012), suggesting there were 2.5 and 3.8 times more black bears than grizzly bears in BNP and GNP, respectively. These differences have been hypothesized to be due to lower productivity in BNP than GNP (Sawaya et al. 2012), as well as higher rates of human-caused bear mortality in this part of BNP.

METHODS

Field methods

In our GNP study area, Kendall et al. (2009) conducted bear rub surveys during 15 June – 7 Sep, 2004. Identification and preparation of bear rubs, sample collection and storage methods, and data quality control were described in Kendall et al. (2009). Field crews were trained to identify naturally-occurring bear rubs based on physical attributes, including surfaces worn smooth by bear rubbing activity, game trails leading to the rub, and the presence of bear hair samples. No bait or attractant was used with bear rub sampling. We attempted to identify and monitor every bear rub that could be reliably relocated at 14-day intervals, which limited searching for bear rubs on maintained trails and similar travel routes. Bear rub density was variable (Fig. 3-1), although it is reasonable that every bear in the study area had an opportunity to be detected at one or more surveyed rubs during the sampling season.

Protocols for identifying, establishing, and surveying bear rubs in BNP were nearly identical to those in GNP. In BNP, bear rub surveys were conducted during 22 May – 27 October, again with relatively short average interval between surveys ($\bar{x} = 18.5$ day). For both study areas, hair samples collected during the first survey of each bear rub were not included in detection histories as we could not determine when they were deposited (Kendall et al. 2008).

Genetic analyses

For both study areas, we considered all hairs found on a set of barbs to constitute a unique sample, which we stored on a silica drying agent until genetic analyses were performed by Wildlife Genetics International (Nelson, BC, Canada). We attempted to obtain multilocus genotypes for samples with ≥ 1 guard hair follicle or ≥ 5 underfur hairs using 7 microsatellite loci following the protocols of Paetkau (2003) and Kendall et al. (2009). For samples that met

quality thresholds, we determined species, individual identity, and sex, for which we used the amelogenin marker (Pilgrim et al. 2005).

For GNP, average observed heterozygosity was 0.73, with 8.6 alleles per locus on average. Our conservative estimate of multilocus genotyping error rate was <0.001 , with the probability of 2 full-siblings sharing the same genotype ($P_{SIB} < 0.0018$) (Kendall et al. 2009). Details of our GNP sample sizes, marker power, and error rates can be found in Kendall et al. (2009). Observed heterozygosity for BNP was similar (0.77), as was the average number of alleles per locus ($\bar{x} = 7.3$), and P_{SIB} at 0.0007. Exhaustive error checking and an independent suite of 13 microsatellite markers that concurred with initial results suggested that BNP multilocus genotyping error rates were <0.001 as with our GNP results. Unlike GNP, we only genotyped one sample per bear rub per visit, thereby reducing the total number of analyzed samples by half. Based on previous results in BNP and GNP (J. Stetz and M. Sawaya, unpublished data), we believe that no bears were excluded from the analysis, although some detection opportunities may have been missed. The fact that bears often leave hairs on multiple bear rubs within the same sampling occasion suggests that any missed detections would not affect encounter histories used in traditional CR models (Sawaya et al. 2012). As with previous analyses (Kendall et al. 2009; Sawaya et al. 2012; Stetz et al. 2014), hair samples were assigned to the two-week sampling occasion in which they were collected.

Modeling detection probability at bear rubs

We developed suites of *a priori* models to explore the effects that biotic and abiotic factors may have on detection probabilities of grizzly bears at bear rubs. We first developed models containing detection events from both study areas. For these models, we used the sampling occasions in BNP that most closely aligned with sampling in GNP, treating each study area and

sex combination as a unique group in MARK. We then developed independent suites of models for each study area, for which we included all detection events. To allow the use of group, individual, and temporal covariates in understanding variation in detection, we used Huggins closed-population models with random effects (Huggins 1991; Gimenez & Choquet 2010) in program MARK (White et al. 2001). The Huggins model maximizes the conditional likelihood, where the total population abundance, N , is conditioned out of the likelihood. This allows the use of individual covariates to improve estimates of detection and recapture probabilities, with abundance then being a derived parameter (Huggins 1991). The random effects extension models the heterogeneity in detection probabilities at the individual level as an additive effect, which allows using AIC methods (Burnham & Anderson 2001) to compare support for models with and without random effects (Gimenez & Choquet 2010). For all models, we treated sexes as different groups, as previous studies have consistently found differences in detection rates at bear rubs for males and females (e.g., Kendall et al. 2009; Sawaya et al. 2012).

Our primary hypothesis was that density of conspecifics influences rubbing behavior and thereby the number of opportunities to detect individual bears. To test this hypothesis, we used spatially-explicit capture-recapture models (Borchers & Efford 2008) to generate predicted density surfaces for each sex in each study area (Fig. 3-1), which we then included as individual covariates in CR models. Briefly, SECR combines a state model that describes the distribution of home range centers with an observation model that relates the probability of detecting an animal at a given site to the distance of that site from the center of an animal's home range (Borchers & Efford 2008). SECR models estimate the density of animal activity centers, D , in a user-defined area that is large enough that animals residing beyond it have a negligible chance of being detected (Borchers & Efford 2008). We therefore used the buffer size suggested by

functions in the *secr* package in R (Efford 2011) for male grizzly bears to define the state space for each study area (GNP=18km; BNP=29km). By treating the distribution of home range centers as an inhomogeneous Poisson process and maximizing the full likelihood, SECR methods can relate variation in environmental conditions to variation in density through the use of spatial covariates as (Efford & Fewster 2013; Royle et al. 2013). We considered combinations and interactions of several environmental factors, including elevation, net primary productivity as measured by the enhanced vegetation index (EVI; Huete et al. 2002), and sympatric species density, to explain variation in density patterns. We assessed model support based on AICc (Burnham & Anderson 2001), and used model averaging when creating density surfaces.

In addition to modeling density, the observation sub-model of SECR models the process of detecting animals by explicitly considering animal movements in relation to the characteristics and distribution of detectors. Two parameters comprise the observation submodel: g_0 is the probability of detecting a given animal at its activity center, and sigma (σ) is the spatial scale parameter describing how detection probability declines with increasing distance between the activity center and each detector. For all SECR models, we used a binomial observation model with a halfnormal detection function to relate the probability of detection to distance from the predicted home range center, which is unobserved and assumed stationary. We modeled each sampling methods (e.g., hair trap, crossing structure) as a different type of proximity detectors (Efford et al. 2004), and used non-binary usage coding to directly account for variation in sampling effort (Efford et al. 2013; Stetz et al. 2014). As with density, we modeled the observation process separately for each species, sex, and season, and considered time (t) effects on detection.

The detection process can also be modeled using spatial covariates, including those that change over time, to relate variation in detection to landscape features. To improve overall model performance, we therefore included biotic and abiotic covariates that we hypothesized could explain detection of grizzly and black bears. Beyond potentially improving model fit, the use of covariates relaxes the assumption of circular home ranges (Royle et al. 2013), although simulations suggest that SECR models are robust to such violations even without the use of covariates (Stenhouse et al. 2015).

For our SECR analyses, we included detection data from intensive hair trapping efforts in both GNP and BNP that were conducted concurrently with bear rub surveys. In GNP, 550 hair traps yielded an additional 209 detections of 147 females, and 145 detections of 101 males (Kendall et al. 2009; Stetz 2016). In BNP, 210 hair traps yielded an additional 65 detections of 38 females, and 34 detections of 19 males. We also included detections of bears at 20 wildlife crossing structures in BNP (Sawaya et al. 2012), which yielded 15 detections of 5 females and 28 detections of 4 males.

We also hypothesized that density of black bears may influence grizzly bear detection rates at bear rubs, as these species have very similar life histories (Aune 1994; Mattson et al. 2005), and are known to use the same bear rubs throughout both study areas (Sawaya et al. 2012; Stetz et al. 2014). We therefore developed independent suites of SECR models for both GNP and BNP to create sex-specific predicted density surfaces of black bears. As with predicted densities of grizzly bears, we calculated the average density of black bears in each grizzly bear idealized home range, as described below. We used these values as well as total bear densities as individual-level covariates in MARK models. Additional details of SECR methods and results can be found in Stetz (2016) and Appendix B.

To create individual covariates, we first plotted the predicted home range center of each bear from our top SECR models in ArcGIS (v.10.2; ESRI). For each study area, we then estimated the home range radius based on the spatial scale parameter, σ , following Noss et al. (2012; Fig. 3-1) separately for each sex, as home ranges of male bears are typical several times larger than those of females (Aune 1994; Bjornlie et al. 2014). Assuming a bivariate normal distribution, these home range radii are expected to include 95% of animal locations, although they may overestimate movements in the presence of sparse detection data (Noss et al. 2012). We then buffered each home range center by the appropriate home range radius to create an idealized home range (Stetz et al. 2014), within which we calculated the average density of male, female, and total grizzly bears, black bears, and both species combined.

To test our hypotheses related to how landscape factors may influence grizzly bear detection at bear rubs, we first considered the relative topographic position of Jenness (2002) as a measure of terrain roughness, which we derived from a 250m digital elevation model. For landcover type, we classified each 500m pixel as consisting of one of six landcover classes that have been found to potentially influence bear space use and density: forest, shrublands, grasslands, permanent wetlands, urban, and croplands (Waller & Mace 1997; Apps et al. 2016). In GNP, we used 2004 MODIS 500m datasets (Nemani & Running 1997; Pettorelli et al. 2014) to classify landcover, whereas we used the North American Land Change Monitoring System (Latifovic et al. 2012) in our BNP study area due to classification issues with MODIS data during our study. For habitat security, we defined areas within national or provincial parks as having the highest security, other public and tribal lands as medium security, and private lands as the lowest security (Mace et al. 1996). For each of these factors, we again used the average values within each idealized home range as individual covariates for CR models.

Previous studies have found that detection probabilities of grizzlies at bear rubs can be partially explained by variation in sampling effort (Kendall et al. 2008, 2009), although sampling effort was used as a strictly temporal covariate that assumed equal effects on both sexes and over time. To improve on this, Stetz et al. (2014) developed an individual-level covariate that quantified effort using an idealized home range based on each bear's average capture location buffered by the sex-specific mean-maximum distance moved (Dice & Clark 1953). We modified this approach to use the idealized home range derived from SECR models, within which we summed the number of days that all bear rubs surveyed in each 14-day sampling occasion were available to collect hair (BRE; Tables 3-1 and 3-2). Finally, the extent that an animal's home range extends beyond the sampled area likely effects its detection probability, as has been found in several studies (Boulianger & McLellan 2001; Kendall et al. 2009; Stetz et al. 2014). We therefore calculated the distance from the predicted center of each bear's home range to the edge of the sampled area (DTE) as a covariate in CR models.

RESULTS

Hair collection and genetic analyses

A total of 5,046 visits to 1,366 bear rubs were conducted in our GNP study area during 15 June-15 September, 2004, from which 3,517 putative bear hair samples were collected (Table 3-1). Multilocus genotypes were obtained for 903 samples (25.6%), from which 144 unique bears were identified (83 M, 61 F). Males were detected more often than females, with 326 and 98 total detection events, respectively. For CR analyses, we collapsed detections to one per individual per sampling occasion, resulting in 169 and 76 detections for males and females, respectively. In GNP we also detected 294 male and 303 female black bears a total of 468 and

307 times, respectively, at hair traps and bear rubs. In BNP, we detected 25 male and 44 female black bears a total of 65 and 88 times, respectively, across our three sampling methods.

In our BNP study area, 2,822 surveys of 485 bear rubs were conducted during 22 May - 27 October, 2008 (Table 3-2). Surveys yielded 2,430 hair samples, 398 (16.4%) of which produced multilocus genotypes of 68 grizzly bears (44M, 24 F) total. As in GNP, males were detected more often than females, with 266 and 81 detections, respectively. These resulted in 124 and 60 detection events of male and female grizzly bears, respectively, for CR analyses. During sampling occasions 2-7, which correspond to bear rub surveys in GNP, 1,760 visits to 455 bear rubs were conducted in BNP, from which 1,660 hair samples were collected. From these, 37 and 19 male and female bears were detected a total of 172 and 48 times, respectively. These resulted in 81 and 29 detection events of males and females, respectively, for use in the joint study area analysis models.

Modeling detection at bear rubs

Results of our joint analysis suggested that the most important factors in explaining detection probabilities at bear rubs were the amount of sampling effort in each bear's idealized home range, bear density, terrain complexity, and proportion of home range in areas of high security (Table 3-4). Consistent with previous studies, sampling effort was the most supported explanatory covariate, with greater effort resulting in higher detection probabilities for both sexes and study areas ($\beta=0.79$, $SE=0.10$; Table 3-5). Male bears had higher detection probabilities than females in both study areas through early August, beyond which female detection was equal to or greater than males, particularly in BNP (Fig. 3-3). Surprisingly, there was no support for modeling GNP and BNP as different groups, with the top model that included a group effect having $\Delta AICc = 14.6$.

Consistent with our predictions, detection probabilities showed a negative relationship with total bear density ($\beta = -0.10$, $SE = 0.017$; Fig. 3-4). Models including total grizzly bear density, female or male grizzly bear density, or total bear density had nearly equal support. Models with just black bear density had little support (i.e., $\Delta AICc > 4$) in the joint analysis. Contrary to predictions, bears with home ranges consisting of greater terrain complexity and higher habitat security had lower detection probabilities ($\beta_{\text{terrain}} = -0.40$, $SE = 0.14$; $\beta_{\text{security}} = -0.20$, $SE = 0.16$; Table 3-5). We found little support for effects of distance to edge or landcover type on detection, which were also inconsistent with our predictions.

Results from the individual study area models were broadly similar to the joint analysis, with detection probabilities varying by time and sex, increasing with greater sampling effort, and decreasing in areas of higher bear density (Table 3-6). Conversely, there was greater support for the distance to edge covariate in the individual study areas than in the joint analysis. The effect, however, differed between the areas, with detection probabilities in GNP being slightly higher for bears with activity centers closer to the edge of the study area ($\beta_{\text{DTE}} = -0.03$, $SE = 0.01$). In GNP there was also support for a negative relationship between detection probability and the proportion of bears' idealized home ranges that consisted of high security areas ($\beta_{\text{high}} = -0.67$, $SE = 0.31$). Finally, there was strong support for a negative relationship between total bear density and grizzly bear detection probability at bear rubs in GNP, particularly for females ($\beta_{\text{female}} = -0.40$, $SE = 0.22$; $\beta_{\text{male}} = -0.17$, $SE = 0.12$).

Unlike the other model sets, there was support for including random effects on detection probability in the BNP models (Table 3-6). In addition to sampling effort and distance to edge ($\beta = 0.68$, $SE = 0.15$), all supported models in BNP included a negative relationship between detection and total black bear density, with similar values for males and females ($\beta_{\text{female}} = -0.37$,

SE=0.33; $\beta_{\text{male}} = -0.37$, SE=0.20). There was also support for negative relationships between detection probability and the proportion of forest cover ($\beta = -0.24$, SE=0.17) and terrain complexity ($\beta = -0.09$, SE=0.20), although effects were not conclusive.

DISCUSSION

Our results suggest that grizzly bear detection probabilities may be influenced by factors not previously considered in CR studies using bear rub detection data, including bear density, terrain complexity, and habitat security at the level of individual home ranges. Our results also found that, consistent with numerous bear NGS studies, detection varied by sex and over time, with sampling effort being the most important explanatory factor. We found these results to be generally consistent for our two study areas, despite the GNP study area having approximately 2.5 and 4 times higher densities of grizzly and black bears, respectively, than BNP.

Our joint study area analysis approach allowed us to consider a larger range of conditions that individual bears were exposed to than study area-specific analyses, as well as increasing sample size (Boulanger et al. 2002). Despite the differences between these populations, there was no support for treating them as distinct groups. This is likely explained by our individual-level sampling effort covariate that has seen strong support in our models, as well as previous studies (Stetz et al. 2010; Sawaya et al. 2012). We believe that treating sampling effort as either a temporal covariate (e.g., Kendall et al. 2016) or a group effect based on sampling intensity (i.e., hair trap cell size; Boulanger et al. 2002) does not capture the heterogeneity of exposure to sampling sites as effectively as our individual-based approach. We recognize that it is impossible to determine each bear's true encounter rate with bear rubs, even with the use of GPS collars and remote cameras at each site. Our approach does, however, directly link known sampling effort in space and time with our best prediction of each animal's home range. Given

the ability of grizzly bears to move large distances in short time periods, it is reasonable that every bear rub assigned to a given bear's idealized home range was, in fact, available to detect that bear in ≥ 1 occasion.

Consistent with our predictions, we found a negative relationship between bear density and grizzly bear detection probability at bear rubs. One plausible explanation for this could be the larger home ranges of bears in lower density areas like our BNP study area resulting in bears encountering more bear rubs and thereby increasing detection rates (Table 3-7; McLoughlin et al. 2003; Bjornlie et al. 2014). Our sampling effort covariate, however, which is a function of home range size, should have controlled for this effect. Given the large numbers of bear rubs monitored in both study areas, it is also unlikely that lower detection rates were a function of missed detections, particularly in GNP where we analyzed every hair sample that met our quality threshold (i.e., ≥ 1 guard hair or 5 under-fur hairs; Kendall et al. 2009). Further, we found considerably higher detection probabilities in BNP (Fig. 3-3), where we analyzed 1 sample per bear rub visit. If subsampling resulted in a large number of missed detections, we would expect the opposite pattern. We hypothesize that grizzly bear rubbing behavior is somehow intrinsically related to bear density or the associated changes in home range size. This appears to be particularly important for female grizzly bears in BNP, which had twice the average detection probability ($\hat{p}_{\text{BNP}}=0.11$, $\text{SE}=0.06$; $\hat{p}_{\text{GNP}}=0.05$, $\text{SE}=0.02$) and twice as many rubs in their idealized home range on average compared to GNP bears ($\bar{x}_{\text{BNP}}=56.2$, $\text{SD}=22.1$; $\bar{x}_{\text{GNP}}=28.5$, $\text{SD}=18.1$; Table 3-7).

Several results from our joint analysis were contrary to predictions, including lower detection probabilities for grizzly bears with home ranges containing less terrain complexity and forest cover, both of which we hypothesized to be related to movement rates. Whereas we

hypothesized that greater terrain complexity may lead bears to use maintained travel routes and thereby encounter more bear rubs, it may be that movement was less constrained in flatter areas, resulting in higher encounter rates. The limited support for a relationship between forest cover and detection probabilities may be related to less variation in home range composition for bears in GNP than BNP. Also contrary to predictions, we found lower detection probabilities in areas of higher habitat security. We suggest that this could be confounded by the fact that the highest densities of bears, namely in the heart of GNP, had the largest proportion of their home ranges in high security areas (Fig. 3-1).

In contrast to previous bear NGS studies (e.g., Boulanger and McLellan 2001; Stetz et al. 2014), our analysis found little support for detection probability being influenced by the distance from a bear's home range center to the edge of sampling. Further, the relationship was negative, suggesting that bears residing closer to the edge of a study area had higher detection probabilities, which is contrary to the predicted effect (Boulanger and McLellan 2001). We suggest that this effect, too, may be confounded with habitat security, as bears living near the edge of the study area had a greater proportion of their home range in medium security areas, which tended to have lower bear densities and thus higher detection probabilities.

Other than sampling effort being the most supported explanatory factor in predicting grizzly bear detection probabilities in both GNP and BNP study areas (Table 3-6), we observed several differences both between the joint analysis and between the individual study areas. Distance to edge was strongly supported for both GNP and BNP individually, although the relationships were different for each study area. Consistent with predictions, there was a strong positive relationship between distance to edge and detection probability for bears in BNP. As with the joint analysis, however, this relationship was negative for bears in GNP. As

hypothesized above, this may be confounded with the lower densities of bears toward the edge of the study relative to within the borders of GNP. This is also consistent with lower detection rates for bears residing in lower security areas, which, again, coincide with areas of lower bear densities. Support for a negative relationship between total predicted bear density and detection probabilities was also strongly supported for the GNP study area. In the BNP study area, however, total black bear density was negatively related to detection probability, with limited support for an effect of total bear density ($\Delta AIC_c=2.55$). We suspect that this was largely driven by several grizzly bears that we detected a single time that had home ranges centered on areas with the highest predicted black bear density in the study area.

That we found partially contradictory results is not uncommon in noninvasive CR studies of bears. For example, camera trapping studies in Minnesota found that adult males were among the least likely to be detected (Noyce et al. 2001), whereas they were the most likely to be detected in Montana (Mace et al. 1994). Although these differences could be due to the timing of the studies, Noyce et al. (2001) determined that individual differences between bears not related to age, sex, or other measurable factors was responsible for the observed heterogeneity in detection, consistent with conclusions from a mark-resight study of grizzly bears in Alaska (Miller et al. 1997).

As the dominant method for bear NGS studies, there has been considerably greater effort to explain variation in detection with hair trap sampling than with bear rubs. For example, several studies have found that the closest distance of a bear to a hair trap is predictive of detection rates, although this, too, can vary influenced by quality of lure, precipitation, wind patterns, and other individual biases (Boulanger et al. 2004; Sollman et al. 2009; Wilton et al. 2016). These studies typically recommend increasing trap density to improve detection rates,

however, doing so can quickly become cost prohibitive (Kendall et al. 2009). The emphasis of trap density and configuration (e.g., Sun et al. 2014) also ignores a fundamental component of hair trap studies, namely that site placement is ultimately based on human perceptions of ideal locations to detect bears. Poor site selection, lure quality, or trap construction may lead to failing to attract bears, or to capture hair when a bear does visit a site (Ebert et al. 2010), all of which may exacerbate heterogeneity in detection rates and are essentially impossible to model.

Multiple hair trapping studies have also found lower detection probabilities for grizzly bears that had been previously live captured, suggesting an avoidance response to baited sites (e.g., Boulanger et al. 2004; Kendall et al. 2009). The opposite effect was observed by Boulanger et al. (2002), however, with collared bears having higher detection rates than non-collared bears, although this may have been related to differences between the exposure of resident and transient bears to hair traps. Study design has also been implicated in introducing bias in detection across sexes (Boulanger et al. 2004), despite this effect being observed in most bear NGS studies (but see Boulanger and McLellan 2001).

Unmodeled heterogeneity in detection probabilities can lead to strong bias in population estimates and their associated estimates of variance (Pollock et al. 1990; Cubaynes et al. 2010; Gimenez & Choquet 2010), and remains a persistent challenge in CR analyses. Causes of heterogeneity can be related to differences in the opportunity to detect individuals, which can be a function of animal movement rates, geographic and demographic closure, and intensity of sampling. Further, inherent differences between individuals related to age, sex, or previous experiences (e.g., live capture), among others, can also induce heterogeneity into the detection process (Pollock et al. 1990). As individual heterogeneity is expected to exist to some degree in nearly all NGS studies (Lukacs & Burnham 2005; Boulanger et al. 2008), a better understanding

of the relationships between a species' behavior and population sampling methods is essential for reliable and efficient sampling design (Sollmann et al. 2012).

Particularly when used in conjunction with other sampling methods (Pollock et al. 1990; Boulanger et al. 2008), bear rub detection data provide a valuable tool to improve the accuracy and precision of population estimates useful in managing bear populations. As with any sampling method, however, potential biases exist with bear rub detection data, the most commonly cited being that males are detected at higher rates than females (e.g., Kendall et al. 2008, 2009; Morehouse and Boyce 2016). Although sampling in late summer and fall alleviates much of this bias, recognizing such issues and designing studies to minimize their effects is critical to obtaining reliable insights into population status and trends. Further, any given sampling method may not be appropriate for every research objective, and bear rubs are no exception. For example, Boulanger et al. (2008) found that abundance estimates for female grizzly bears using bear rub data alone were significantly lower and less precise than estimates from joint hair trap-bear rub data. And although SECR methods show great promise in improving density estimates using NGS data, we are not aware of any published SECR analyses using bear rub-only data. We suggest that such a comparison would be valuable given the interest in using bear rubs to monitor grizzly and black bear populations (Stetz et al. 2010; Morgan Henderson et al. 2015; Morehouse & Boyce 2016).

Our results provide insights into the potential underlying mechanisms causing heterogeneity in detection probabilities of grizzly bears at bear rubs, and should be useful in improving future study designs. We suggest that bear rub surveys should avoid, or at least be less sensitive to, some of the factors thought to induce detection heterogeneity in hair trap sampling. Passive sampling methods such as those based on bear rubbing behavior should not be

influenced by history of previous capture, behavioral responses to sites that do, or do not, provide a food reward, or unpredictable weather events (Ebert et al. 2010). Further, unlike with hair trap, remote camera, or live trap placement, bear rubs offer a powerful advantage by providing direct evidence of bear use of a site. Bear use of bear rubs occurs with or without human influence, and we know of no evidence of bears changing their rubbing behavior based on human presence or sample collection. Further, the efficiency of establishing and repeatedly surveying large numbers of bear rubs across large areas is a major strength when considering that CR models that account for detection heterogeneity require large sample sizes (Skalski et al. 2005; Boulanger et al. 2004; Ebert et al. 2010).

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TABLES

Table 3-1. Results from bear rub surveys in our Glacier National Park, MT, study area. We conducted surveys between 15 June - 15 September, 2004.

Occasion	No. bear rubs ¹	Bear rub effort ²	No. samples	No. grizzly bear samples ³	No. unique bears	
					M	F
1	176	5433	410	91	18	0
2	788	12406	765	227	35	7
3	767	13499	568	132	37	12
4	704	17325	556	133	28	14
5	1155	26904	688	165	33	25
6	1177	19915	530	86	18	18
Total	1366	95482	3517	834	83	61

¹ The total number of bear rubs includes all bear rubs surveyed at least once.

² Bear rub effort is the sum number of days that all bear rubs surveyed in a given occasion were available to collect hair.

³ The number of grizzly bear samples includes only those samples with accepted multilocus genotypes.

Table 3-2. Results from bear rub surveys in our Banff National Park, AB, study area. We conducted surveys between 22 May - 27 October, 2008. Shaded cells represent sampling occasions that correspond with sampling in our Glacier National Park study area (Table 3-1).

Occasion	No. bear rubs ¹	Bear rub effort ²	No. samples	No. grizzly bear samples ³	No. unique bears	
					M	F
1	48	3043	197	48	14	0
2	172	3156	347	52	12	0
3	229	4529	304	52	15	1
4	308	5614	230	34	17	5
5	270	5302	221	25	10	5
6	319	6290	254	39	10	7
7	372	8066	304	55	15	11
8	308	6483	252	34	10	7
9	282	5986	168	25	8	7
10	269	5585	101	17	6	3
11	73	2073	52	17	6	4
Total	497	56127	2430	398	44	24

¹ The total number of bear rubs includes all bear rubs surveyed at least once.

² Bear rub effort is the sum number of days that all bear rubs surveyed in a given occasion were available to collect hair.

³ The number of grizzly bear samples includes only those samples with accepted multilocus genotypes.

Table 3-3. Distribution of the combined number of detections of individual grizzly bears (*Ursus arctos*) and American black bears (*U. americanus*) by sex at all sampling sites in our Glacier and Banff National Park study areas. Also shown is the observed and expected number of individual bears detected for the most supported model. The expected number was calculated as $E(n) = \int p.(X)D(X)dX$, with $p.(X)$ is the probability a given individual was detected at least once and $D(X)$ is the expected density at X for the most supported model.

Study area	Species	Sex	Distribution of number of detections					Total	No. individuals	
			1	2	3	4	≥ 5		Observed	Expected
Glacier	Grizzly	F	90	44	22	9	5	307	170	169.99
		M	52	34	18	7	28	468	139	138.99
	Black	F	223	57	9	8	6	430	303	302.92
		M	181	73	29	7	5	494	295	294.99
Banff	Grizzly	F	6	2	2	3	14	149	27	26.99
		M	11	6	4	1	23	315	45	45.06
	Black	F	24	10	3	3	4	88	44	43.99
		M	9	9	1	4	2	65	25	24.82

Table 3-4. Model selection results for explaining grizzly bear detection probabilities at bear rubs from Huggins (1991) models in program MARK. Sampling occurred during 15 June - 15 September, 2004, in Glacier National Park, and 6 June – 3 September, 2008, in Banff National Park. Sigma=random effect of individual heterogeneity on detection probability, with sigma(-) indicating no random effect was included, and sigma(.) including a random effect; *t* = detection allowed to vary by time; rtp = relative topographic position; bre = bear rub sampling effort; high/med = index of habitat security; forest/grass/shrub = proportion of home range assigned to that landcover type; gb = grizzly bear; bb = black bear.

Model ^a	Deviance	Num. Par	ΔAIC _c	AIC _c Weight	Model Likelihood
sigma(-), (sex*t)+bre+rtp+high	1155.53	14	0.00	0.12	1.00
sigma(-), (sex*t)+bre+rtp+total gb density	1156.42	14	0.89	0.08	0.64
sigma(-), (sex*t)+bre+rtp+female gb density	1156.49	14	0.95	0.08	0.62
sigma(-), (sex*t)+bre+rtp+med+total bear density	1154.61	15	1.13	0.07	0.57
sigma(-), (sex*t)+bre+rtp+total bear density	1156.84	14	1.31	0.06	0.52
sigma(-), (sex*t)+bre+rtp+male gb density	1156.84	14	1.31	0.06	0.52
sigma(-), (sex*t)+bre+rtp+forest	1156.97	14	1.43	0.06	0.49
sigma(-), (sex*t)+bre+dte+rtp	1156.98	14	1.45	0.06	0.48
sigma(-), (sex*t)+bre+rtp	1157.02	14	1.48	0.06	0.48
sigma(-), (sex*t)+bre+rtp+high+total bear density	1155.13	15	1.65	0.05	0.44
sigma(-), (sex*t)+bre+rtp+high+total gb density	1155.19	15	1.71	0.05	0.43
sigma(-), (sex*t)+bre+rtp+high+male gb density	1155.47	15	1.99	0.05	0.37
sigma(-), (sex*t)+bre+rtp+med	1158.31	14	2.78	0.03	0.25
sigma(.), (sex*t)+bre+rtp+total gb density	1156.42	15	2.94	0.03	0.23

sigma(-), (sex*t)+bre+rtp+grass	1159.54	14	4.00	0.02	0.14
sigma(.), (sex*t)+(female+total bb density, male+total bear density)+bre	1161.66	13	4.08	0.02	0.13
sigma(-), (sex*t)+bre+rtp+shrub	1159.72	14	4.19	0.02	0.12
sigma(-), (sex*t)+(female+total bb density, male+total bear density)+bre+rtp	1157.84	15	4.35	0.01	0.11
sigma(.), (sex*t)+(female*t*male gb density, male+total bear density)+bre+rtp	1149.88	19	4.64	0.01	0.10
sigma(-), (sex*t)+bre+total gb density	1162.42	13	4.84	0.01	0.09

Table 3-5. Model averaged parameter estimates and associated cumulative AIC_c weights from Huggins (1991) models to explain detection probabilities of grizzly bears using detection data from our Glacier and Banff National Parks study areas. Results are from models in Table 3-4 with $\Delta AIC_c \leq 2$.

Parameter	Cum.		SE	95% CI	
	AIC _c wt	β		LCL	UCL
Bear rub effort	0.80	0.79	0.10	0.59	0.99
Relative topographic position	0.80	-0.40	0.14	-0.67	-0.12
High security	0.27	-0.20	0.16	-0.52	0.12
Total bear density	0.19	-0.10	0.17	-0.43	0.23
Total grizzly bear density	0.13	-0.11	0.16	-0.43	0.21
Male grizzly bear density	0.11	-0.05	0.17	-0.38	0.27
Female grizzly bear density	0.08	-0.12	0.16	-0.43	0.20
Medium security	0.08	0.25	0.16	-0.07	0.57
Distance to edge	0.06	-0.03	0.16	-0.34	0.28
Forest cover	0.06	-0.04	0.16	-0.36	0.29

Table 3-6. Results for the most supported models of grizzly bear detections at bear rubs from Huggins (1991) models in program MARK. Sampling occurred during 15 June - 15 September, 2004, in our Glacier National Park study area and during 22 May - 27 October, 2008, in Banff National Park.

	Model ^a	Deviance	Num. Par	ΔAIC_c	AIC _c Weight	Model Likelihood
Banff	sigma(.) (sex*t)+bre+dte+total bb density	658.21	24	0.00	0.17	1.00
	sigma(.) (sex*t)+bre+dte+forest+total bb density	656.23	25	0.17	0.16	0.92
	sigma(.) (sex*t)+bre+dte+rtp+total bb density	656.77	25	0.70	0.12	0.70
	sigma(.) (sex*t)+bre+dte+(sex*total bb density)	658.21	25	2.14	0.06	0.34
	sigma(.) (sex*t)+bre+dte+forest	660.45	24	2.25	0.06	0.33
Glacier	sigma(-), (sex*t)+bre+dte+low+total bear density	803.64	15	0.00	0.25	1.00
	sigma(-), (sex*t)+bre+dte+low+rtp+total bear density	803.23	16	1.67	0.11	0.43
	sigma(-), (sex*t)+bre+dte+low+(sex*total bear density)	803.41	16	1.84	0.10	0.40
	sigma(-), (sex*t)+bre+low+total bear density	807.63	14	1.92	0.10	0.38
	sigma(-), (sex*t)+bre+med+total bear density	808.88	14	3.16	0.05	0.21
	sigma(-), (sex*t)+bre+dte+low+rtp+(sex*total bear density)	803.00	17	3.51	0.04	0.17

Table 3-7. Estimated per-occasion detection probability, \hat{p} , from the most supported models of grizzly bear (*Ursus arctos*) detections at bear rubs from Huggins (1991) models in program MARK for Glacier and Banff National Parks. Also shown are the estimated spatial scale parameter, σ , from the most supported spatially-explicit capture-recapture models, estimated home range sizes derived from σ using the equation from Noss et al. (2012), and the number of bear rubs per idealized home range by sex and study area. Sampling occurred during 15 June - 15 September, 2004, in our Glacier National Park study area and during 22 May - 27 October, 2008, in Banff National Park

Study area	Sex	Avg. \hat{p} (SE)	σ (SE)	Home range		No. rubs per idealized home range			
				Estimate	95% CI	min	max	avg	SD
Glacier	F	0.05 (0.02)	4196 (190)	331	278-396	0	92	28.50	18.05
	M	0.13 (0.04)	5330 (157)	535	476-600	0	255	95.89	52.63
Banff	F	0.11 (0.06)	3173 (303)	189	125-267	10	95	56.15	22.12
	M	0.18 (0.6)	8189 (372)	1262	1057-1508	10	197	80.57	47.71

FIGURES

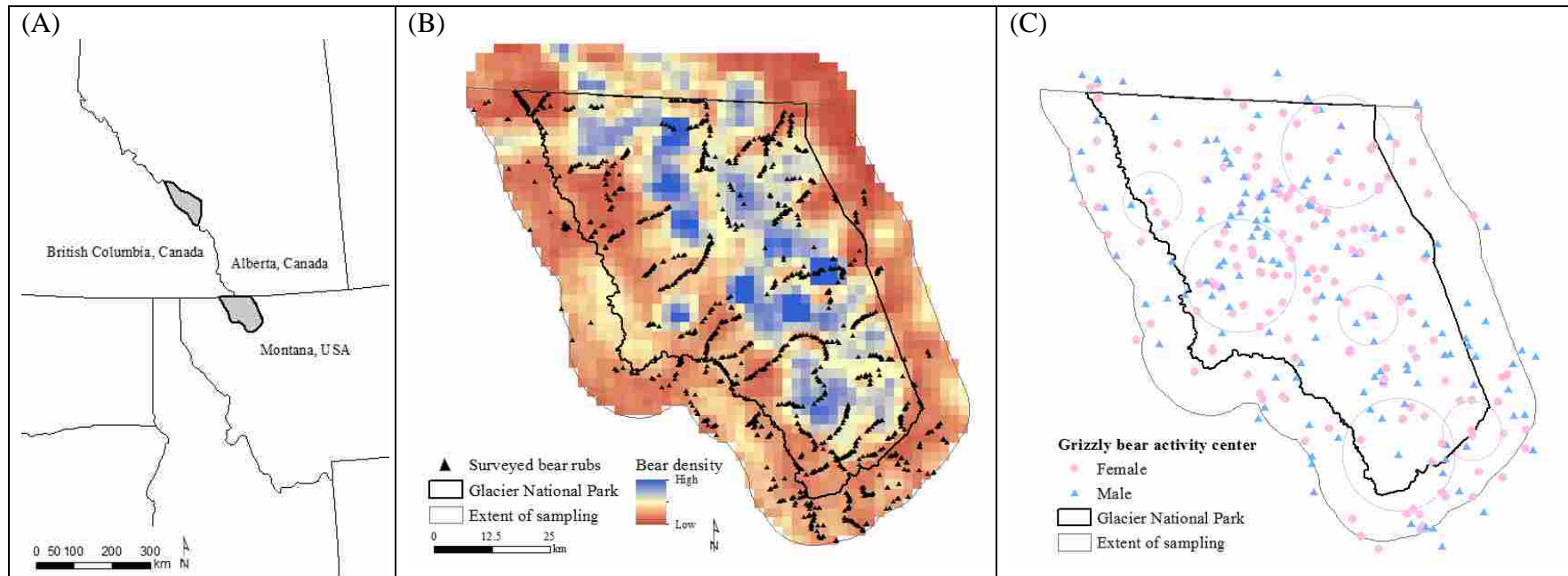


Figure 3-1. (A) Location of our Banff National Park and Glacier National Park (GNP) study areas. (B) Locations of bear rubs surveyed during June-September, 2004, in our GNP study area with an example of a predicted density surface from spatially-explicit capture-recapture (SECR) models. (C) Predicted activity centers from SECR models for all grizzly bears used in our analyses. For visual clarity, we show the idealized home ranges of six bears. We defined home ranges by buffering each activity center by the sex-specific home range radius calculated in R as $(qchisq(0.95,2)^{0.5}) \times (\text{sigma})$ (Noss et al. 2012), where sigma was the spatial scale parameter from the most supported SECR models.

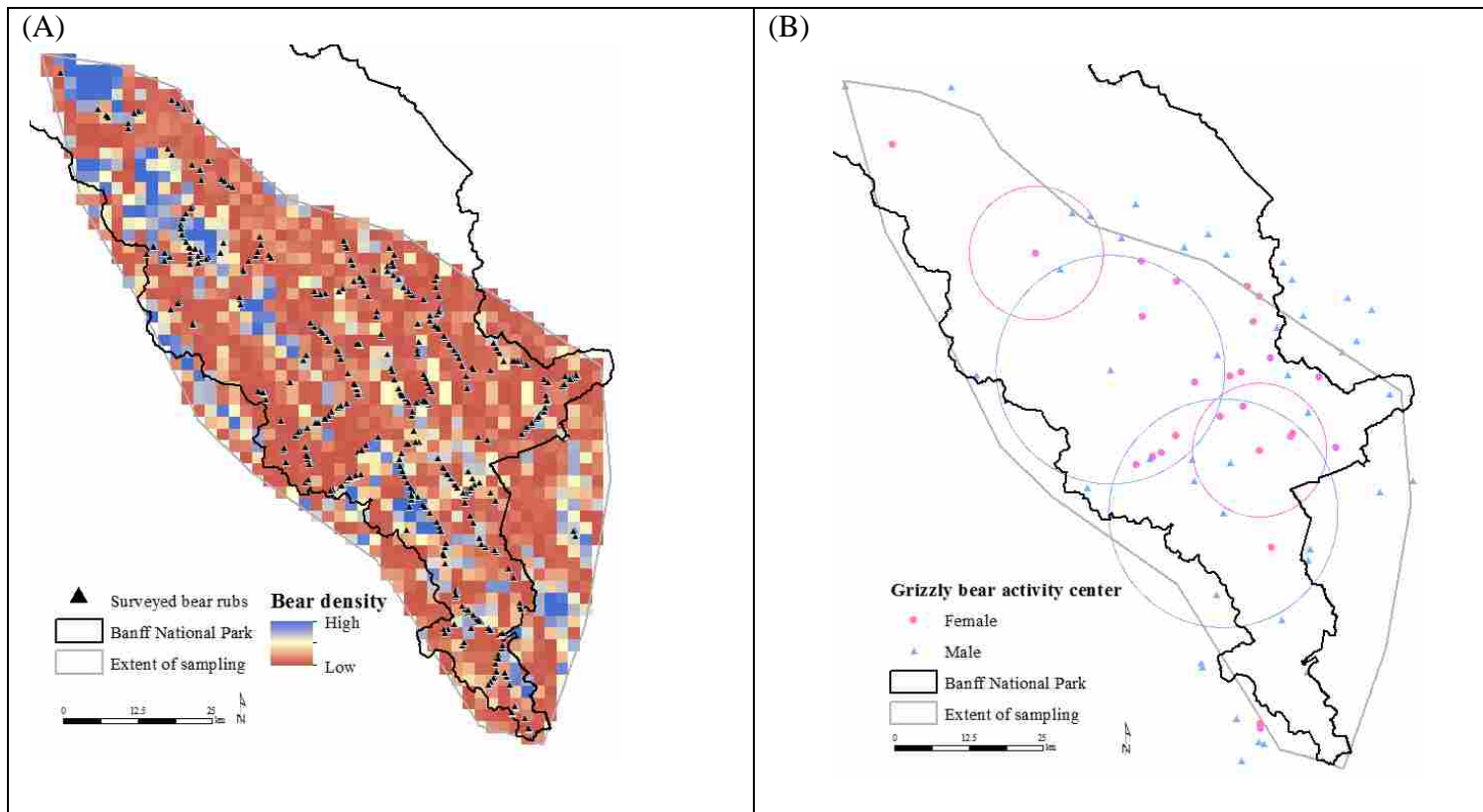


Figure 3-2. (A) Locations of bear rubs surveyed during May-October, 2008, in our Banff National Park study area with an example of a predicted density surface from spatially-explicit capture-recapture (SECR) models. (B) Predicted activity centers for grizzly bears from SECR models. The idealized home ranges for four bears are also shown.

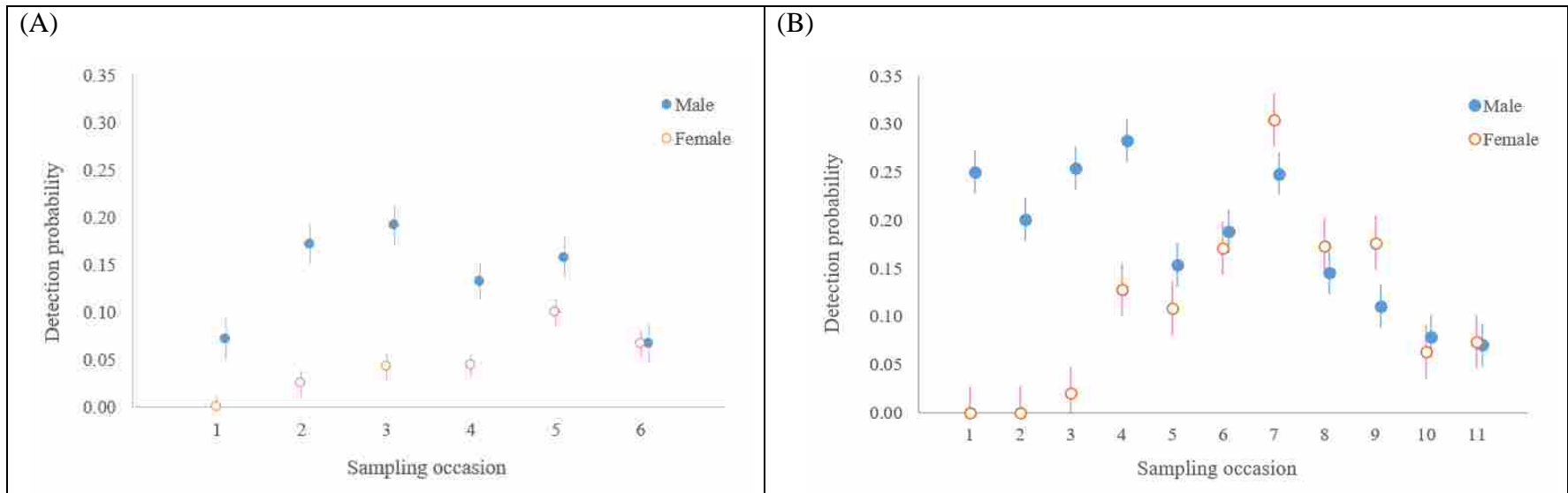


Figure 3-3. Estimated detection probabilities for male and female grizzly bears in our (A) Glacier National Park (GNP) and (B) Banff National Park (BNP) study areas. Sampling occasions lasted 14 days each during 15 June - 15 September, 2004, in GNP, and 22 May - 27 October, 2008, in BNP. Estimates and standard errors (bars) are from model-averaged Huggins (1991) models in program MARK

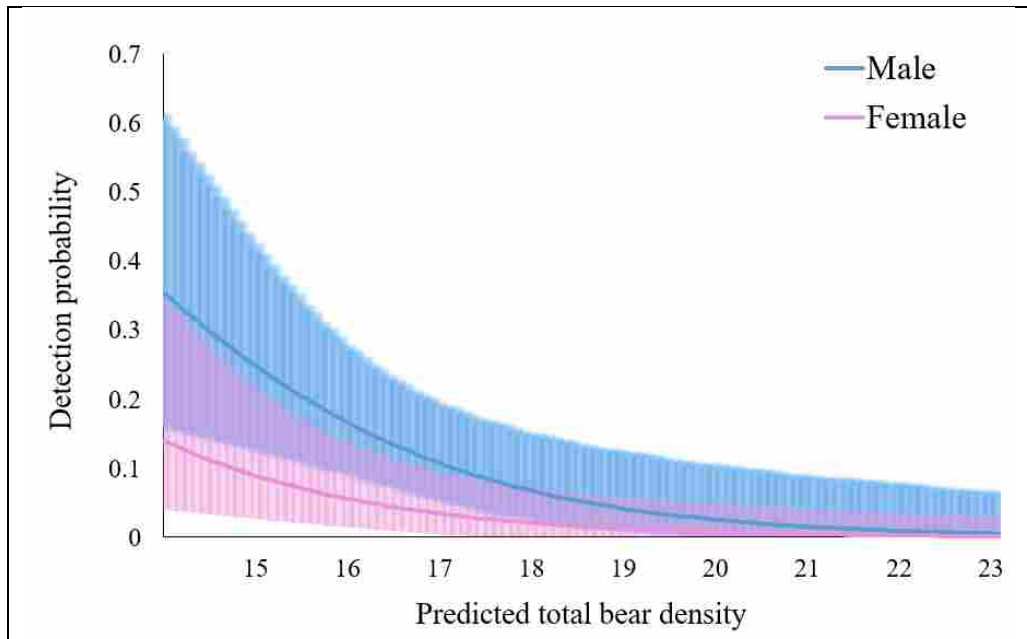


Figure 3-4. Individual covariate plot showing relationship of predicted total bear density on capture probabilities of male and female grizzly bears from joint Glacier and Banff National Park study areas. Results are from the most supported Huggins model for the fourth sampling occasion. Shaded areas are 95% confidence intervals

APPENDIX B. SUPPLEMENTAL MATERIALS

Table 3-S1. Complete model selection results for grizzly bear (*Ursus arctos*) detections at bear rubs from Huggins (1991) models in program MARK. Sampling occurred during 15 June - 15 September, 2004, in our Glacier National Park, USA, study area.

Model ^a	Deviance	Num. Par	Δ AICc	AICc Wts	Model Likelihood
sigma(-), (sex*t)+low+bre+dte+total bear density	803.64	15	0.00	0.25	1.00
sigma(-), (sex*t)+low+bre+rtp+dte+total bear density	803.23	16	1.67	0.11	0.43
sigma(-), (sex*t)+(sex* total bear density)+low+bre+dte	803.41	16	1.84	0.10	0.40
sigma(-), (sex*t)+low+bre+total bear density	807.63	14	1.92	0.10	0.38
sigma(-), (sex*t)+med+bre+total bear density	808.88	14	3.16	0.05	0.21
sigma(-), (sex*t)+(sex* total bear density)+low+bre+rtp+dte	803.00	17	3.51	0.04	0.17
sigma(-), (sex*t)+(sex* total bear density)+low+bre+rtp+dte+forest	803.22	17	3.73	0.04	0.15
sigma(-), (sex*t)+low+bre+rtp+total bear density	807.63	15	3.99	0.03	0.14
sigma(-), (sex*t)+low+bre+dte+total bb density	807.65	15	4.00	0.03	0.13
sigma(-), (sex*t)+high+bre+total bear density	809.78	14	4.07	0.03	0.13
sigma(-), (sex*t)+bre+total bear density	811.92	13	4.14	0.03	0.13
sigma(-), (sex*t)+dte+bre+total bear density	809.97	14	4.25	0.03	0.12
sigma(-), (sex*t)+bre+rtp+dte+total bear density	808.14	15	4.50	0.03	0.11
sigma(-), (sex*t)+forest+bre+total bear density	810.56	14	4.85	0.02	0.09
sigma(-), (sex*t)+bre+total bear density	811.31	14	5.59	0.02	0.06

sigma(-), (sex*t)+rtp+bre+total bear density	811.39	14	5.68	0.01	0.06
sigma(-), (sex*t)+(sex* total bear density)+bre	811.49	14	5.78	0.01	0.06
sigma(-), (sex*t)+shrub+bre+total bear density	811.86	14	6.15	0.01	0.05
sigma(-), (sex*t)+(male+total bear density)+low+bre+rtp+dte	807.74	16	6.17	0.01	0.05
sigma(-), (sex*t)+(male+total bear density)+bre	815.21	13	7.43	0.01	0.02
sigma(-), (sex*t)+(male+male gb density)+bre	815.28	13	7.50	0.01	0.02
sigma(-), (sex*t)+dte+bre	815.47	13	7.69	0.01	0.02
sigma(-), (sex*t)+bre+total gb density	815.52	13	7.74	0.01	0.02
sigma(-), (sex*t)+(male+female gb density)+low+bre+rtp+dte	809.39	16	7.82	0.01	0.02
sigma(-), (sex*t)+low+bre+rtp+dte	811.96	15	8.32	0.00	0.02
sigma(-), (sex*t)+(male+female gb density)+low+bre+rtp+dte	809.97	16	8.40	0.00	0.02
sigma(-), (sex*t)+bre	816.31	13	8.53	0.00	0.01
sigma(-), (sex*t)+dte+bre+total gb density	815.04	14	9.32	0.00	0.01
sigma(-), (sex*t)+bbt+bre	815.24	14	9.52	0.00	0.01
sigma(-), (sex*t)+dte+bre+male gb density	815.47	14	9.76	0.00	0.01
sigma(-), (sex*t)+low+bre+rtp+dte+total gb density	811.38	16	9.82	0.00	0.01
sigma(-), (sex*t)+(male+female gb density+male gb density)+low+bre+rtp+dte	809.38	17	9.89	0.00	0.01
sigma(-), (sex*t)+(male+female gb density, total bear density)+low+bre+rtp+dte	811.79	16	10.22	0.00	0.01
sigma(-), (sex*t)+low+bre+rtp+dte+male gb density	811.96	16	10.39	0.00	0.01

sigma(-), (female+T, male*t)+bre+total bear density	830.85	10	16.90	0.00	0.00
sigma(-), (female+T)+bre total bear density	850.21	5	26.07	0.00	0.00
sigma(-), (sex*T)+bre+total bear density	849.73	6	27.62	0.00	0.00
sigma(-), (sex+t)+bre+total bear density	845.70	9	29.70	0.00	0.00
sigma(-), (sex*t)+total bear density	856.60	12	46.76	0.00	0.00
sigma(-), (sex*t)	861.08	11	49.18	0.00	0.00
sigma(.), (sex*t)	860.18	12	50.33	0.00	0.00
sigma(.), (female+T, male*t)	875.73	9	59.73	0.00	0.00
sigma(.), (sex*T)	895.89	5	71.75	0.00	0.00
sigma(.), (sex+t)	890.32	8	72.28	0.00	0.00
sigma(.), (sex+T)	915.61	4	89.45	0.00	0.00

Table 3-S2. Complete model selection results for grizzly bear (*Ursus arctos*) detections at bear rubs from Huggins (1991) models in program MARK. Sampling occurred during 22 May - 27 October, 2008, in Banff National Park

Model	Deviance	Num. Par	Delta AICc	AICc Wts	Model Likelihood
sigma(.) (sex*t)+bre+dte+total bb density	658.21	24	0.00	0.17	1.00
sigma(.) (sex*t)+bre+dte+total bb density+forest	656.23	25	0.17	0.16	0.92
sigma(.) (sex*t)+bre+dte+total bb density+rtp	656.77	25	0.70	0.12	0.70
sigma(.) (sex*t)+bre+dte+(sex*total bb density)	658.21	25	2.14	0.06	0.34
sigma(.) (sex*t)+bre+dte+forest	660.45	24	2.25	0.06	0.33
sigma(.) (sex*t)+bre+dte+total bear density	660.76	24	2.55	0.05	0.28
sigma(.) (sex*t)+bre+dte	662.99	23	2.65	0.05	0.27
sigma(.) (sex*t)+bre+dte+(sex*rtp)	658.81	25	2.74	0.04	0.25
sigma(.) (sex*t)+bre+dte+forest+total bear density	659.21	25	3.14	0.04	0.21
sigma(.) (sex*t)+bre+dte+med	661.48	24	3.27	0.03	0.19
sigma(.) (sex*t)+bre+dte+high	661.86	24	3.65	0.03	0.16
sigma(.) (sex*t)+bre+high+total bear density	661.93	24	3.72	0.03	0.16
sigma(-) (sex*t)+bre+dte	666.25	22	3.78	0.03	0.15
sigma(.) (sex*t)+bre+dte+med+total bear density	659.90	25	3.83	0.03	0.15
sigma(.) (sex*t)+bre+dte+total gb density	662.59	24	4.39	0.02	0.11
sigma(.) (sex*t)+bre+dte+low	662.79	24	4.58	0.02	0.10

sigma(.) (sex*t)+bre+dte+rtp	662.91	24	4.70	0.02	0.10
sigma(-) (sex*t)+bre+dte+med	665.18	23	4.84	0.02	0.09
sigma(.) (sex*t)+bre+dte+(female+total bb density, male+total bear density)	661.24	25	5.17	0.01	0.08
sigma(.) (sex*t)+bre+dte+(sex*total bear density)	661.79	25	5.72	0.01	0.06
sigma(.) (sex*t)+bre	668.73	22	6.26	0.01	0.04
sigma(.) (sex*t)+bre+dte+(sex*total gb density)	662.59	25	6.52	0.01	0.04
sigma(.) (sex*t)+(sex*bre)	668.50	23	8.15	0.00	0.02
sigma(.) (sex*t)+bre+total bear density	668.71	23	8.37	0.00	0.02
sigma(.) (sex*t)+dte+total bear density	679.06	23	18.72	0.00	0.00
sigma(.) (sex*t)+dte	682.90	22	20.43	0.00	0.00
sigma(.) (sex*t)+(sex*dte)	682.07	23	21.73	0.00	0.00
sigma(.) (sex*t)+dte+total gb density	682.81	23	22.47	0.00	0.00
sigma(.) (sex+t)+bre+dte	703.24	15	26.03	0.00	0.00
sigma(-) (sex*t)	712.08	20	45.37	0.00	0.00
sigma(.) (sex*t)	711.49	21	46.89	0.00	0.00
sigma(-) (sex*t)+total bear density	711.03	22	48.56	0.00	0.00
sigma(.) (sex*T)	751.05	5	53.26	0.00	0.00
sigma(-) (sex+t)	748.84	12	65.40	0.00	0.00
sigma(.) (sex+T)	770.79	4	70.98	0.00	0.00
sigma(.) (sex*t)+bre+male gb density+dte	887.93	1	182.07	0.00	0.00

sigma(.) (sex*t)+(female+male gb density, male+female gb density)+bre+dte	889.43	3	187.59	0.00	0.00
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CHAPTER 4 : POPULATION MONITORING OPTIONS FOR AMERICAN BLACK BEARS IN THE NORTHEASTERN UNITED STATES AND EASTERN CANADA

INTRODUCTION

By the first half of the twentieth century, American black bear (*Ursus americanus*) populations in many areas in North America had substantially declined from historic levels due to excessive killing by humans for their fur, meat, and fat, and to reduce conflicts with humans (Hristienko and McDonald 2007). As awareness of their ecological and cultural value grew, black bears were classified as a game species in most jurisdictions. Consequently, population recovery from overexploitation was an important management goal in the 1960s through early 1990s (Miller 1990). In recent decades, bear populations throughout North America have increased in abundance and distribution as a result of habitat recovery and conservative hunting regulations (Fig. 4-1) (Garshelis and Hristienko 2006, Scheick and McCown 2014). Forty states in the U.S., 12 Canadian provinces and territories (all except Prince Edward Island), and 6 states in northern Mexico have black bear range (Scheick and McCown 2014). In a survey of states and provinces (hereafter, jurisdictions) with black bear populations in both 1988 and 2001, 32 jurisdictions reported population increases during that time period, 10 jurisdictions reported stable populations, and 2 reported declines (Hristienko and McDonald 2007).

Concomitant with increasing and expanding bear populations, human-bear conflicts have increased in 34 jurisdictions (Hristienko and McDonald 2007). Accordingly, black bear management in many portions of North America has gradually shifted from population recovery to enhancing harvest opportunities and reduction of human-bear conflicts (Organ and Ellingwood 2000). This is particularly true for jurisdictions in northeastern North America, where hunting of black bears has been the primary mechanism to pursue population objectives in

a cost-effective manner (Sawaya et al. 2013b). Hunting is a significant source of funding for wildlife conservation and management activities in many northeastern jurisdictions (eastern Canada and the northeastern U.S.). In Pennsylvania for example, residents are required to purchase bear hunting licenses, totaling more than \$2 million in revenue per year. Also, conservation funds are generated in the U.S. from a tax on sporting arms and ammunition (i.e., Federal Aid in Wildlife Restoration Act; 16 U.S.C. 669-669i; 50 Stat. 917). These funds may be applied toward habitat management, land acquisition, conflict reimbursement programs, research, or other activities to foster wildlife management and conservation. Although hunting remains the primary mechanism for bear management in most areas, and is considered the primary management tool in 70% of northeastern jurisdictions (Sawaya et al. 2013b), hunting participation and revenues are declining across most of the region, as across most of North America (U.S. Census Bureau 2006). Increasing and expanding black bear populations across the region, combined with decreasing hunter participation and revenue, present substantial challenges to successful black bear management (Hristienko and McDonald 2007). Ultimately, managers need to be able to link population parameter estimates such as density and population growth rates with the drivers of population change to effectively implement adaptive management to accomplish their objectives (Nichols and Williams 2006).

Clearly, wildlife management agencies need reliable information and tools to effectively respond to changing management circumstances without putting long-term viability of bear populations at risk. In some areas, agencies faced with increasing bear populations need information on how best to reduce human-bear conflicts, and on population monitoring methods that allow them to determine if management actions are having the desired effects (Organ and Ellingwood 2000). A further challenge in this region is that populations often cross geopolitical

boundaries, where jurisdictions may have different management objectives or priorities. Nonetheless, coordinating efforts across wildlife management programs may yield benefits from data compatibility, complementary methods, and economies of scale (Lindenmayer and Likens 2010) to better meet the shared objective of sustainable bear populations in the Northeast (Garshelis and Hristienko 2006).

There are many rapidly evolving techniques for population monitoring, but uncertainty about applicability and efficacy of each technique can make it difficult for wildlife managers to decide which methods are most appropriate to assess their success in reaching management objectives (Garshelis and Hristienko 2006). Some population monitoring methods lack sufficient precision to detect small but meaningful changes in population parameters and may not be feasible at spatial and temporal scales most beneficial to managers, or may provide little information on underlying population processes (Coster et al. 2011). More importantly, many ecological monitoring programs lack well-defined objectives and neglect sources of variation or uncertainty (Yoccoz et al. 2001, Nichols and Williams 2006), with financial constraints often determining the scope of programs and the techniques considered (Caughlan and Oakley 2001).

Given these challenges, the Northeastern Black Bear Technical Committee was interested in evaluating black bear management and monitoring options for jurisdictions in the northeastern U.S. and eastern Canada, taking into consideration the range of agency resources, bear population status, and management objectives present across this large and diverse region. Our overall goal was to assess available methods that incorporate statistical rigor and precision, feasibility, and cost-effectiveness for a range of population scenarios and management objectives that we developed working closely with bear biologists and managers from across the Northeast and beyond. Our specific objectives were to (1) provide an overview of current status and

management of American black bears in the region, (2) produce an accessible review of reliable techniques to estimate population parameters and monitor population trends, and (3) provide guidance to agencies to better enable them to choose monitoring tools that best meet their management objectives and available resources. Although wildlife managers in the Northeast provided the impetus for this work, our findings are broadly applicable to bear management across North American jurisdictions and beyond.

MATERIALS AND METHODS

Study Area

Northeastern North America (hereafter referred to as the Northeast, Fig. 4-1) is characterized by diverse geographic and climatic conditions, landcover types, and land management regimes, which result in a wide range of suitable black bear habitat types, ranging from Atlantic Coastal Wetlands in the east and north to Interior Highlands in the west (Alexander 1967). The granitic Appalachian Mountains dominate much of the region, reaching their highest elevation at Mt. Washington, New Hampshire (1,917 m), with the Atlantic Ocean being the eastern and northern borders for many of the jurisdictions responsible for managing black bears. The climate of the 13 U.S. states within the study area is classified as humid mid-latitude, with cold winters, warm summers, and distinct autumn and spring seasons (Alexander 1967). The climate of the 6 Canadian Provinces is generally colder with shorter summers and more days of lingering snow, so forests typically produce less hard and soft mast. Daylight is much longer in summer so lowland habitats can produce an abundance of berries that are consumed by bears (Young and Ruff 1982).

Forests in Connecticut, Delaware, Maryland, New Jersey, Pennsylvania, Rhode Island, Virginia, and West Virginia are predominated by oak (*Quercus* spp.) and hickory (*Carya* spp.),

which provide abundant hard mast for black bears in autumn (Ryan 2009). The forests of Maine, New Hampshire, New York, Ontario, Quebec, and Vermont primarily consist of maple (*Acer* spp.), American beech (*Fagus grandifolia*), and paper birch (*Betula papyrifera*), with only beech providing a valuable, but variable, source of hard mast (McLaughlin et al. 1994). Massachusetts is a transition zone between those 2 major forest types. Southern Newfoundland, Nova Scotia, and Prince Edward Island are dominated by relatively unproductive boreal spruce-fir forests, which transition to barren ground near the Atlantic Coast and above the Arctic Circle. Forest regeneration after logging and extensive land clearing for agriculture from the early 1700s through the mid-1900s has resulted in a notable expansion of forest habitat (Hall et al. 2002), which may have been a contributing factor to increasing black bear populations in the Northeast.

The Northeast is one of the most densely populated areas in North America because of its agricultural productivity, proximity to waterways, and early history of settlement. The region is home to almost 100 million people with 72 million people inhabiting the northeastern U.S. and 23 million residing in eastern Canada. The sizes of jurisdictions vary widely: Rhode Island and Prince Edward Island each are <6,000 km² whereas Quebec is nearly 1.4 million km². The lowest density of humans in the Northeast occurs in Newfoundland, whereas the greatest densities are concentrated near New York City, New York and Toronto, Ontario. The 13 United States included in our study area contain almost 25% of the entire U.S. population of >311 million people, but constitute only 7% of the total land area (681,748 km²) (U.S. Census Bureau 2010). Almost 70% of the entire Canadian population of >33 million people resides in the 6 provinces of our study area, while occupying only 32% of the total land area of Canada (Statistics Canada 2011).

Human populations in the Northeast are experiencing dramatic variation in growth rates among jurisdictions. Between 2000 and 2010, the U.S. population grew by 9.7%, but the average population growth rate in the 13 northeastern United States was only 4.7% (U.S. Census Bureau 2010). Between 2006 and 2011, Canada's population grew by 5.9%, whereas eastern Canadian provinces grew by 11.4% (Statistics Canada 2011). Ontario and Delaware, which differ considerably in size and density, experienced approximately 15% growth from 2000 to 2010. Other jurisdictions recorded less growth but only Newfoundland reported a decrease in the human population.

About 232,000 black bears inhabit the 3.6 million km² encompassed by our study area, although density and population growth rates vary greatly among jurisdictions (Noyce 2011). Historically, the entire Northeast was occupied by black bears (Feldhamer et al. 2003). At present, no resident black bear populations exist in Delaware or Prince Edward Island (Fig. 4-1), but during the past two decades, bear range has expanded in Connecticut, Massachusetts, New Jersey, New York, Pennsylvania, Rhode Island, Virginia, and West Virginia, and sightings recently have been reported in Delaware (Scheick and McCown 2014).

High and increasing human densities in the Northeast, combined with increasing bear numbers and close proximity of bears to humans in many areas, have resulted in increased human-bear conflicts in recent years. Twelve of 17 jurisdictions in the Northeast occupied by black bears reported increasing human-bear conflicts between 2000 and 2010 (Noyce 2011). Black bears are omnivorous and are often drawn to anthropogenic foods such as garbage, bird feeders, and agricultural crops. Although black bear attacks on humans are rare, incidents do occur and have resulted in injuries or death, costly litigation, and negative perceptions of bears by the public. Also, vacation or retirement properties owned by urban residents are becoming

more commonplace in the Northeast and the owners often have little experience dealing with wild animals. Such changing dynamics present many challenges to black bear managers in the Northeast. Noyce (2011) reported that 53% of black bear management jurisdictions in the Northeast had experienced an increase in human-bear conflicts over the preceding 10 years, with no jurisdictions reporting a decrease. Despite the rapid growth in bear populations and in human-bear conflicts reported in Noyce (2011), 67% of northeastern bear managers we surveyed indicated that <40% of their populations were at or beyond social carrying capacity.

Bear hunting has a long history in the Northeast. Of the 17 jurisdictions that have black bear populations, 14 use hunting as a primary management tool (Noyce 2011). Other population management tools have been proposed (e.g., immunocontraception, relocation) but few, if any, are deemed adequately effective or economically feasible at the spatial and temporal scales of concern to management agencies.

Population Parameters for Monitoring

Regrettably, monitoring of wildlife populations often consists of simply following trends in population abundance or other parameters with little understanding of what is driving the trend and how to modify it (Nichols and Williams 2006). Here, we use the term monitoring to describe the estimation of demographic parameters useful for assessing biological aspects of wildlife population performance across multiple years. This includes improving our understanding of the drivers of those parameters and ideally obtaining estimates of parameter precision.

Obtaining estimates of demographic parameters for black bears requires intensive and often expensive study designs to achieve reasonable levels of accuracy and precision (Settlage et al. 2008, Harris et al. 2011). Estimates that are accurate (low bias) and precise (low uncertainty)

are the most beneficial to wildlife management (Mills 2013). Perhaps the most dangerous are estimates that are precise but inaccurate, as they may lead managers to have false confidence in their decisions. Some parameters are inherently more difficult to reliably estimate than others and there is no universal definition of reliability that is suitable in all situations. What constitutes acceptable level of precision will vary by agency or management objective but managers should decide *a priori* how that level should be determined based on how the data are to be used, and what are the consequences of a given degree of uncertainty in the chosen monitoring metrics. Although Pollock et al. (1990) suggested that estimates with coefficients of variation <20% are probably acceptable for wildlife management decision making, there has never been a formal analysis of how the precision of estimates can influence the success of management actions. Consequently, researchers should work with managers to determine acceptable levels of precision based, in part, on how the results will be used. In the following, we describe population parameters that may be useful to monitor effects of bear management actions, empirical examples and estimation challenges of each, and techniques used to overcome those challenges.

Abundance and density - indirect estimates

Abundance remains one of the most important parameters to bear managers, particularly in jurisdictions that use harvest quotas, to monitor temporal changes in population status and to gain a better understanding of population dynamics (Nichols and Hines 2002, Lukacs and Burnham 2005). Abundance estimates themselves are, however, only implicitly tied to a defined spatial extent. To make meaningful comparisons across, or track changes within, populations, it is necessary to make this relationship explicit by defining the area to which an abundance estimate relates (Dice and Clark 1953, Wilson and Anderson 1985).

Generally, precision of abundance estimates increases with greater sampling intensity, which usually means greater cost. Thus, most managers must consider the tradeoffs between sampling intensity (i.e., cost) and reliability (i.e., accuracy and precision). Abundance is usually thought of as a discrete number of animals inhabiting a particular space and time, but indirect measures of abundance, or indices, may potentially be useful depending on the management objective (Lancia et al. 2005). Reliable indices can provide insights into population trend in response to perturbations, which may be all that is needed for certain jurisdictions, and can cost far less than a population estimate. The best indices are those that have a known, linear correlation with population size. Non-linear relationships can be useful as well if the curvilinear form can be quantified. Unfortunately, the strength and shape of the relationships for most indices of black bear abundance have not been investigated. Below, we discuss commonly used methods to estimate black bear abundance, beginning with indirect and followed by direct estimation methods.

Bait-station index

Bait-stations have been used by >15 wildlife management agencies in North America as an indirect estimate of black bear abundance (Garshelis 1990). The method evolved from pre-baiting for black bear trapping (Johnson and Pelton 1980), and involves establishing a series of bait-station routes, often along roads or trails. Bait, often opened cans of sardines or bakery products, is suspended by a string from a tree branch about 3 m above the ground at each of a series of sampling sites. A bear visiting the site will generally climb the tree to obtain the bait, leaving claw marks as an indication that the site was visited. Baits are usually checked after 5–7 days and the proportion of visited bait sites is used as an index of abundance. Bait-station surveys are usually conducted annually to monitor bear population trends.

Several potential problems exist with bait-station surveys. First, a site not being visited does not mean that bears are not in the area of the bait; 20–30% of bait sites are often not visited even where bear densities are high. Therefore, detection is not perfect (i.e., <100%) and can vary by factors not associated with population abundance, such as fluctuations in natural bear foods or live trapping efforts in the vicinity of bait stations (Brongo et al. 2005a). Further, the relationship is likely curvilinear and asymptotic because bear populations may continue to increase even when the bait-station index has reached 100%. Another potential issue is that this method may add to the food-conditioning of bears, whereby they become less wary of humans, similar to effects of trapping with bait (Ternent and Garshelis 1999, Brongo et al. 2005a).

The only rigorous evaluations of bait-station surveys and population trend were performed by Clark et al. (2005) and Rice et al. (2001). Clark et al. (2005) found that bait-station indices were not a good predictor of population growth on a 330-km² study area in Great Smoky Mountains National Park, Tennessee. Bait-station indices were, however, correlated with indices of acorn abundance, suggesting that the availability of natural foods affected visitation rates. Rice et al. (2001) used a power analysis and concluded that bait-station surveys in Idaho could detect large declines in abundance (i.e., 50% over three years), whereas surveys in Washington lacked adequate power to detect even gross population declines. Year-to-year fluctuations in bait-station indices are likely affected by sampling error and extraneous factors such as natural food availability, so we view bait stations as a method potentially capable of detecting gross population trends over a long period of time (i.e., decades) in a broad geographical context (i.e., multi-state or province wide), which clearly will not be adequate for many populations. Occupancy estimation methods might be used with detections based on bait-station data if the sites were surveyed repeatedly (MacKenzie et al. 2006). Given such data,

Royle et al. (2005) described methods for directly estimating abundance, but this has not been attempted with bears. Finally, bait-station data could be used as auxiliary data for integrated population models to improve estimates of population parameters, but these methods are still in development (Chandler and Clark 2014).

Observations

We define observations as any attempt to record, in a standardized way, visual records of bear occurrence, either by design (e.g., via remote camera) or incidental (e.g., human-bear conflict complaints). For example, many jurisdictions track annual occurrences of nuisance bear complaints received from the public as an indirect measure of bear abundance. Other jurisdictions have recorded observations of bears by the public, usually for small, re-establishing populations. These types of observational data are affected by factors other than population abundance (e.g., mast failures usually coincide with increasing nuisance bear complaints or road kills), so these data should only be used as a general measure of population trend. Additionally, road kill data are affected by traffic volume, which has been steadily climbing for decades throughout eastern North America (van Manen et al. 2012). Considering factors such as the increasing popularity of remote cameras, greater efforts to monitor wildlife-vehicle collisions (e.g., smartphone apps), and the general increase in the number of potential observers, relying on *ad hoc* observation data is unlikely to provide reliable insights into population trends.

Formalized observational air or ground surveys for black bears are, however, feasible in areas where cover is sparse and bears are easily detected (Schwartz et al. 2002), but except in more northerly units of some Canadian provinces, this method is usually not used in the Northeast. Sightability is strongly dependent on cover type (e.g., meadows, alpine); however, methods exist to estimate sightability and correct for its influence on observations, including

double sampling and multiple observers (Samuel et al. 1987, Lubow and Ransom 2016). Observations may be easier to obtain at known feeding sites (e.g., garbage dumps, berry patches), but the same assumptions and complexities with using nuisance reports probably apply. Remote cameras are seeing ever increasing use as an indirect measure of abundance, or at least occupancy (Burton et al. 2015, Steenweg et al. 2016), even for species that cannot be individually identified (i.e., marked). Advances in camera and sensor technologies including the ability to record thousands of images between visits and long-lasting batteries have reduced earlier issues of differential success among camera types (Kelly and Holub 2008) and small sample sizes (Mace et al. 1994b). Further, as camera costs have declined, it is now feasible to cover large areas following statistical sampling designs (Burton et al. 2015). Issues remain, however, with designing studies to minimize variable detection rates among different age classes or seasonal differences in movement rates, similar to other noninvasive sampling techniques (Long et al. 2012).

Harvest data

Jurisdictions with hunting seasons monitor annual harvest and many require physical checking of harvested bears to obtain data on sex, weight, age (e.g., cementum annuli analysis of teeth) (Stoneberg and Jonkel 1966, Harshyne et al. 1998), and collect tissue for genetic analyses. Stable harvest trends may suggest that the bear population is in fact remaining stable, given some knowledge of hunter effort. Of course, an important assumption is that harvest opportunities and reporting levels are known (or constant). For example, declining populations may sometimes show stable trends in harvest for a period of years because more hunting effort (i.e., more hunters afield, more hunter days) is being invested. Given that harvest indices can be sensitive to

sampling variation (Diefenbach et al. 2004), harvest trend data should be considered insensitive to all but gross population changes at best and misleading at worst.

If effort can be quantified (e.g., number of hunter days), the harvest per unit effort (sometimes referred to as catch per unit effort or CPUE) could be calculated and used as an index of abundance (Harley et al. 2001). Variables other than population abundance affect hunter success (e.g., weather, duration of hunt, methods allowed) and would have to be included in any CPUE models, but positive relationships have been demonstrated elsewhere (e.g., for moose [*Alces alces*], Schmidt et al. 2005). Analyses of fisheries data, however, have indicated CPUE can remain stable while abundance declines (Hilborn et al. 1992). Further, even under the best conditions, precision of CPUE indices of abundance is generally low compared with other estimators of abundance (Harley et al. 2001).

Abundance and density - direct estimates

Although indices may be capable of detecting large magnitude changes in abundance, direct enumeration of abundance will be more suitable to support common management objectives, particularly those involving harvest. Ideally, however, abundance estimates are tied to a defined area and reported in terms of animals per unit area (i.e., density). For example, maintaining viable harvest levels usually benefits from having reliable estimates of population abundance (N). The simplest population enumeration concept is a census or total count, whereby every animal in the population can be observed and counted (Mills 2012). In that special case, the detection or capture probability (p) equals 1 (i.e., perfect detection). In most instances, however, detection probabilities are not perfect ($p < 1$) and only a portion of the population is captured or detected (C). In those cases, population size can be estimated if that proportion (p) is known, where $N = C/p$ (Otis et al. 1978). Consequently, almost all abundance estimation methods focus

on the estimation of p and a variety of methods (i.e., mark-recapture, mark-resight, search-encounter, occupancy) have been developed for such purposes.

Heterogeneity in detection rates is a major concern with mark-recapture abundance estimates for bears because it is prevalent, difficult to account for in models, and can result in biased estimates (Pollock et al. 1990, Boulanger et al. 2004c). For example, larger bears may be able to step over the barbed wire at a hair snare, resulting in lower capture probabilities than smaller bears, which would produce an abundance estimate that is biased low. A variety of methods have been developed to detect and account for this bias (e.g., Pledger mixture models, Huggins individual heterogeneity models, Jackknife models) but they may not perform well when capture probabilities are low (Huggins 1991, Pledger 2000, Boulanger et al. 2004b, Laufenberg et al. 2013).

The most popular method for estimating p for bears is capture-mark-recapture (CMR). The basic assumptions are that the population is closed to additions or removals, marks are not lost and are read correctly, and all animals have the same probability of capture (Williams et al. 2002). Biases may be difficult to discern, but can be prevalent even in large-scale studies (Garshelis and Noyce 2006). Violation of some or all of these assumptions is common (e.g., ear tag loss, mortality, trap shyness) and sophisticated methods have been developed to estimate or reduce such biases. For example, open population estimators have been developed when geographic (immigration and emigration) or demographic (births and deaths) closure violations occur between sampling occasions (Jolly 1965, Seber 1965). Black bears are particularly prone to some sampling biases, such as geographic closure violation, and these issues should be taken seriously when designing CMR studies (Settlage et al. 2008, Laufenberg et al. 2013).

Great variation exists in the design of mark-recapture studies that can lead to violating assumptions and affect parameter estimates. For example, black bear researchers have used both rewarding (e.g., bakery products) and non-rewarding lures (i.e., scents) to entice bears to enter sampling sites. Rewarding lures have commonly been used in eastern North America to attract bears, but bears may exhibit a positive behavioral response, which can result in negatively biased abundance estimates if not modeled appropriately or if data are too sparse to detect the effect. Further, if bait at a site is consumed, it may be more difficult to entice bears that subsequently encounter the site to enter. Researchers in the western U.S. and Canada have often used a mixture of aged cattle blood and decomposed fish with success, but recapture probabilities are lower than for rewarding lures, which can lead to problems in modeling capture heterogeneity (i.e., differences in capture probability among individuals not related to previous capture). This can be exacerbated by negative behavioral responses following live capture, which can be difficult to know for all bears in a population (Kendall et al. 2009). Following the marking of animals, the ability to recapture them is central to mark-recapture studies and the effects of lure or bait on detections should be further explored, which is no simple task.

The density of trap sites on the landscape is also a key determinant influencing detection probabilities. For example, one assumption for mark-recapture studies is that all animals have the same probability of capture regardless of their location on the landscape, which can easily be violated if large gaps exist in site distribution. Although equal detection rates are rarely realistic, studies to estimate abundance should be designed to ensure that all animals have at least some opportunity to be detected in more than one sampling occasion, which can often be improved through use of multiple sampling methods. Thus, at a minimum, trap spacing should be no greater than the smallest seasonal home-range diameter of bears within the sampled area

(Boulanger et al. 2004b, 2006). Because most hair sampling surveys take place in summer and black bear home ranges are smaller for females than males, summer home ranges of females are thus useful for guidance.

Below, we discuss some of the more commonly used methods to obtain detection data for use with estimating bear density, then discuss some of the models themselves. For mark-resight, traditional mark-recapture, and the newer spatially-explicit capture-recapture models, we performed simulations using empirical data from the Northeast to give an overview of how these models perform across a broad range of population and sampling conditions.

Live-capture data

A variety of techniques have been used to obtain observation data for estimating p . Live capture is a common form of initial marking and recapturing. Live capture is relatively expensive but allows for the attachment of radio transmitters and collection of age and sex data along with other individual attributes to use as covariates to improve estimating capture probabilities or for other purposes. Live capture studies for bears often have small sample sizes and limited geographic extent, although exceptions exist (e.g., ~600 ear-tagged bears per year in Pennsylvania; Ternent 2006). Even for relatively small efforts, data on animals marked during live-capture projects can be used to augment detection data from other methods such as through genetic sampling (e.g., Kendall et al. 2009), or used in mark-resight models (Mace et al. 1994b), as discussed below.

Biomarker data

Biomarkers such as tetracycline and radioisotopes have been used with some success in black bear populations in Michigan and Minnesota to estimate abundance, although there are issues regarding assumptions of the method and potential social concerns (Garshelis and Visser 1997).

For example, radioisotopes are effective markers but, where bears are hunted, there is concern about health risks posed by consuming meat of marked bears. Baits laced with non-toxic tetracycline, which fluoresces in bone tissue under ultraviolet light, have been used in Minnesota and Michigan to estimate statewide bear populations (Garshelis and Visser 1997, Belant et al. 2011). Tooth or rib samples were obtained from hunter-killed bears and examined under a microscope to detect the tetracycline. Cautions include the failure of tetracycline to fluoresce in some tooth samples (because of inadequate dosage or slow growth during some seasons and in old animals), markers fading over time in bone samples, and bears emigrating from the sampled area, all of which positively biases estimates of population size. Further, if non-target species take a significant proportion of the tetracycline baits, which are used to infer the number of marks in the population, estimates will be positively biased. Wide spacing between baits is necessary to ensure that individual bears do not consume >1 bait. Additionally, animals that are more prone to consume tetracycline baits may also be more prone to harvest, thereby introducing bias (Garshelis and Noyce 2006). The method is attractive because most jurisdictions in the Northeast occupied by black bears allow hunting, which would enable easy access to recapture samples, although this may not represent a random sample of the marked population (Garshelis and Visser 1997). Unfortunately, biomarkers do not enable researchers to individually identify animals, which limit the choice of population estimators that can be used. Biomarker projects in New Hampshire and New York were unsuccessful because of low bait consumption and insufficient marking of bears (A. Timmins, New Hampshire Fish and Game Department; J. Hurst, New York Department of Environmental Conservation; personal communication).

Noninvasive genetic sampling data

Mark-recapture methods based on DNA extracted from bear hair or scat samples have become among of the most widely used research and monitoring tools across North America and beyond (Boersen et al. 2003, Tredick and Vaughan 2009, Latham et al. 2012, van Manen et al. 2012, Karamanlidis et al. 2015). Rather than capturing and marking animals directly, biological samples (usually hair or scat) are collected and genotyped, thus producing records of capture analogous to those that might be obtained by live capture and marking with ear tags. This is largely due to technical breakthroughs in the 1990s based on polymerase chain reaction (PCR), enabling small amounts of DNA from hair or scat to be amplified and then genotyped (Foran et al. 1997). Woods et al. (1999) devised a hair trap by stringing barbed wire around a series of trees to form an enclosure around a baited center. This type of sampling is often referred to as noninvasive genetic sampling because, following medical terminology, biological samples are obtained without breaking the skin. An added benefit of noninvasive genetic sampling data is that it can be used to estimate other population parameters in addition to abundance (e.g. population growth, survival, reproduction) and to understand how bear populations are demographically and genetically connected (Proctor et al. 2005, Sawaya et al. 2013a).

Noninvasive genetic sampling, however, is not without its challenges. The DNA in hair and scat samples is often of low quantity and quality compared with blood or tissue samples and thus may be prone to genotyping errors (allelic dropout, false alleles; Taberlet et al. 1999, Mills et al. 2000). This can lead to animals losing their “marks”, thereby introducing spurious individuals into the sample. Not only does this inflate the minimum count, but it lowers detection probabilities, both of which contribute to overestimates of population abundance (Taberlet et al. 1999). Also, if the ability to reliably distinguish individuals (i.e., marker power)

is insufficient, it may not be possible to distinguish between closely related individuals, leading to underestimates of abundance (Mills et al. 2000). Methods have been developed to identify and minimize genotyping errors from datasets, however, substantially reducing the influence of these errors on population estimates (Taberlet et al. 1997, 1999, Paetkau 2003, McKelvey and Schwartz 2004). Pilot genetic sampling studies should be conducted to ensure that desired genotypic discrimination and genotyping success rates can be achieved (Kalinowski et al. 2006, Settlage et al. 2008). In small isolated bear populations with low genetic variation, a greater number of markers may be required for successful genotyping. Wildlife managers may be reluctant to embrace genetic monitoring methods because unfamiliarity with methods and models (Schwartz et al. 2007). Stetz et al. (2011) developed an online resource for managers to help bridge this barrier (http://alaska.fws.gov/gem/mainPage_1.htm).

One potential concern with noninvasive genetic sampling is that >1 bear can leave hair samples on the same barb, resulting in a mixed sample. As part of a large laboratory test, Kendall et al. (2009) submitted >800 blind samples, including 115 intentionally mixed samples consisting of hair from closely related (i.e., full siblings) bears. Their results were conclusive in that no discrepancies among known individual genotypes (e.g., spurious genotypes) were detected. Mixed samples should not constitute a major problem as long as standard laboratory protocols and error checking procedures are used (Paetkau 2003). Researchers may select different heights of wire depending on the physical characteristics (i.e., body size) of bears in the sampled population. Ideally, every adult bear that enters a hair trap would leave hair as they pass over or under the wire, but a number of studies have documented lower detection rates for males than females (Sawaya et al. 2012). One contributing factor for this difference may be that males have different molting schedules or may be tall enough to step over the wire without leaving

hair. Because male detection probabilities are often lower than females at hair traps, some researchers have used two strands of barbed wire set at approximately 40 and 60 cm or 20 and 50 cm in an attempt to capture more males (Drewry et al. 2013, O'Connell-Goode et al. 2014, Wilton et al. 2014). Laufenberg and Clark (2014) found that none of 13 cubs that were known to be present on their study area were detected at sites that used a 2-wire configuration. Also, of the 30 genotypes from live-captured bears that matched noninvasive genotypes, 0, 3, and 17 were first detected as cubs, yearlings, and 2-year olds, respectively. Thus, vital rate estimates based on similar wire configurations for black bears most likely exclude cubs of the year.

In eastern North America, where bear home ranges are relatively small and bear densities can be high, hair traps often need to be less than a few kilometers apart to avoid gaps in the sampling coverage that can lead to some individuals not being able to be detected (Settlage et al. 2008). Further, in these populations the high density of sampling sites can yield a large number of hair samples, leading to untenable lab expenses. In those cases, DNA analysis of only a subset of the total number of hair samples collected may be an option (Tredick et al. 2007, Settlage et al. 2008, Dreher et al. 2009). Excessive subsampling likely reduces detection probabilities, however, so minimizing the likelihood of missing individuals is important (Laufenberg et al. 2013). This can be aided by, for example, using auxiliary information such as partial genotypes to target samples for complete analysis (Stetz et al. 2014). Conversely, analyzing a single sample per site-visit may favor detection of individuals that leave larger clumps of hair, which may have a high probability of successful genotyping, resulting in capture biases (Augustine et al. 2014).

Subsampling may also make it more difficult to model behavioral biases because of missed detections. For example, the first occasion that an animal is captured may actually be a

recapture of an animal whose hair was previously collected but not genotyped (Laufenberg et al. 2013). Such undetected positive trap responses can lead to overestimation bias of N (Augustine et al. 2014). Subsampling also assumes that individual hair captures are independent, which may not be the case with, for example, animals traveling in family groups. In these situations, animals would not be randomly sampled (i.e., only 1 of the group can be selected) resulting in a potential bias. More work needs to be done to address issues caused by subsampling.

Another consideration is whether or not to move hair traps between sampling sessions. Leaving sites in place and rebaiting them takes considerably less work than moving them, but capture probabilities are generally greater when sites are moved when no food rewards are used (Boulanger et al. 2006). Sites with rewarding lures may have greater detection rates when they are not moved due to a positive behavioral response. Many other variables may influence hair trap capture probabilities, including weather conditions that can affect sample quality and lab standards for genetic analysis. Previous live captures can negatively affect capture probabilities with hair traps as bears may develop wariness of similar sites (Boulanger et al. 2008, Kendall et al. 2009). Similar to other bear species, American black bears rub on trees, posts, and other objects and may provide an opportunity to collect high-quality hair samples for use in mark-recapture studies. Hair from rubs was used to successfully estimate grizzly and black bear abundances in Glacier National Park, Montana (Kendall et al. 2008, Stetz et al. 2014). Researchers used detections from bear rubs and hair traps to estimate grizzly and black bear abundance in Banff National Park, Alberta (Sawaya et al. 2012) but found very low bear rub detection rates for black bears relative to grizzlies. Hair collected at wildlife crossing structures (Sawaya et al. 2012), harvest samples (Dreher et al. 2007), and from nuisance or research bears

(Kendall et al. 2009) have also been used in conjunction with samples from hair traps to reduce effects of detection heterogeneity from a single sample source.

Although hair traps are generally used for genetic sampling (Long et al. 2012), Clevenger et al. (2010) used barbed wire strung across wildlife crossing structures to collect bear hair and this method could be adapted to any type of known crossing location. Hirth et al. (2002) found ample black bear hair for genetic analysis on bark and broken twigs of crab apple trees (*Malus pumila*) when bears were climbing trees to eat ripening fruit in fall. They suggested that, given the broad distribution of current and abandoned orchards in the Northeast, sampling in apple orchards could potentially replace or augment DNA collection from hair traps, but this would need be evaluated on a per-project basis (Hirth et al. 2002). Bear scat can provide a source of DNA as well. Studies have shown the use of scat detection dogs greatly improves efficiency of scat surveys (Wasser et al. 2004, Long et al. 2007), but low microsatellite amplification rates can still severely limit detection probabilities. Considerable effort has been directed at identifying the best methods for scat collection (e.g., swab of epithelial cells from surface of the scat) and storage, but with current technologies, capture probabilities typically remain too low to use scat alone for abundance estimation (Murphy et al. 2007). Newer techniques, however, such as single nucleotide polymorphisms (SNPs), are providing demonstrable improvements in genotyping success rates across a range of sample types and conditions for many species, as well as allowing insights into other population genetic questions involving traits under natural selection (Allendorf et al. 2010). Also, estimators based on the use of scat detector dogs within a spatially unstructured grid may work well for estimating bear abundance in the future (Thompson et al. 2012, Davidson et al. 2014).

Mark-resight methods

Mark-resight models attempt to estimate p via marking a subset of a population and reencountering some proportion of those marked animals through sightings (e.g., remote cameras). They differ from strictly live-capture methods because all animals marked during a single marking event do not have to be captured and handled again. Sightings of marked and unmarked individuals are recorded during sighting surveys, which also differs from standard mark-recapture methods. Advantages to mark-resight methods include reduced costs due to requiring only a single capture (i.e., marking) event, the reduced potential for harming animals during physical capture and chemical immobilization (Cattet et al. 2008), or biasing estimates by modifying the behavior of captured individuals (Moa et al. 2001). A key component of the mark-resight method is that the number of marked animals available for resighting must be known or at least estimable. One way that likely satisfies this requirement is to mark animals immediately before resighting efforts take place. If this is not possible and enough time elapses between marking and resighting occasions, it may be necessary to use radio collars, for example, to determine how many marked animals are present (Higgs et al. 2013). For large or long-term studies, this may be cost-prohibitive. Although this requirement can be overlooked for some models (e.g., the Minta-Mangel estimator, Minta and Mangel 1989), the necessity of large sample sizes and other assumptions led to limited use (McClintock et al. 2009), although extension of this class of models and access to analytical tools has increased their popularity (McClintock and White 2009, Higgs et al. 2013).

As with any study, it is important to first define the population with respect to geographic boundaries and time periods of interest (Pollock 1991). Other design criteria include whether it is feasible to mark a reasonable number of animals with field-readable marks and whether marks

are individually identifiable. While the latter is not strictly necessary (Table 4-1), individual identification is essential for the use of heterogeneity models, which are typically useful in black bear abundance estimation due to the prevalence of detection heterogeneity in essentially all sampling methods. Another consideration is whether animals are resighted with replacement or not. Sampling with replacement is appropriate for remote camera studies where animals may visit more >1 camera station during the resighting period. Sampling without replacement occurs when individuals may be detected at most once per resighting occasion. Although the parameters being estimated for either situation are the same, the choice of estimator is not (Table 4-1).

Mark-resight methods to estimate abundance of black bears is challenging because individual identification is difficult without supplemental marking. To remedy this, Mace et al. (1994b) and Martorello et al. (2001) affixed colored ear streamers to live-captured bears that were later observed at camera stations, with capture histories being generated from the photos. Advantages of the technique are that the remote cameras are relatively inexpensive to operate and lack of avoidance behavior typically associated with live trapping. Drawbacks include the inability to identify individuals because of poor picture quality or the head position of the bear, streamers can break or fall out, and the method may raise ethical issues about encumbering an animal with such tags and the undesirable aesthetics to wildlife observers (Murray and Fuller 2000). Further, resighting rates can be dramatically affected by external factors such as weather or changes in availability of natural foods that can influence bear movement rates (Mace et al. 1994b). Observations of marked bears by airplane have also been used to estimate bear abundance (Miller et al. 1997), but that technique is largely infeasible in the Northeast due to heavy canopy cover. Mark-resight methods based on natural marks have been successfully used

on species that exhibit differences in pelage or other physical characteristic (e.g., tigers [*Panthera tigris*], Royle et al. 2009; Asiatic black bears [*Ursus thibetanus*], Ngoprasert et al. 2012) but black bears often are not naturally visually identifiable. This class of models has recently seen rapid improvements, with more powerful and flexible likelihood-based methods being readily accessible to researchers and managers (McClintock and White 2012). These new methods can make use of detections of animals that are unmarked, marked, individually marked, and combinations of the three; populations that are or are not geographically closed; and by sampling with or without replacement (Table 4-1). These models may provide powerful, economical alternatives to other observation methods in the future.

Mark-resight abundance simulations

Because many black bear managers in the Northeast obtain data from live-captured bears (Noyce 2011), we explored the potential to use mark-resight with the Poisson log-normal estimator (PNE, McClintock and White 2009). The PNE model requires individually identifiable marks, but does not require that the number of marks be known (i.e., in case of emigration from the study area), although the number of marks is often determined via telemetry prior to camera surveys. As with other robust-design mark-recapture models (Ivan et al. 2013), the assumption of geographic closure may be relaxed with the PNE model given an estimate of the proportion of time radiocollared bears spend off the study area.

We simulated a population of 600 bears with a 50:50 sex ratio. For each sex, we treated 100 bears as known (i.e., marked), with a mean detection probability of 0.55 and 0.5 for males and females respectively, similar to detection rates from Matthews et al. (2008). We used apparent survival rates of 0.85 and 0.9 for males and females, respectively, based on plausible values for black bears in the northeast (Table 4-5). We assumed a 0.05 probability that an

individual transitions to an unobservable state (i.e., leaves the study area), with a 0.5 probability that they return to being available for resighting. We ran simulations in program MARK for 500 iterations, and assessed model performance based on percent relative bias (PRB), coefficient of variation (CV), and confidence interval coverage (CIC; percent of runs where the true value is within the confidence interval). We calculated PRB as the difference between the estimated parameter value and truth (i.e., the value used to generate simulated data; $PRB = [(estimate - truth) / truth] \times 100\%$).

Over the set of parameters we considered, model performance was generally poor (Table 4-2). Male abundance estimates had an average negative bias of 28%, with females being negatively biased by 21%. Estimates for both sexes were precise, with $CV=9\%$. This combination of high precision with significantly biased estimates resulted in poor CIC, particularly for males (5.6%). Females were slightly better ($CIC=23.7\%$), although still far below nominal values. Even without simulating heterogeneity in detection rates, the models performed poorly and present the dangerous scenario of precise but biased estimates.

Traditional mark-recapture

Mark-recapture data analysis is an active area of research and a variety of methods have been developed to deal with sampling biases and data types. Perhaps the greatest contribution to the access to these methods is the development of Program MARK (White and Burnham 1999) software that is free, relatively user-friendly, and is adaptable to a wide array of data types. This software package has made it possible for field biologists to analyze their own data using sophisticated maximum likelihood estimation methods. Also, recent developments in the use of hierarchical models employing Bayesian analytical methods have enabled those estimators to be more routinely used (Gardner et al. 2009).

Capture heterogeneity is a major concern with all types of mark-recapture abundance estimates and a variety of methods have been developed to model such biases but they may not perform well when capture probabilities are low (Huggins 1991, Pledger 2000, Boulanger et al. 2004b, Laufenberg et al. 2013). The effect of capture heterogeneity can also be reduced with the use of multiple sampling methods (Dreher et al. 2007, Boulanger et al. 2008). For example, researchers in Pennsylvania mark bears by live-trapping whereas they are recaptured (recovered) via harvest, which can be used to augment other types of detection data, thus reducing sampling biases (e.g., Dreher et al. 2007). Finite mixture models that categorize individuals into ≥ 2 groups that share similar traits (Pledger 2000), or random effects models that allow individual detection to differ from the population mean (Coull and Agresti 1999, Gimenez and Choquet 2010) have been shown to perform well (Laufenberg and Clark 2014). It is also now common to use individual covariates such as each animal's average distance to the edge of the sampling grid in the case of non-spatial mark-recapture models (Boulanger and McLellan 2001), history of previous live capture (Boulanger et al. 2004c, van Manen et al. 2012), and time-varying sampling effort (Sawaya et al. 2012, Efford et al. 2013) to improve model performance. Despite continuing advances in modeling, detection heterogeneity remains a concern for all types of mark-recapture estimation methods.

Because of relatively large home ranges of bears, one of the greatest challenges in using closed population models for estimating abundance is violation of the assumptions of geographic closure (Boulanger and McLellan 2001, Gardner et al. 2009). If geographic closure is violated, estimated abundance is that of the super-population (i.e., includes animals moving on and off the study area; Crosbie and Manly 1985, Kendall 1999). Sampling large areas can reduce such violations, but resource limitations may result in a sampling intensity too sparse for reliable

parameter estimation (Boulanger et al. 2004b). Regardless, not knowing the geographic bounds to which the abundance estimate applies persist and estimates of density ($N/\text{area sampled}$) are difficult to interpret. A number of *ad hoc* methods have been proposed for estimating the sampled area (Karanth and Nichols 1998) but such approaches have no true statistical foundation and, therefore, may produce biased density estimates (but see Stetz et al. 2014).

Mark-recapture simulations

We evaluated a number of black bear mark-recapture study designs by conducting closed-population abundance simulations using estimates of detection probability spanning the range found in the primary literature, focusing on studies conducted in the Northeast (Appendix C). Using the Program R (Team 2013) package WiSP (Wildlife Simulation Package, Zucchini et al. 2002), we simulated populations ranging in true abundance N from 100 to 900 in increments of 100 individuals (Table 4-3), within square study areas with sampling grids composed of 100 or 200 sampling sites on each side, each with uniform bear density. We assumed that sampling effort was constant across k occasions ($k = 5, 7, \text{ or } 10$), depending on the particular simulation. This is reasonable as most mark-recapture studies deploy the same number of traps each occasion, although the number and length of occasions may vary. We used a minimum per-occasion capture and recapture probability of 0.005 (i.e., assuming that all bears had at least some opportunity to be detected), a maximum per-occasion value of 0.5, and we assumed no change in detection across occasions (i.e., no behavioral response). All simulations used a jackknife model to allow for the variation in detection probabilities imposed by the simulated sampling design (Burnham and Overton 1978, Otis et al. 1978). We derived nonparametric bootstrap 95% confidence intervals with 99 runs. To assess performance, we estimated the

average relative bias and coefficient of variation across replicates and assessed confidence interval coverage. We provide annotated code in Appendix C.

For those simulation scenarios with adequate data for models to converge, estimates showed decreasing bias and increasing precision as true population abundance and the number of sampling occasions increased (Fig. 4-2). One exception, however, was decreasing CIC due to overly precise estimates as abundance increased with the smaller study area scenario. For all but the sparsest scenarios, the coefficient of variation (CV) remained below 20%, and was rarely >10% for populations of ≥ 200 animals. These results suggest that, across a range of population sizes, the detection probabilities achieved in black bear mark-recapture studies in the Northeast have been adequate for robust abundance estimates. As expected, larger study areas produced less biased and more precise estimates than did smaller study areas. Near nominal coverage was, however, achieved for the majority of scenarios and bias rarely exceeded 5% for populations of ≥ 300 animals. Higher detection probabilities and more complex models would likely result in even more precise estimates although examples of such data (e.g., mixture probabilities) were rare in the literature and likely too specific to a particular region or study to be useful in simulations. We reiterate that studies designed to maximize detection probabilities while minimizing heterogeneity induced by closure violation or other factors will produce the most reliable estimates. Proper modeling (e.g., using covariates) and supplementary data can reduce estimate bias, but more complicated models also tend to require larger sample sizes and detection rates (Boulanger et al. 2004c).

Spatially-explicit mark-recapture

To address the challenges with defining the spatial extent to which abundance estimates pertain, spatially explicit capture-recapture (SECR) models have been developed that combine elements

of distance sampling with mark-recapture estimation (Efford 2004, Borchers and Efford 2008, Royle et al. 2013b). Unlike non-spatial capture-recapture models that ignore the spatial location of detection sites, SECR models use the spatial distribution of sites to estimate home-range size and detectability, assuming that the probability of detection is greatest at the home range center and detectability decays as a function of distance from the center (see Borchers 2012 for a nontechnical review of SECR models). SECR models use maximum likelihood (Borchers and Efford 2008) or Bayesian methods (Gardner et al. 2009, Royle et al. 2013b) to estimate detection probabilities. Obbard et al. (2010) conducted a comparison of density estimators for black bears in Ontario and concluded that density estimates from SECR models were lower and presumably less biased than estimates from non-spatial mark-recapture models. Their study design, however, deployed sites along secondary roads and used a rewarding bait, which could have induced a behavioral response. Conversely, Stetz et al. (2014) compared traditional and SECR density estimates of black bears in Glacier National Park, MT, using two concurrent genetic sampling methods and found no difference in point estimates or their precision. The authors attributed this to sampling a large area relative to bear home ranges and the use of >1 sampling method, despite a trap density lower than typically used for black bears (Stetz et al. 2014).

SECR methods are most commonly used to directly estimate population density, but estimation of abundance is also possible and may be more robust to spatial heterogeneity in capture probabilities than are strictly non-spatial methods. Efford and Fewster (2013) found that spatially explicit models for estimating N were robust to gaps in detector spacing and heterogeneous animal distributions. One important advantage of SECR models is that the correlation of density at individual trap sites with habitat covariates can be directly integrated into the estimation process, enabling researchers to predict density in areas not sampled (Drewry

et al. 2013). Finally, SECR methods are based on estimating the relationship between detection probability and distance of the trap from an estimated home range center; it is not necessary that every animal has the same probability of capture regardless of its location within the sampling grid. This enables researchers to employ a series of intensive trap clusters placed within the context of a larger overall study area, enabling the estimation of abundance and density in areas not sampled, perhaps with the help of habitat and other covariates (Drewry et al. 2013, Efford and Fewster 2013). Clusters or arrays must, however, take a sample that is representative of the area of extrapolation or severely biased estimates may result (Wilton et al. 2014).

Expanding on recent advances in mark-resight and spatially explicit capture-recapture models, Sollman et al. (2013) developed a spatial mark-resight model that combines spatially-referenced resighting data (e.g., remote camera stations) and telemetry data. Such an approach is particularly advantageous if sampling stations are placed too far apart (Sollman et al. 2012) or when animals are not always individually identifiable (Chandler and Royle 2013). The telemetry data are used to inform estimation of movement-related parameters (Sollman et al. 2013). Applications of SECR models are myriad and represent a fertile area for future research, including monitoring changes in density patterns using open population models. SECR models are not a panacea, however, because non-spatial individual heterogeneity issues persist as do some biases associated with other estimators of abundance such as differential detection rates between males and females that can produce biased density estimates.

Despite assumptions that SECR models are less biased than traditional approaches, it is usually impossible to discern the degree of bias in a parameter estimate from a field study. Estimates of precision are typical, but as noted above, even the most precise estimates can be severely biased, which is perhaps the most dangerous result upon which to base policy or

management decisions. Therefore, simulations are typically used to estimate and compare the potential biases and precision of estimation methods and study designs. In such simulations, populations with known characteristics (e.g., abundance, survival rate) are created by the user, and then “sampled” according to the prospective study design. For example, Boulanger et al. (2004a) used simulated detection data to estimate the bias of grizzly bear abundance estimates in hair trapping studies due to the heterogeneity in cub capture probabilities. They were able to evaluate the performance of multiple study designs (i.e., size and number of grid cells with hair traps) and thereby make recommendations on study design that reduce this form of heterogeneity. Simulation studies such as those have become instrumental in designing bear research and monitoring programs (Boulanger et al. 2008, Stetz et al. 2010, Laufenberg et al. 2013).

Spatially explicit capture-recapture density simulations

We conducted simulations in Program R to evaluate the performance of SECR methods to inform study design for estimating density of black bear populations. We conducted experiments covering a range of plausible sampling scenarios and population parameters based on the literature (Appendix C), focusing on the maximum likelihood approaches of Borchers and Efford (2008). To perform the simulations, we used the secr package (Efford 2012) to generate and sample populations, then derive estimates of density from which we assessed bias and precision relative to true density. Again, we estimated bias as the average PRB across replicates and precision based on the average CV and average CIC.

We conducted a large number of SECR simulation scenarios resulting in approximately 1,400 combinations of parameters (Table 4-4). We assumed a half-normal function to relate detection rate to the distance between an animal’s estimated home range center and a given

proximity detector. We also assumed detection was uniform across sampling events, and the population was demographically closed, given most bear studies occur when births and deaths are at their minimum. We simulated populations ranging from 10-150 bears per 100 km² to cover the majority of density estimates from the literature in the Northeast. We varied detection at the home range center, g_0 , from 0.05-0.15, with the spatial scale parameter, σ , ranging from 400-3,000m. For sampling design variables, we considered trap spacing from 1,000-3,000m, with 5, 7, or 10 sampling occasions. Finally, we considered sampling grid sizes of 10×10 and 25×25 sites, with a mask buffer ≥ 4 times the σ value. We provide annotated code in Appendix C.

Results of SECR simulations were generally similar across the two grid sizes we considered, with the biggest exception being that data-rich scenarios (i.e., high density) consistently failed because of computer memory constraints for a 25×25 trap layout, regardless of distance between traps. Similarly, for the 10×10 grid, we excluded spurious results for several low-density scenarios from further consideration.

Our SECR simulation results indicated the greatest bias in density estimates, both positive and negative, occurred for low-density populations, with smaller home ranges (i.e., the spatial scale parameter, σ), and with greater spacing of sampling sites. Specifically, low-density populations were more likely to produce positively biased estimates, even with high detection rates, with large home ranges relative to site spacing. Negative bias was also associated with small home ranges in conjunction with large site spacing, even with high detection rates and slightly higher population density. Low CIC (95%) for 10 × 10 grids also occurred with sparse data scenarios, such as low-density populations with small σ and large site spacing, with a lesser effect due to detection probability or number of sampling occasions. Only 21% of scenarios with

the smallest home range achieved nominal (95%) CIC, however, these estimates were heavily biased and CIC was achieved simply because of poor precision that resulted in large confidence intervals. We found the same pattern of poor precision for 25×25 grids, but with only 15% of scenarios achieving 95% CIC. The number of sampling occasions seemed to be the least influential parameter overall, although more occasions did result in greater precision, particularly among sparse data scenarios. We observed the same patterns for 25×25 grids but associated CVs were consistently better than the 10×10 grid scenarios.

In summary, SECR model performance was best in low density populations, with relatively large home ranges, and larger sampling areas. Detection probability, site spacing, and number of occasions were less important. The smaller study area scenarios were less consistent in terms of the influence of population density and detection rate on model performance, although home range size, both in absolute terms and relative to site spacing, again was the most important factor in model performance. Thus, given the level of sampling typical of black bear DNA-based mark-recapture studies, our results suggest that SECR models may produce biased and imprecise estimates for populations when home ranges are small relative to the sampling intensity.

Our simulation results are consistent with empirical estimates of Wilton et al. (2014), who compared two sampling designs for SECR models using DNA-based detections of black bears in Missouri. They found that intensive sampling designs covering a smaller geographic area produced more precise estimates than more extensive, lower-density sampling of the same area due largely to sparse recaptures in the latter (Wilton et al. 2014). More importantly, density estimated from the intensive sampling design was 5.5 times greater than from the extensive design, reinforcing the significance of trap spacing to produce reliable estimates (Wilton et al.

2014). Our results are also similar to those of Sun et al. (2014), who found that study design parameters such as sample site spacing were directly linked to the reliability of inference from spatial models. Conversely, Stetz et al. (2014) used a larger trap spacing originally designed to sample the sympatric grizzly bear population in conjunction with detections at bear rubs in SECR models. Despite the sparse sampling intensity relative to black bear home range size and moderate subsampling, they produced precise (i.e., $CV < 18\%$), sex-specific density estimates. Further, density estimates were nearly identical to those obtained by traditional closed-population abundance models with an effective sample buffered by $\frac{1}{2}$ the mean maximum distance moved by bears during the study (Stetz et al. 2014), contrary to several studies that routinely report lower density estimates from SECR models (Obbard et al. 2010, Noss et al. 2012). This was likely a function of sampling a large area (4,100 km²; approximately 66 times larger than average male home ranges in this region), which served to reduce edge effects (Stetz et al. 2014).

Although SECR methods appear to overcome some of the fundamental challenges of estimating density, techniques continue to see rapid development. For example, recent extension of SECR models to incorporate landscape resistance suggests that models using Euclidian distance between activity centers and sampling sites to estimate σ may drastically underestimate density (Royle et al. 2013a). Again, these models are undergoing rapid growth and require further theoretical development, simulation, and empirical evaluation.

Survival

Abundance is probably the most difficult population parameter to estimate. Estimates of survival, however, may be useful in place of abundance for monitoring effects of harvest, evaluating harvest changes, and better understanding population dynamics (Sorensen and Powell

1998). Furthermore, black bear population growth is particularly sensitive to changes in adult female survival (Beston 2011) and survival estimates are not as sensitive to the detection biases that plague abundance estimates, making robust estimation possible with less cost and effort. Estimates may be biased, however, if a representative sample of the population is not acquired or if undetected permanent emigration occurs.

Black bear survival can be estimated by tracking their fates with radio collars or by mark-recapture techniques, noninvasive or otherwise. Survival typically varies with age and sex and, ideally, survival would be estimated for bears of every age, sex, and reproductive status (i.e., females with and without cubs or yearlings). Fortunately, little information is usually lost by pooling data into age categories (e.g., old adults [8+ yrs], young adults [3–8 yrs], subadults [2–3 yrs], and cubs of the year [<1 yr]). Annual survival rates are calculated as the proportion of each age or sex class that survived each year. While it may be easier to pool data into cohorts such as these, it may limit the ability to reduce bias relative to individual-based analyses.

Radiotelemetry methods

The most common method to estimate bear survival is to capture animals, radiocollar them, and monitor their signals to determine if, when, and why the animal died. Estimating survival with radiotelemetry data does not require that locations be obtained, but the status (dead, alive, unknown) must be monitored regularly and frequently, preferably over a number of years to estimate annual variation. Adult females are often targeted in telemetry survival studies because population growth rates are most sensitive to survival of that population segment (Beston 2011). Cub and yearling survival are other population parameters of interest to managers and expandable radio collars that allow for substantial body growth have been developed for cubs and yearlings (Vashon et al. 2003). Whichever age classes are monitored, it is important to

determine sample sizes needed to provide an estimate that will meet study objectives. For example, if an agency desires to detect a 5% decrease in annual adult female survival, it is important to know how many radio-collared animals would be required to meet that objective. In general, precision of survival estimates can be high (e.g., confidence interval width <0.10) even when sample sizes are moderate (e.g., 20–30 females/year), although Brongo et al. (2005b) suggested that this requires monitoring for at least five years to obtain reliable estimates of trend. Further, large samples may be required to isolate sampling variance from process variance in parameter estimates (Harris et al. 2011, Mace et al. 2012).

Modern radio collars often have activity sensors that emit uniquely pulsed mortality signals when collar stops moving, presumably indicating the animal has died. If the carcass can be recovered, the cause of death may be determined which is usually not possible with mark-recapture methods. Radiotelemetry methods have greatly improved in recent years because of the integration of Global Positioning System (GPS) technology, satellite data transfer capabilities, smaller and lighter transmitter designs, and increased battery life. GPS collars have revolutionized the study of wildlife with the sheer volume of highly accurate location data that may be stored in the collar, sent to handheld receivers, or even sent directly to satellites and emailed to researchers. An added advantage of radiotelemetry methods for estimating survival is that other attributes of bear ecology (e.g., fine-scale movements, habitat use) can be examined as well.

Annual survival can be calculated by dividing the number of living animals after 1 year by the number originally collared. That calculation is accurate, however, only if all animals are collared at the same time and every animal is located on every occasion. If an animal is captured and collared halfway through the study period, for example, the survival estimate for the

population will be biased high because that animal has already survived half the sampling season whereas another animal that may have died is no longer available for sampling. Procedures have been developed to accommodate different starting dates for survival data (staggered entry design), which base survival rates on short intervals of time (e.g., 1 week) and whereby the number of surviving animals is divided by the number at risk, excluding animals whose signal was not located during that interval (Kaplan and Meier 1958, Pollock et al. 1990). The product of the individual survival rates during those sampling intervals (e.g., 52 weeks) produces an unbiased estimate of the annual survival rate. The method, in effect, estimates the time of death as the mid-point of the sampling interval. Thus, it is important in telemetry-based survival studies that the animals are located frequently and regularly. The Kaplan-Meier known-fate method has been implemented in Program MARK to estimate survival, thus enabling users to use information-theoretic methods for model selection. If telemetry data are not regularly collected, it may still be possible to obtain a reliable estimate of survival using nest survival models, also in Program MARK. Such data are sometimes referred to as staggered entry data. Unfortunately, no goodness-of-fit test for known-fate models is available. Therefore, there currently is no way to evaluate fit or adjust estimates of variance to account for possible overdispersion. In addition to monitoring adult survival, cub and yearling survival can be monitored by visually observing radio-collared adult females with cubs throughout the non-denning period (Elowe and Dodge 1989). Oftentimes, cubs can be treed and counted while the female remains nearby. Litter and cub survival can likewise be estimated using the known-fate or nest survival methods.

Mark-recapture methods

Black bear survival can also be reliably estimated with mark-recapture methods. Because emigration usually cannot be distinguished from mortality with mark-recapture methods, survival estimates from these models actually represent apparent survival (ϕ) which is the probability an animal lived *and* remained on the study area. With this method, animals are captured and marked (either traditionally or using genetic sampling) and their recaptures are monitored over time (usually years). A number of estimators using mark-recapture data have been developed, of which the Cormack-Jolly-Seber (CJS) method (Cormack 1964, Jolly 1965, Seber 1965) is most commonly used because it estimates only 2 parameters, detection probability (p) and ϕ . Other methods such as Jolly-Seber (Jolly 1965, Seber 1965) or robust design (Pollock 1982, Kendall et al. 1995) are more general because other population parameters can be estimated (e.g., abundance, population growth). The robust design combines open and closed population models by sampling multiple times within each year over the course of multiple years. The within-year (i.e., secondary) occasions allow estimation of detection probabilities and abundance, whereas across-year (i.e., primary) occasions allow estimation of other parameters such as survival, immigration, and temporary emigration from the study area. These models can accommodate covariates and can be extended to multi-state data types (Brownie et al. 1993) to estimate transition probabilities between different states, for example, between breeder and non-breeder status. One advantage of estimating survival with mark-recapture methods is that survival estimation is not as prone to capture biases as other parameters (e.g., N).

Finally, there may be potential to use band recovery methods, which are commonly used to estimate survival rates in birds, but have yet to be applied to bears. Brownie et al. (1985) developed a method whereby animals are tagged each year for a successive number of years and

tags are recovered when those animals are harvested or found dead. The advantage of that technique is that parameter estimates are not sensitive to capture biases (particularly capture heterogeneity) in the marking process (Nichols et al. 1982, Pollock and Raveling 1982). In addition to survival, the method also provides an estimate of recovery rate, the proportion of the marked animals that are killed and retrieved by hunters and then identified as a marked animal (Mace et al. 1994a). If marked animals do not emigrate from the area where the samples are recovered (i.e., hunted areas), the method returns true estimates of survival (S) rather than apparent survival (ϕ). However, if a large proportion of the marked population emigrates outside the areas open for hunting, the estimate of S will be biased low. Overall, data would have to be collected over a longer period of time and at greater expense to detect a 10% difference in survival compared with some other options discussed previously. The major advantage is that relatively few sample sites would have to be established and their spatial locations would be less strict than for estimating abundance because recapture rates are not being estimated, resulting in savings in personnel time required to obtain samples.

Survival simulations

To explore the influence that sample size, duration of study, and population characteristics have on the precision of survival estimates from radiotelemetry data, we conducted a suite of simulations in MATLAB using code modified from Harris et al. (2011) with published vital rate estimates of northeastern black bears (Table 4-5). Briefly, this simulation routine allows the user to vary parameters related to sample design (i.e., the number of individuals per age class monitored over a designated number of years) and population characteristics including cub, yearling, subadult, and adult survival, and fecundity. The model also uses variances of vital rate estimates to assess uncertainty in survival (or reproduction or population growth) estimates as

the number of years of monitoring increases. Parameter estimation can then be viewed in terms of the tradeoffs between sample size and precision, thereby providing an informed starting point for project design. The simulation routine also allows for defining covariance of vital rates, for example cub and yearling survival, although we followed the suggestion of Harris et al. (2011) and did not include such effects because of limited evidence of covariance in the literature.

Another factor not included in our simulations is the removal of sampling variance. Because of typically small samples, estimating and removing sampling variance is rarely done, resulting in less precise estimates from known-fate models (Harris et al. 2011). Whenever possible, however, sampling variance should be accounted for when estimating vital rates.

We reviewed the literature for estimates of vital rates for black bear populations in the Northeast, drawing on the summary provided by (Beston 2011). We initially considered combinations of estimates representing either best- or worst-case scenarios (i.e., highest or lowest vital rates from across studies), with the intent of capturing the extreme situations that managers may encounter with similar analyses. We elected, however, to use more realistic combinations of vital rates from real populations that black bear managers may be familiar with (Table 4-5). As an example population with lower values for the vital rates of interest, we chose a study in east-central Ontario (Kolenosky 1990). For an example of greater vital rates, we combined estimates from 3 studies in Virginia (Table 4-6). In all cases, variance of vital rate estimates were from the same study as the vital rate estimates themselves. In addition to using estimates from different populations, we varied the number of animals and the number of years monitored for each vital rate. For a small population design, we used combinations of 10 or 30 animals monitored per age class for 3, 5, 10, and 20 years. For a large population design, we used combinations of 30 or 100 animals monitored per age class for the same range of years. For

more details on simulation methods, see Harris et al. (2011), Doak et al. (2005), and our annotated MATLAB code (Appendix C). We assessed precision of estimates based on their CV.

For all age classes, survival estimates were least precise (largest CV) for the lower vital rate population (i.e., Ontario) with the smallest number of individuals ($n = 10$) monitored (Fig. 4-3). The lowest CVs were obtained with the largest sample size ($n = 100$) for all age classes, although the influence of low or high vital rates was less consistent. Specifically, adult and subadult survival rate estimates were most precise for the “low” scenario, whereas cub and yearling survival were most precise for the “high” scenario. These results likely reflect the magnitude of variance in the vital rate estimates used (Table 4-6), as cub and yearling estimates were more precise for the “high” population, and subadult and adult estimates were more precise for the “low” population.

We obtained rapid gains in precision up to 10 years of monitoring, with gains declining between 10 and 20 years (Fig. 4-3). In fact, CVs for all time period scenarios within each age class were within ~5% after 20 years of monitoring. As a general rule, increasing the years of sampling from 3 to 10 resulted in the same improvement in precision of estimate as increasing the number of individuals monitored from 10 to 100 per age class.

Reproduction

Black bear populations in the Northeast have relatively high fecundity (i.e., number of female cubs/breeding age female/year) and low age of first reproduction (i.e., primiparity; Beston 2011; Table 4-5). Reliable estimates of reproduction are important for predicting population growth rates and can reflect annual fluctuations in habitat conditions. Measures of female reproductive success for black bears include litter size, cub sex ratio, age of primiparity, and fecundity. These data are often used in concert with survival and age structure data to project population growth

using matrix or individual-based models. Primiparity, litter size, and cub sex ratios for black bears are usually estimated by radio-marking and monitoring female bears in den sites. True litter sizes will seldom be known because mortality occurs immediately after (and even prior to) birth. Thus, litter size estimates depend on when the cubs are counted, which can lead to estimation errors. For example, if litter sizes are based on placental scars (Klestil 2014) and cub survival is based on radio telemetry of cubs beginning at about 2 months of age, cub recruitment will be overestimated because mortality between birth and 2 months is not accounted for.

Reproductive tract methods

Female black bear reproductive tracts can be examined to count corpora lutea on ovaries and placental scars on the walls of the uterus. Corpora lutea indicate the number of eggs that were shed in the mammalian reproductive process each reproductive cycle and placental scars indicate the number of embryos that were implanted (Stickley 1962, Kordek and Lindzey 1980, Klestil 2014). Consequently, the average number of corpora lutea is generally greater than the number of placental scars because not all eggs will be fertilized and implanted. Similarly, not all placental scars will become successfully birthed fetuses, and that number will typically be greater than cub counts in winter dens. Reproductive tracts can only be obtained from dead bears and are thus dependent on harvest.

Den visits

Visiting black bear dens in winter can provide data on a number of reproductive parameters. Bear cubs are born in the den and may experience mortality prior to emerging in spring. Therefore, entering dens to count newborns provides a reliable estimate of litter size and sex ratio (McDonald and Fuller 2001, Samson and Huot 2001), unless mortality occurred prior to the den visit, which is difficult to confirm. The proportion of cubs observed the following year in

dens as yearlings can be used to estimate cub survival. Conversely, 1-year recruitment can be directly estimated (the number of female cubs recruited into the 1-year-old age class per adult female). Research suggests that remote photography methods could be used in conjunction with den visits to improve accuracy of reproductive and cub survival estimates (Bridges et al. 2004).

Direct observations

Throughout most of their forested range, black bears generally have low sightability. Thus, unless bears are radio-collared, visual observations for estimating reproductive parameters is typically not feasible in the Northeast. In open habitats or places where black bears develop strong preferences for foraging locations (e.g., berry patches, garbage bins, agricultural fields), observations may be used for estimating age of first reproduction and fecundity. If a relatively large sample of radio-collared females exists and den visits are not feasible or risk cub abandonment, researchers can use telemetry to approach them to tree cubs in the field after den emergence. This technique enables estimation of litter size, cub and yearling survival, age of primiparity, and fecundity, assuming dependent offspring can be reliably associated with their mother, which may be difficult given that females are known to occasionally adopt cubs (Alt 1984). As with known-fate analyses, observations should be frequent to obtain sufficient precision and to reduce bias from undercounting that sometimes occurs using this method. Differences in sightability due to group size, landcover and topography, individual behaviors, and survey effort must all be considered when relying on observation data, particularly when few marked individuals are available to help calibrate results (Jonkel 1971).

Mark-recapture methods

One alternative to estimating recruitment that does not necessarily require handling animals is through mark-recapture modeling. Specifically, the Pradel (1996) temporal symmetry models,

which use detection histories both forward and backward in time, can provide robust estimates of not only realized population growth (λ), but recruitment (f), apparent survival (ϕ), and seniority (γ). Apparent survival, which includes both true survival and emigration, models detection events in standard forward-time, conditional on the first detection of individuals. Recruitment can be derived as a function of ϕ and γ , the latter being defined as the probability that, if an animal was alive and in the population in time period i , it was also alive and in the population at $i-1$. Seniority, which is the proportion of the population that was detected in the previous sample, can be viewed as the reverse-time analogue of survival (Pradel 1996; Hines and Nichols 2002). Simulation studies have explored the performance of Pradel models for estimating these important parameters (Hines and Nichols 2002, Stetz et al. 2010), concluding that estimates are generally unbiased and precise, given reasonable amounts of data. Further, empirical studies with bears and other taxa have compared Pradel to traditional methods (Sandercock and Beissinger 2002, Clark and Eastridge 2006), and have found them to perform at least as well, potentially providing useful insights into the causes of population change as well as precise estimates (Boulanger et al. 2004a).

Genetic methods

Although outside the scope of our evaluation, it is worth noting that in some special cases it may be possible to measure recruitment by directly documenting reproduction through parentage analyses (i.e., pedigrees). For small, intensively monitored populations it may be possible to derive precise estimates of reproduction and recruitment via pedigrees (Kasworm et al. 2007). For larger populations, however, it may be difficult to sample a large enough proportion of the population to do so.

Fecundity simulations

In addition to providing estimates of precision for survival, the simulations described in the Survival section allowed us to evaluate influence of sample size and variance on precision of fecundity estimates. We again used the MATLAB simulation routine of Harris et al. (2011) with the vital rate estimates presented in Table 4-5, varying the sample size and number of years of monitoring (see annotated MATLAB code, Appendix C).

Similar to results of the adult survival simulations, the differences between the fecundity of these populations was quite pronounced, with a considerably lower, but more precise, estimate for the Ontario population compared with the composite Virginia scenario. As with adult survival, the greatest gains in precision were obtained from increasing the sample size of radio-monitored bears as opposed to duration of monitoring (Fig. 4-4). We observed the same general improvement in precision as the duration of monitoring increased, with the most rapid gains occurring in early years. Again, increasing the sampling duration from 3 to 10 years was approximately equivalent to increasing sample size from 10 to 30 or from 30 to 100 individuals per age class (Fig. 4-4).

Population Growth

Population growth refers to changes in abundance over time (i.e., increases, decreases, or no change) reflecting the cumulative influences of birth, death, immigration, and emigration on the demography of a population (Pollock et al. 1990, Mills 2012). Population growth is the most important parameter to many black bear managers, and there are many potentially reliable methods to estimate it even across a large gradient of population densities, trajectories, and funding levels. Across most of black bear range, however, Garshelis and Hristienko (2006) found that state and provincial estimates of black bear abundance over time often reveal growth

patterns that differed from true trends. Although they speculate these discrepancies were sometimes due to managers using conservative estimates to avoid overharvest (Garshelis and Hristienko 2006), they may also be due in part to movements of bears among jurisdictions, which could easily confound estimates of density or growth rate (Pollock et al. 1990, Kendall et al. 1995).

Such movements across management boundaries may also result in source-sink dynamics (Pulliam 1988) if differences in habitat or management are strong enough to influence survival or reproduction among subpopulations. And similar to the findings of Garshelis and Hristienko (2006), failure to account for meta-population dynamics may mask the true performance of the larger population. Given the extensive opportunities for exchanges of animals among populations, or at least jurisdictions, in the Northeast, regional bear management would benefit by considering the operational definition of sources and sinks developed by Runge et al. (2006) where a source is any population that has a net positive contribution to the growth of itself (via recruitment) and other populations (via emigration). As such, it is possible that a population that appears to be experiencing negative growth could in reality be a source if it is successfully exporting a large number of animals to surrounding populations (Mills 2012, Newby et al. 2013). Recognizing such dynamics could provide valuable insights into larger population processes including how bears respond to differences in management and habitat across this diverse region.

In its simplest form, population growth is calculated by dividing population size during a particular period of time by population size of the previous time period, $\lambda = N_t/N_{t-1}$ (i.e., realized population growth). This differs from projected population growth rate estimates, which use estimates of population vital rates such as survival and reproduction to predict how the

population will change in the future. Below, we discuss various advantages and disadvantages of each measure, along with a range of methods to estimate them.

Population reconstruction

Population reconstruction has been used to monitor bear population growth and estimate abundance, recruitment, survival, and harvest rate. The technique has been used in fisheries management for decades (Fry 1949, Pope 1972), but was popularized for wildlife management by Downing (1980), who estimated minimum population size and trend for white-tailed deer (*Odocoileus virginianus*). The technique is based on total harvest by year and a sample of ages of harvested animals to back-calculate the age distribution at the time the oldest animals were born, thus estimating minimum population size. The population size estimate is a minimum because deaths from causes other than harvest are not included. The greatest advantage of Downing reconstruction is that it requires only the total annual harvest and a subsample of annual harvest with age data (Downing 1980). Thus, no additional costs are incurred other than cementum annuli analysis to age a subsample of the harvested population. Davis et al. (2007) found that such reconstruction techniques performed best when harvest rates were high and natural mortality was low, as may be the case with bears in the Northeast. The authors also found, however, that the estimates of λ could be negatively biased if harvest rates trended even moderately upward (1%/yr) or were highly variable. This could be the case in many jurisdictions because bear harvests are greatly affected by food availability and other factors, and many changes in harvest regulations have occurred in recent years.

Population reconstruction relies on the assumption that harvest and natural mortality rates do not change over time. Additionally, this method is based on the assumption of a stable age distribution and a constant harvest reporting rate. Population reconstruction relies on a number

of other assumptions that are difficult to meet in many wildlife studies. Williams et al. (2002) provided a comprehensive critique of population reconstruction and identified 3 main flaws of the method: 1) survival estimates are inferred from a population model; 2) biases in the reconstruction will manifest themselves in the estimates; and 3) even if assumptions are met, estimates of sampling variation will not include the sampling error of the harvest. Also, Williams et al. (2002) suggested that population reconstruction based on age-at-harvest data alone is theoretically flawed because the method does not account for non-hunting mortality and the age and sex distribution of the harvest is probably not reflective of the sampled population. They concluded that population reconstruction should not be considered if more reliable estimation methods are available (Williams et al. 2002).

To address these and other problems, Gove et al. (2002) introduced maximum likelihood methods to estimate harvest rates and population size given auxiliary data on survival from radiotelemetry and hunter reporting rates from a telephone survey. One of the advantages of using maximum likelihood techniques for population reconstruction is that various assumptions (e.g., constant harvest, increasing harvest) can be tested using information-theoretic methods (Burnham and Anderson 1998) and statistical uncertainty can be measured. Recently, attention has been placed on model evaluation for statistical population reconstruction through the use of residual analyses, sensitivity analyses, and model predictions as reviewed in Skalski et al. (2012). Model evaluation differs from model selection (i.e., based on AIC values) in that goodness-of-fit measures are used to determine how well the observed data match what is expected given a certain model. Model selection, however, is simply the relative support for each model among a given set of models that may, in theory, all be inappropriate (Johnson and Omland 2004). Thus, model evaluation precedes model selection and averaging, but does not

replace it. One suggested approach is to delete one or more consecutive year's data from the beginning or end of the series to determine model stability. If results change substantially, it is likely that inadequate data are being used. Estimability of such population reconstruction models requires auxiliary data, as even the simplest of models is over-parameterized when only age-at-harvest data are used (Skalski et al. 2012). These auxiliary data can include catch per unit or harvest effort, index data, mark-recapture, or radiotelemetry data (Skalski et al. 2007, 2012). Such combinations would permit an integrated analysis of data collected by many jurisdictions, be more statistically rigorous, and provide estimates of precision for all parameters. Further, statistical population reconstruction models appear robust to pooled age classes (i.e., when actual ages are not known), providing greater flexibility of use (Skalski et al. 2012). Unfortunately, these relatively complex methods are still in development and a detailed treatment is beyond the scope of our review.

Integrated population models

Integrated population models can be used to estimate population growth for black bears by integrating multiple types of data. One advantage of integrated models is that they can synthesize various relevant data into a single analysis. This approach can be considered similar to Downing (1980) population reconstruction methods that are scaled by intermittent abundance estimates, but that can also be used to investigate relationships between harvest rates and factors such as hunter effort. These methods can be particularly powerful in populations where hunting is the primary source of bear mortality, which is true for most managed bear populations (Garshelis 1990, Beston 2011). Fieberg et al. (2010) used this approach to synthesize age-at-harvest data, periodic large-scale estimates of abundance, and measured covariates thought to affect black bear harvest rates. The authors concluded that integrated population models were

unbiased and hold great promise for black bear population monitoring, but they recognized the assumption of age distribution being representative of the greater population may often be unreasonable. Instead of maximum likelihood, Conn et al. (2008) used Bayesian analysis to estimate similar population parameters for black bears, again by coupling age-at-harvest data with mark-recapture data. Further, Chandler and Clark (2014) used Bayesian analysis coupled with mark-recapture data to develop a spatially-explicit integrated population model. The computational and conceptual complexities of this approach are considerable, and we refer readers to Buckland et al. (2004), Abadi et al. (2010), and Schaub and Abadi (2011) for detailed reviews.

Demographic analyses

Growth rate can be estimated from vital rate statistics in matrix or individual-based projection models but may require robust estimates of population size, age- and sex-specific survival and fecundity, sex ratios, population age or stage structure data, and age of primiparity (Clark and Eastridge 2006, Clark et al. 2010). Sometimes called life-table methods or demographic analyses (Harris et al. 2011), they are data intensive, often requiring both mark-recapture and radiotelemetry techniques. Also, harvest rates can easily be accommodated in population projections to evaluate different management alternatives. Like any projection, assumptions are usually based on constant environmental conditions and variance, so these models should be updated often as uncertainty increases dramatically the longer the time period of the projection (Caswell 2001).

Matrix population models to estimate population growth and can be used with either age-based or stage (e.g., juvenile, adult) data. The age-based Leslie (1945) matrix requires that each animal either die or advance to the next age, which is always a constant time step. Conversely,

stage based, or Lefkovitch (1965), matrices are more flexible, allowing animals to transition between any, or remain in the same, stage. As the exact age of bears can be difficult to determine, stage-based matrices are more commonly used, although defining stages important to bear biology, and to which animals can be reliably assigned, is important (Mills 2012).

Assuming vital rates of a population remain relatively constant, most matrices will eventually converge on a stable stage (or age) distribution, although these can be disturbed by management actions or harvest, at least temporarily. Stochastic models can address natural or management related variance in population processes by either randomly selecting from a range of known values or by drawing vital rates from a distribution of values. Given that increasing variance in population processes tends to decrease growth rates, it is important to include these effects in projection models whenever possible (Doak et al. 2005).

For long-lived species that tend to produce few offspring with high survival, such as black bears, population growth rates are generally more sensitive to adult female survival than reproductive rate (Pfister 1998, Gaillard and Yoccoz 2003). In other words, changes to adult survival rates are expected to have a larger effect on population growth than other vital rates. Given that the magnitude of vital rates is not uniform (e.g., survival rates are always 0-1 whereas reproduction can be in the thousands), sensitivities are often scaled to describe how a proportional change in a vital rate results in a proportional change in population growth (Doak et al. 2005). These rescaled values, called elasticities, can be compared across studies, can be summed to predict overall effects on a population, and can be used to obtain insights into how a population will respond to changes in vital rates due to any number of causes via sensitivity analyses (Mills 2012). A number of matrix-based software tools (e.g., Poptools; PopTools version 3.2.5 <http://www.poptools.org/>) have been developed that enable users to perform

sensitivity analyses and to explore the effects that perturbations to vital rates have on population growth. Other, individual-based models have been used to model bear population growth (e.g., Riskman, GAPPS, R package *demonic*). The alternate-year breeding in black bears is more easily accommodated in these individual-based models and thus have particular appeal.

Precision of life table-based estimates of population growth are strongly correlated with the precision of age-specific vital rate estimates. Because black bear population growth is most sensitive to changes in adult and subadult female survival and fecundity, precise estimation of those parameters is particularly important to obtain reliable estimates of projected population growth (Freedman et al. 2003, Mitchell et al. 2009). Generally, the precision and accuracy of vital rate estimates increases with the number of individuals monitored and the duration of monitoring (Harris et al. 2011). Even with long-term monitoring, many life table analyses estimate λ imprecisely with 95% confidence intervals (CIs) that often overlap 1.0, indicating the possibility of a stable, declining, or increasing population. Perhaps the most difficult parameter required for many projection models is an estimate of the standing age distribution. Unless a population is sampled almost completely, some age and sex classes are usually more susceptible to sampling, which can lead to bias (Conn and Diefenbach 2007). It is possible to project asymptotic population growth assuming a stable age distribution, but this is probably rare for black bears because of their long lifespan and annual fluctuations in abundance of food resources.

Population projection simulations

We again used a MATLAB simulation routine modified from Harris et al. (2011) to explore the influence of study design, vital rate values, and vital rate variances on estimates of population growth rate based on matrix projections using survival and fecundity rate estimates. Managers

are typically most interested in the lower bound of λ estimates, so we assessed precision of λ estimates based on the width of 90% confidence intervals, which produces a 5% probability that the estimate falsely exceeds true λ , assuming accurate estimates are used with a reasonable model (Harris et al. 2011). We used vital rate estimates and variances from the published literature on northeastern black bears (Table 4-6) to parameterize the simulations.

For all scenarios, precision rapidly improved as the number of monitoring years increased with relatively small gains between 10 and 20 years of monitoring (Fig. 4-5). Consistent with Harris et al. (2011), we found the greatest improvements in precision for all scenarios by increasing the number of monitored litters. When considering single vital rates, however, the greatest improvement in precision for the lower vital rate scenarios (i.e., Ontario) was gained through monitoring more adults, whereas the higher vital rates scenarios (i.e., Virginia) showed the greatest improvement by monitoring fecundity more intensively. This latter finding may seem somewhat contradictory to expectations given the known importance of adult female survival on population projections (Garshelis et al. 2005, Beston 2011), and may have been due to the very small variance used in the lower vital rate scenario. Variance of adult survival estimates is, however, typically low so gains in precision can be more easily accomplished with other vital rate estimates, as others have found (Mitchell et al. 2009). This tendency to canalize traits (Gaillard and Yoccoz 2003) of greatest importance to population growth has been observed in a large number of long-lived species (Gaillard et al. 1998). An important consideration is that density dependent responses are likely to manifest in such canalized or buffered traits later than in more variable stages, such as juvenile survival (Gaillard et al. 1998).

Mark-recapture

The most intuitive method of estimating population growth rate is to compare estimates of abundance at two or more points in time. Consequently, time series of abundance estimates have often been used to estimate λ , which may appear problematic given the challenges we discussed previously, but there are some potential advantages to this approach. For example, if N is consistently biased over time, the ratio (λ) may be relatively unbiased. Further, many of these estimators allow the use of covariates to improve estimate bias and precision, including the effects of variable sampling effort or environmental factors influencing sampling or animal behavior. Conversely, time series are often short relative to the dynamics of studied populations, making it difficult to detect, let alone explain, differences in abundance over time (Humbert et al. 2009).

As with other techniques to estimate population growth, time series analyses should include estimates of both process and sampling variance, although this has often not been the case (Mills 2012). In fact, two of the most well-known approaches to estimate growth rates fail to incorporate both forms, with one attributing all variance to observation error (Caughley 1977), whereas the other assumes that abundance is known exactly and all variance is due to population processes (Dennis et al. 1991). Although these may work reasonably well if the source of variance is strongly skewed (e.g., populations are essentially censused) and the appropriate method used, such situations are rare. More likely, the opportunity for substantial and confounded variance in both observation and population processes can be better accommodated by the exponential growth state-space model of Humbert et al. (2009). This model has been shown to work well under a wide range of conditions (i.e., magnitude and nature of variance), although it requires a minimum of five abundance estimates over a 10-year period (Mills 2012).

In fact, the authors suggest that investing resources in obtaining fewer, more precise estimates is better than more frequent, less precise ones (Humbert et al. 2009, Mills 2012).

Open-population mark-recapture models are generally more robust to capture heterogeneity biases than are abundance estimators (Pollock et al. 1990, Schwarz 2001). Based on that notion, Pradel (1996) and Schwarz and Arnason (1996) developed maximum likelihood methods for estimating population growth (λ) directly from mark-recapture data without the need for estimating N . These temporal symmetry models use detection data with normal ordering in time to estimate recruitment (f) and seniority (γ) concurrently with using the data in reverse order to estimate apparent survival (ϕ) (Hines and Nichols 2002). When used with the robust-design (Kendall et al. 1995) these models can also estimate abundance. Subsequent research has shown that the Pradel method is robust to moderate capture heterogeneity, the most difficult of all capture biases to estimate (Schwarz 2001, Hines and Nichols 2002, Marescot et al. 2011). Clark and Eastridge (2006) used the Pradel model with live-capture data in a small population of black bears in Arkansas collected over a period of 5 years to produce a precise (CV=7%) estimate of population growth. Those estimates were consistent with estimates from hair-sampling and population modeling based on radiotelemetry data. The Pradel model has been used to investigate the effect of salmon availability on grizzly bear population growth in British Columbia, Canada (Boulanger et al. 2004a). More recently, bear rub tree detection data were successfully used with a Pradel model in Banff National Park, Alberta, to estimate λ for grizzly bears (Sawaya et al. 2012).

Mark-recapture methods not only evaluate changes in the population over time, but enable researchers to evaluate the proximate causes of the population trend (e.g., survival, fecundity). Also, detection probabilities can be lower than those desired for estimating

abundance with closed or robust design methods, thus making this technique more cost effective. Hines and Nichols (2002) found, however, that behavioral differences among animals could lead to biased estimates, particularly with short-term data sets. Sampling sites should be systematically spaced so that all bears have a reasonable opportunity for detection and locations should be changed annually to reduce behavioral bias. Recent work on adapting Pradel (1996) models to spatially explicit data may relax some of those restrictions (Royle et al. 2013b).

Open population mark-recapture simulations

We conducted a suite of open population simulations with the Pradel (1996) model in program MARK to provide reference points for estimating population growth rate in black bear populations in the Northeast. Again, we reviewed the literature and extracted estimates of λ , ϕ , and p from DNA-based mark-recapture studies (Table 4-7). We simulated populations of 100 or 500 bears that were either monotonically increasing ($\lambda = 1.05$) or decreasing ($\lambda = 0.95$) for 5 or 10 years, with moderate or relatively high detection probabilities (0.38 or 0.70, respectively). We conducted 250 replicates per scenario, and assessed model performance with average PRB, CV, and CIC.

Results of our simulations using the Pradel model based on noninvasive detections found that all scenarios produced unbiased (i.e., PRB < 1%) and precise (i.e., CV < 5%) estimates of population growth rate. Simulations based on larger populations and longer studies performed best. Despite being unbiased, however, those scenarios had extremely small confidence intervals resulting in low CIC values (Fig. 4-6). Population abundance did not seem to affect CIC, but reflecting the decreasing CV of estimates, longer studies tended to have poorer CIC than shorter studies. Greater detection probabilities did not effectively improve estimator performance; even the near doubling of female detections from $p = 0.38$ to $p = 0.7$ resulted only in a 1.4%

improvement in CV for the sparsest data scenario (i.e., scenario 2, smaller and declining population with lower survival). Our results suggest that even with relatively small populations and moderate detection probabilities, robust, sex-specific estimates may be obtained within 5 years of sampling. These population and sampling parameters are very similar to those of (Coster et al. 2011) who conducted a study on a small area (223 km²) with 51 grid cells of 5.2 km².

Tradeoffs will exist with field studies, which will almost certainly encounter capture biases, annual variation in λ and ϕ , and the realities of sampling wild populations. Data from field studies, however, can allow use of more complex models to accommodate those realities, including robust design or mixture models that make use of covariates and potentially multiple data types (Boulanger et al. 2004a, 2006, 2008; Stetz et al. 2010). Therefore, these scenarios should be viewed as a starting point for exploring more realistic study designs depending on the specific objectives, population characteristics, and available resources.

Population Monitoring Scenarios

We provide study design options for monitoring American black bear populations based on the collective findings from published studies and results of our simulation analyses. Although we initially developed these scenarios and study design options for jurisdictions in the Northeast, they are applicable to most black bear populations in North America. For simplicity, we focus our discussion and evaluation of black bear monitoring options on the methods that have been used in previous research in the Northeast (Table 4-8) for estimating the two population parameters most important to managers: abundance and population growth. We present our evaluation of monitoring options for 6 population scenarios developed in collaboration with biologists and managers familiar with the challenges of monitoring bear populations across this

region. We considered situations ranging from small to large population sizes and from declining to stable or increasing population trends. We based our population size classes of small, ($N \leq 500$), medium ($N = 500-2,500$) and large ($N > 2,500$) on the range of black bear population sizes found in Northeastern jurisdictions or management units. We pooled monitoring options for stable and increasing populations because most managers already classify population trends accordingly. Although some managers may not know the exact status of their populations, the scenarios we present here should provide useful guidance for study design.

Small, declining population ($N \leq 500$, $\lambda < 1.0$)

Populations with this status are of the greatest management concern and advantages of monitoring should be carefully weighed against the potential disadvantages. For example, mortality due to capture and handling is an increasing concern as population size becomes smaller because management efforts are often directed to increasing adult survival. Managers may consider monitoring adult survival rather than population growth for small, declining populations. Accurate and precise estimates are particularly important for small, declining populations because there is little room for error. The value in monitoring smaller populations has been questioned, however, because resources could be used more effectively to secure habitat or reduce human-bear conflicts. Nonetheless, we recommend using DNA-based mark-recapture (e.g., robust design Pradel model) to estimate abundance and population growth for small, declining populations because this method does not involve capture or handling, is affordable at small scales, can provide precise estimates of λ in a shorter time period compared with radiotelemetry, and may provide insights into drivers of population changes through use of covariates (Table 4-6).

Because DNA-based mark-recapture abundance estimates for small populations generally have poorer precision than larger populations, managers must compensate by increasing sampling effort (e.g., number of occasions, number of sampling sites per unit area) to achieve the same level of precision. For example, a large population study may achieve a CV < 20% for abundance with 4 sampling occasions, whereas a small population would require at least 7 occasions to obtain a CV < 20%. Open population or SECR models should be considered as smaller areas may amplify capture heterogeneity because a large proportion of animals have home ranges extending beyond the edge of sampling grid.

Small, stable or increasing population ($N \leq 500$, $\lambda \geq 1.0$)

Black bear populations of this size are typically not harvested so population reconstruction is not an option (Table 4-8). If the population is small and growing, then an index such as bait-station surveys may be sufficient to monitor gross changes in abundance or assess range expansion. Managers interested in estimating abundance or population growth should consider DNA-based mark-recapture methods. Population growth aside, these methods provide the best baseline data on population size, density, and sex ratios to use as benchmarks to gauge future population dynamics related to management actions. Radiotelemetry may also be considered to estimate population growth, but managers should be aware that at least 5 years of monitoring will be required, and more if vital rates are highly variable, to obtain a precise estimate. Again, because DNA-based mark-recapture abundance estimates for small populations generally have lower precision than larger populations, managers must compensate by increasing sampling intensity (e.g., number of occasions, number of sampling sites) to achieve their desired level of precision.

Medium, declining population ($N = 500-2,500, \lambda < 1.0$)

We suggest that managers interested in abundance, or more appropriately, density, use DNA-based mark-recapture as these methods provide the most reliable estimates (Table 4-8).

Managers interested in monitoring population growth may consider using either DNA-based mark-recapture or radiotelemetry-based methods. Radiotelemetry-based methods may be inappropriate when the age distribution of the population is believed to be non-stable or if management decisions must be made prior to acquiring sufficient data to use projection models (Table 4-8). Although both methods are suitable for estimating population growth, if capture-related mortality is not a concern, radiotelemetry is the better method to use for this scenario as it may detect the drivers of trends better than mark-recapture methods (Table 4-9), which may be valuable to long-term management.

Medium, stable or increasing population ($N = 500-2,500, \lambda \geq 1.0$)

DNA-based mark-recapture may be a viable option for managers interested mainly in monitoring population growth because that can be accomplished with lower capture probabilities, meaning that fewer samples need to be genotyped and sites could be sampled for fewer occasions. When estimating abundance, however, the number of sample sites needed for larger populations may be daunting, particularly if home-range sizes are small. In such cases, estimating population growth rates using radiotelemetry-based methods may be a better alternative.

Large, declining population ($N > 2,500, \lambda < 1.0$)

As described previously, sampling requirements may be too intensive to make DNA-based mark-recapture feasible for estimating abundance of large populations, and may not be the most important parameter for effecting sound management. Population growth projection using radiotelemetry or DNA-based mark-recapture with open population models would probably be

better alternatives. Also, the economies of scale are better for radiotelemetry than for DNA-based mark-recapture because the precision of parameter estimates from known-fate models is independent of population size, whereas costs increase with population size for DNA-based studies (i.e., more samples collected and more bears to identify).

Large, stable or increasing population ($N > 2,500$, $\lambda \geq 1.0$)

A common scenario among North American jurisdictions are large, stable or increasing black bear populations. In these areas, the establishment of regional monitoring programs is an important consideration, particularly where bear populations are shared among multiple jurisdictions (e.g., Pennsylvania and New York, or Maryland and West Virginia in the Northeast). Pooling resources to collaboratively monitor population growth using radiotelemetry or DNA-based mark-recapture techniques would provide long-term benefits. We suggest that managers interested in estimating abundance of these large populations use DNA-based mark-recapture because this method provides the most reliable estimates. This would most likely entail a series of estimates for population subsets and using extrapolation techniques. As in the previous example, use of population projection or estimation of population growth using mark-recapture methods is a more reasonable regional or jurisdiction-wide approach, although SECR methods based on cluster sampling may make DNA mark-recapture more feasible at these scales.

CONCLUSIONS

Many suitable monitoring options exist for black bear managers and there is no single appropriate method for all bear populations and management objectives. One of the greatest dilemmas for bear managers today is that the monitoring methods that provide the most accurate and precise estimates of population parameters (i.e., radiotelemetry, DNA-based mark-recapture) are also the most expensive. Less expensive methods are ultimately a poor investment when

money and resources are used to collect data that reveal little about bear populations and provide limited inference regarding the drivers of population change.

When developing a program for black bear population monitoring, managers should first identify the parameter(s) of interest (e.g., abundance and density, survival and reproduction, population growth) that would meet well-defined management objectives. Selection of monitoring techniques should then focus on assessing which techniques can produce estimates with the desired level of accuracy and precision. Once these techniques have been identified, managers can then consider the potential advantages and disadvantages of each, along with any special considerations (e.g., data collection requirements), to select effective techniques monitoring program (Table 4-8).

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TABLES

Table 4-1. Mark-resight model assumptions and requirements^a (from McClintock and White 2012).

Model	Marks are			
	Number of marks known	individually identifiable	Geographic closure	Sample with replacement
Immigration-emigration logit-normal	Required	Not required	Not required	Not allowed
Logit-normal	Required	Not required	Required	Not allowed
(Zero-truncated) Poisson log-normal	Not required	Required	Required	Allowed

^a Note that all models require demographic closure within primary sampling occasions.

Table 4-2. Parameter definitions and values used in mark-resight simulations of the Poisson log normal estimator (PNE) (McClintock and White 2009) in program MARK to simulate estimation of American black bear population abundance.

Simulation inputs			Estimates from simulations		
Parameter	Definition	Value	PRB ^a	CV ^b	CIC ^c
N_{male}	Abundance (M)	300	-27.7%	9.1%	5.6%
N_{female}	Abundance (F)	300	-21.2%	9.2%	23.7%
n_{male}	No. known marks (M)	100			
n_{female}	No. known marks (F)	100			
Σ	Individual detection rate heterogeneity	0			
α_{male}	Mean detection rate (M) ^d	0.55			
α_{female}	Mean detection rate (F)	0.5			
U_{male}	No. unmarked individuals (M)	200			
U_{female}	No. unmarked individuals (F)	200			
ϕ_{male}	Apparent survival (M)	0.85			
ϕ_{female}	Apparent survival (F)	0.9			
γ'	Transition probability ^e	0.05			
γ'	Probability of not transitioning to previous state	0.5			

^a PRB = percent relative bias $((\text{estimate} - \text{truth}) / \text{truth}) \times 100\%$.

^b CV = coefficient of variation.

^c CIC = percent of simulations with confidence interval including true abundance.

^d Mean detection rate for primary sampling occasion.

^e The probability of leaving the study area (i.e., transition from observable to unobservable state).

Table 4-3. Population and sampling parameters used in closed population abundance simulations with WiSP package (Zucchini et al. 2007) in program R. Minimum and maximum capture probabilities were per occasion (k). Not every combination was run because of computational limitations.

Study area dimension (no. grid cells east- west)	Study area dimension (no. grid cells north-south)	Population abundance (N)	No. sampling occasions (k)	Min. capture probability (p)	Max. capture probability (p)
100, 200	100, 200	100–900	5, 7, 10	0.005	0.5

Table 4-4. Population and sampling parameters used in SECR simulations of American black bear (*Ursus americanus*) populations using the secr package (Efford 2012) in Program R. Not all combinations were run because of computational limitations.

Density (no. bears/km ²)	g_0^a	σ^b (m)	No. sampling occasions (k)	Grid size	Site spacing (m)
0.1	0.05	400	5	10 × 10	1,000
0.5	0.10	1,000	7	25 × 25	2,000
1.0	0.15	2,000	10		3,000
1.5	0.20	3,000			
	0.25				

^a g_0 = average detection probability at the individual's center of activity.

^b σ = shape of the half-normal detection function; we converted σ into an estimate of home-range radius in R using $(qchisq(0.95, 2)0.5)^* \sigma$.

Table 4-5. American black bear (*Ursus americanus*) survival and reproductive rate estimates from studies in the northeastern United States and eastern Canada.

Jurisdiction	Adult female survival ^a	Subadult female survival	Cub survival	Age at first reproduction	Average litter size	Fecundity	Reference
MA	0.87						Cardoza, personal communication ^b
MA		0.66	0.59	3.70			Elowe and Dodge (1989) ^b
MA			0.53-0.63				Fuller (1993) ^b
MA			0.74				McDonald and Fuller (2001) ^b
ME	0.96	0.78	0.79	4.91		0.58	McLaughlin (1998) ^b
ME	0.84	0.76	0.65	5.10		0.61	McLaughlin (1998) ^b
ME	0.96	0.71	0.59	4.47		0.58	McLaughlin (1998) ^b
NH	0.87		0.74				Timmins (2008) ^b
NJ	0.94		0.72	3.00			McConnell et al. (1997) ^b
NJ			0.70				New Jersey (2004) ^b
ON	0.87	0.78	0.46	7.81			Obbard and Howe (2008) ^b
ON		0.86	0.44	6.70			Obbard and Howe (2008) ^b
ON	0.84	0.76	0.53	6.17		0.46	Yodzis and Kolenosky (1986), Kolenosky (1990) ^b
PA			0.84	3.20	3.00		Alt (1980, 1981, 1989) ^b
PA	0.59						Diefenbach and Alt (1998) ^b
PA				3.53		0.62	Ternent and Sittler (2007) ^b
QC	0.85		0.71	6.00		0.47	Jolicoeur et al. (2006) ^b
QC	0.96			5.33		0.58	Jolicoeur et al. (2006) ^b
VA	0.93		0.70	4.00		0.50	Carney (1985) ^b
VA		0.78	0.72				Hellgren (1988) ^b
VA	0.87			4.00	2.30	0.57	Hellgren and Vaughan (1989) ^b
VA	0.73		0.73	3.89		0.66	Kasbohm et al. (1996) ^b

VA	0.81						Klenzendorf (2002) ^b
VA		0.87					Lee and Vaughan (2005) ^b
VA			0.70	2.83		0.69	(Ryan 1997) ^b
VA	0.92	0.90	0.87	3.80	2.50		Bridges et al. (2011)
VT			0.26	5.33		0.87	Hammond (2002) ^b
WV	0.76	0.79		3.11	2.65		Ryan (2009)

^a We defined an adult bear as >3 years old and subadults as bears 2–3 years old.

^b See Table S1 in Beston (2011)

Table 4-6. Estimates for American black bear (*Ursus americanus*) vital rates and their variances used in demographic analysis simulations.

Rates	Vital rate estimates					Variance estimates				
	Cub <i>S</i> ^a	Yrlg <i>S</i>	Subad <i>S</i>	Adult <i>S</i>	Fecundity	Cub <i>S</i>	Yrlg <i>S</i>	Subad <i>S</i>	Adult <i>S</i>	Fecundity
Low ^b	0.53	0.76	0.87	0.84	0.4570	0.00778	0.00793	0.00213	0.00063	0.00049
High	0.73 _c	0.87 _d	0.93 ^c	0.93 ^e	0.6875 ^c	0.00493	0.00435	0.00360	0.00271	0.02000

^a Survival estimate.

^b Kolenosky (1990); 241 adult females monitored.

^c Ryan (1997); 34 bears monitored (6M, 28F).

^d Lee and Vaughan (2005); 54 yearling bears monitored (34M:20F).

^e Carney (1985).

Table 4-7. Population and sampling parameters used with Pradel (1996) open population model simulations in program MARK to estimate population growth rate of American black bear (*Ursus americanus*) populations.

Scenario	N	λ	φ_M	φ_F	p_M	p_F	No. years
1	100 or 500	0.95	0.93	0.87	0.4	0.38	5 or 10
2	100 or 500	0.95	0.85	0.80	0.4	0.38	5 or 10
3	100 or 500	1.05	0.93	0.87	0.4	0.38	5 or 10
4	100 or 500	1.05	0.85	0.80	0.4	0.38	5 or 10
5	100 or 500	0.95	0.93	0.87	0.7	0.70	5 or 10
6	100 or 500	0.95	0.85	0.80	0.7	0.70	5 or 10
7	100 or 500	1.05	0.93	0.87	0.7	0.70	5 or 10
8	100 or 500	1.05	0.85	0.80	0.7	0.70	5 or 10

Table 4-8. Suitability of monitoring methods for estimating population parameters for American black bears (*Ursus americanus*) in the Northeast.

Method suitability ^a	Bait stations	Population reconstruction	Radiotelemetry ^b	Mark-recapture					Remote cameras
				Biomarking	DNA-based	Ear tags	Harvest	Observations	
Parameter of interest									
Abundance	+	+		+	++	+	+	+	+
Density			+	+	++	+	+	+	+
Survival			++	+	+	+	+	+	+
Reproduction			++	+	+	+	+	+	+
Population growth	+	+	++	+	++	+	+	+	+
Advantages									
Proven track record of precise estimates		+	++		++	+			
Identify individual bears ^c			+		++	+	+	+	
Determine sex ratio		+	+	+	++	+	+	+	
Provide data on multiple wildlife species									++
Can also examine genetic structure and dispersal			+		++	+	+		
Can be used with other sampling methods			+	+	+	+	+	+	+
No additional costs if harvest monitored ^d		+					+		
Can identify drivers of parameter			++		+				

Disadvantages						
Relatively expensive	-		-	-		-
Logistically difficult	--	-	--	-		-
Capture, handling, or removal required	-	--		-	-	
Baiting bears may lead to habituation	--	-	--	-	-	
Concern for human consumption ^e		--	-		-	
Dependent on constant harvest and mortality		--				
Cannot positively identify species (i.e., bears)	--		-			
Individual marks can be lost		-		--		-
Special considerations						
Provides coarse data on many individuals ^c				++	+	+
Provides fine-scale data on few individuals		++				
Best for heavily harvested populations (>20%)	++				+	+
Best for highly visible populations					+	++
Requires specialized lab/field equipment		+	+	+	+	+
>1 year of data collection required	++	++	+		+	+
>5 years of data collection required	++	++				
>10 years of data collection required	++	+				

Table 4-9. Ability of various estimation methods to detect different factors of American black bear (*Ursus americanus*) population growth rates.

Potential causes of trend ^a	Bait stations	Population reconstruction	Radiotelemetry ^b	Mark-recapture				
				Biomarking	DNA-based	Ear tags	Harvest	Observations
Excessive human-caused mortality								
Excessive legal hunting		+	++	+	+		+	
Unreported mortality (e.g., poaching)		+	++		+			
Hunting-related mortality		+	++	+	+		+	
Conflict bears		+	++		+	+	+	
Net emigration								
Disturbance		+	++	+	+			
Decline of habitat quality		+	+	+	+			
Attractive sinks		+	++	+	+			
Density-dependent dispersal		+	++	+	+	+		
Increased road or trail density								
Vehicle collisions		+		+				
Access for hunters or poachers		+	++	+	+			
Fragmented habitats		+	+	+	+			
Intraspecific killing								
Related to high density		+	++	+	+			
Reduced carrying capacity		+	+	+	+			
Skewed sex ratio		+	+	+	++	+	+	
Hunger		+	++	+	+			

Poor reproduction								
Decline of habitat quality	+	+		+	+			
Displacement from high-quality habitat	+	++		+				
Advanced age in female cohort	++	++		+	+	+		
High cub mortality								
Predation		+						
Poor nutrition		++						
Disease		+						
Accidents (e.g., vehicle collisions)		++						
Orphaning		++						
Other useful analytical abilities								
Habitat modeling, fine-scale	+	++	+	+	+	+		
Occurrence modeling, coarse-scale	+	++	+	++	+	+	+	+
Core and linkage habitat prediction	+	++	+	++	+	+		
Coarse bear movement info	+	++	+	++	+	+		
Movement data, fine-scale	+	++	+	+	+	+		
Population estimation	+	+	+	++	+	+		
Condition of the bears, health, disease	+	++	+		+	+	+	+
Diet studies, fine-scale (species of food)	+	++	+	+	+	+		
Diet studies, coarse-scale (isotope)	+	++	+	++	+	+		
Fragmentation and connectivity	+	++	+	++	+	+		
Sex and age structure	++	++	+	+	+	+		
Home-range size or overlap, dispersal	+	++	+	+	+	+		

FIGURES

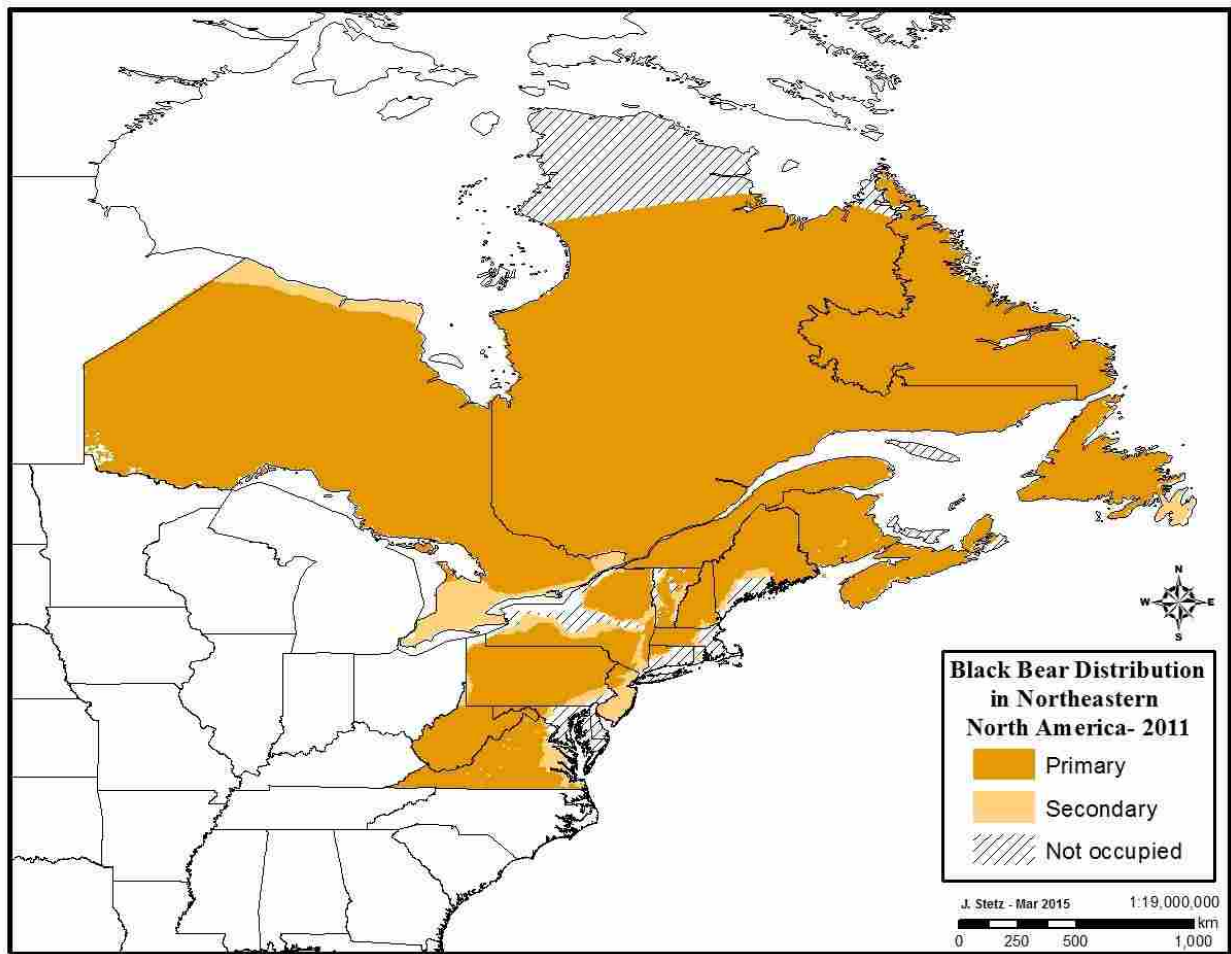
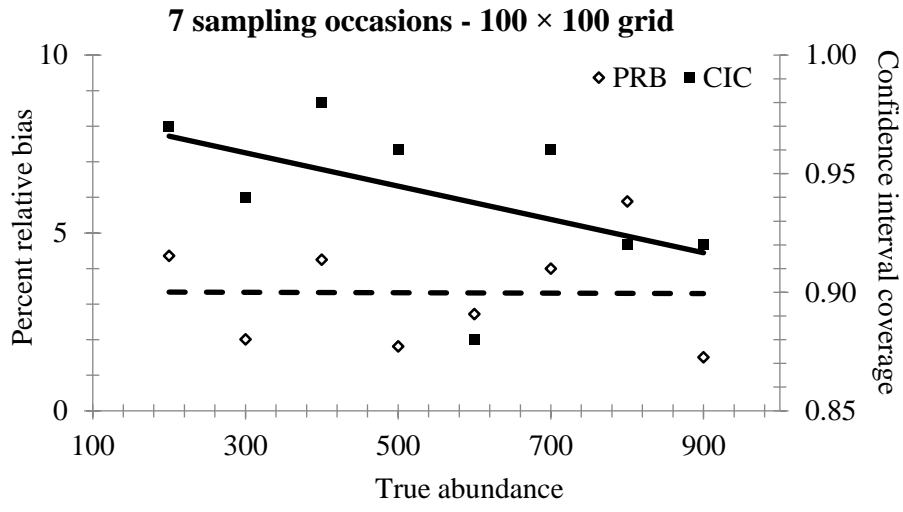
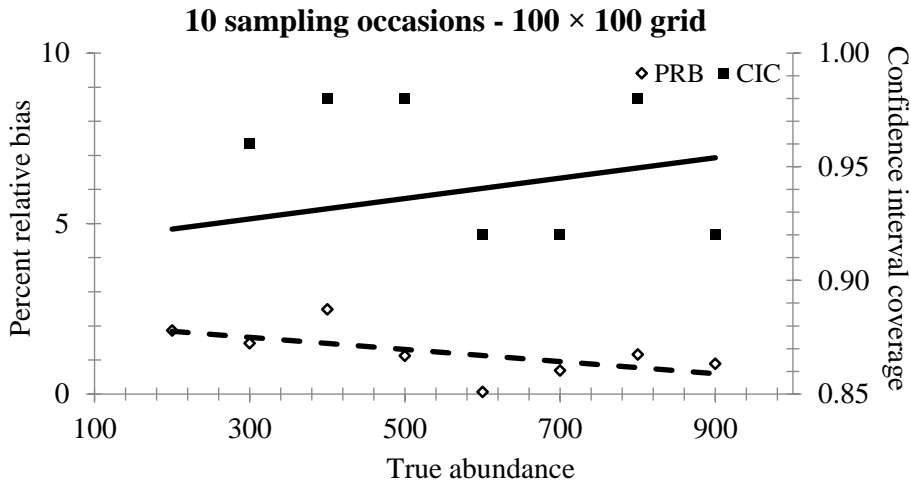


Figure 4-1. American black bear (*Ursus americanus*) distribution in North America. From Scheick and McCown (2014). Bear distributions were mapped by state and provincial biologists using 36-km² hexagonal grid cells to identify primary and secondary occupied range

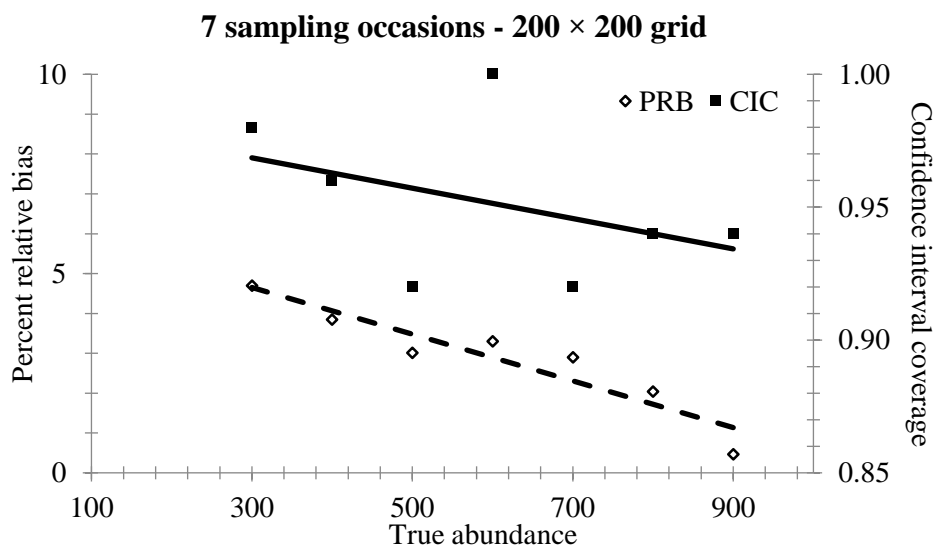
A.



B.



C.



D.

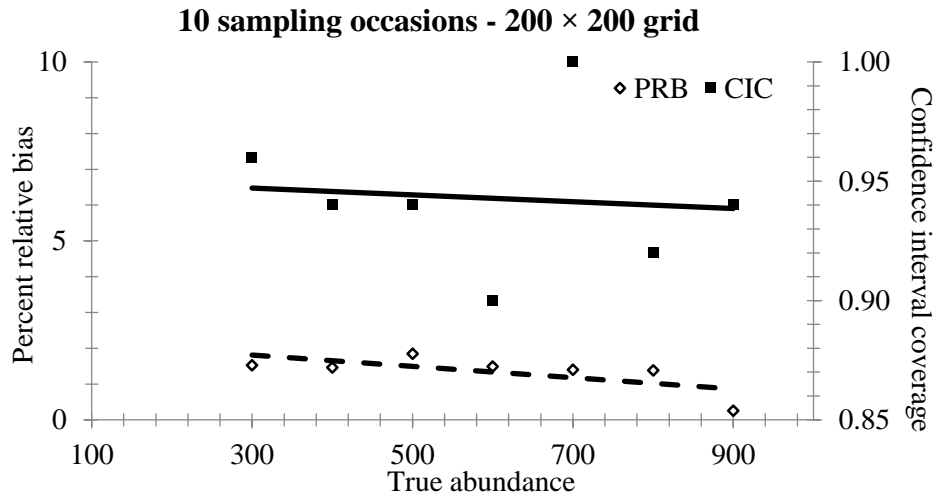
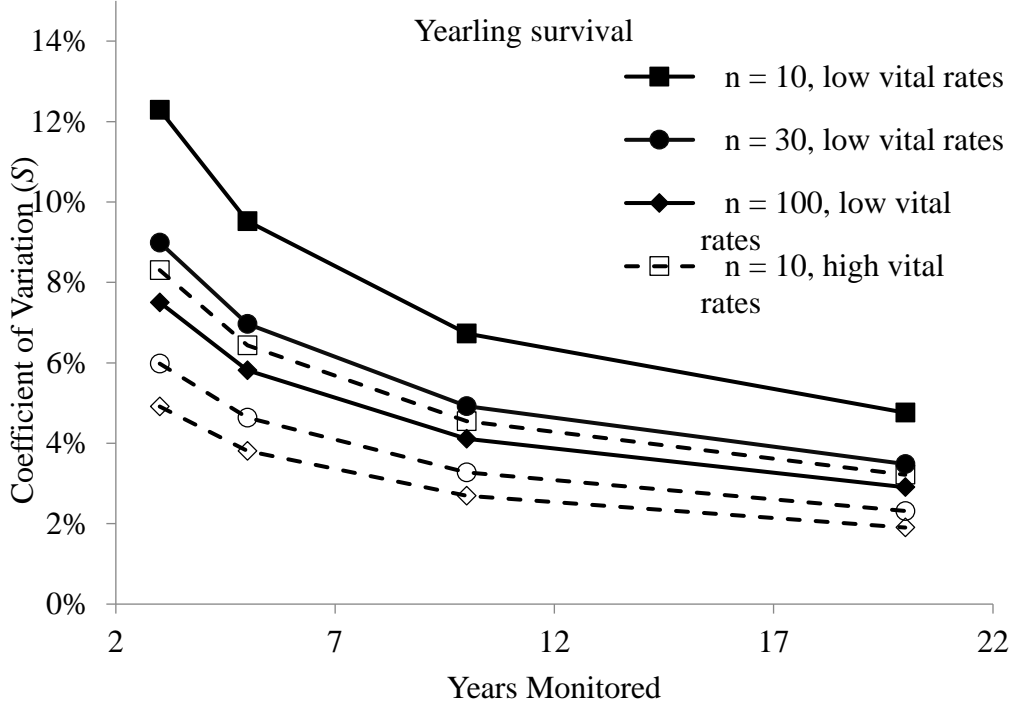
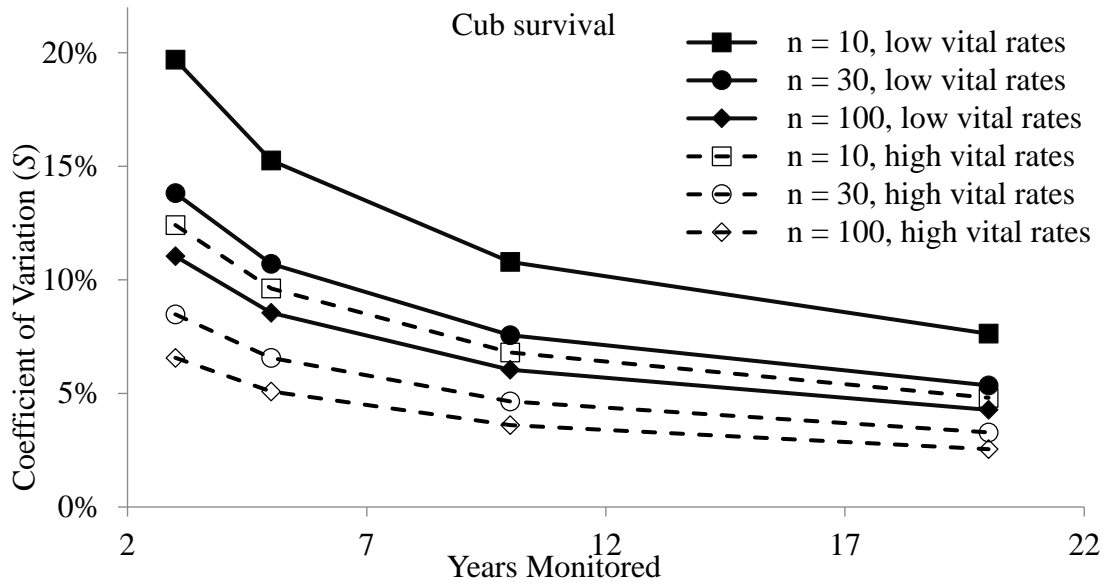


Figure 4-2. Percent relative bias (PRB) of estimates of American black bear (*Ursus americanus*) abundance estimates as a function of the number of sampling occasions (7 or 10), true abundance (ranging from 200-1,000), and study area dimensions (i.e., number of sampling sites per side of trapping grid, either 100 or 200). Simulations performed with WiSP package (Zucchini et al. 2007) in program R. PRB = percent relative bias; CIC = confidence interval coverage.



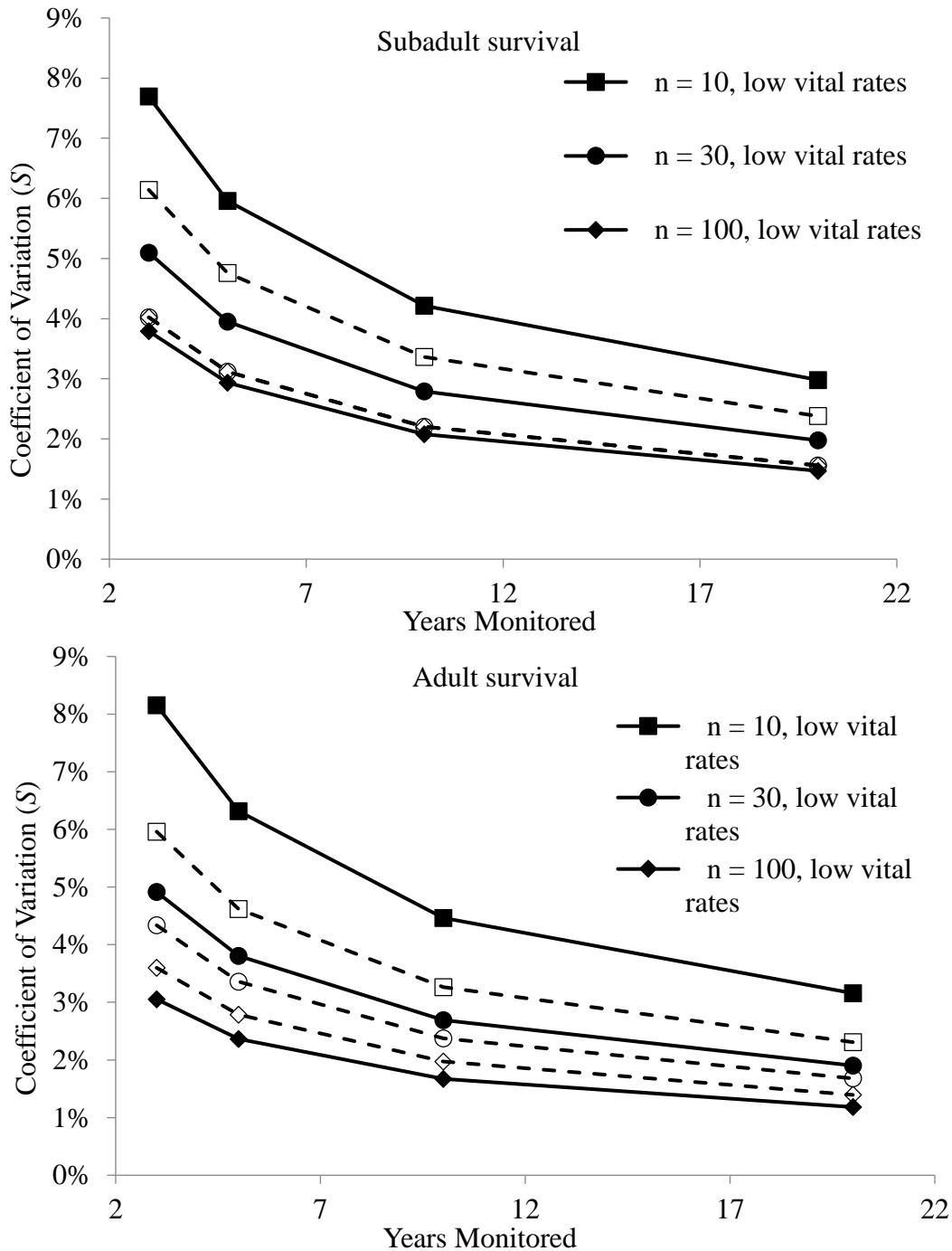


Figure 4-3. Age class-specific estimates of precision for survival estimates of American black bears (*Ursus americanus*) from radiotelemetry data as a function of sample size and number of years monitored (3, 5, 10, or 20). “Low” vital rates are from Ontario (Kolenosky 1990); “high” vital rates are a composite from Virginia populations (see citations in Table 5). Here we define adult as >3 year old and subadult as 2-3 years old. Note that the y-axes differ.

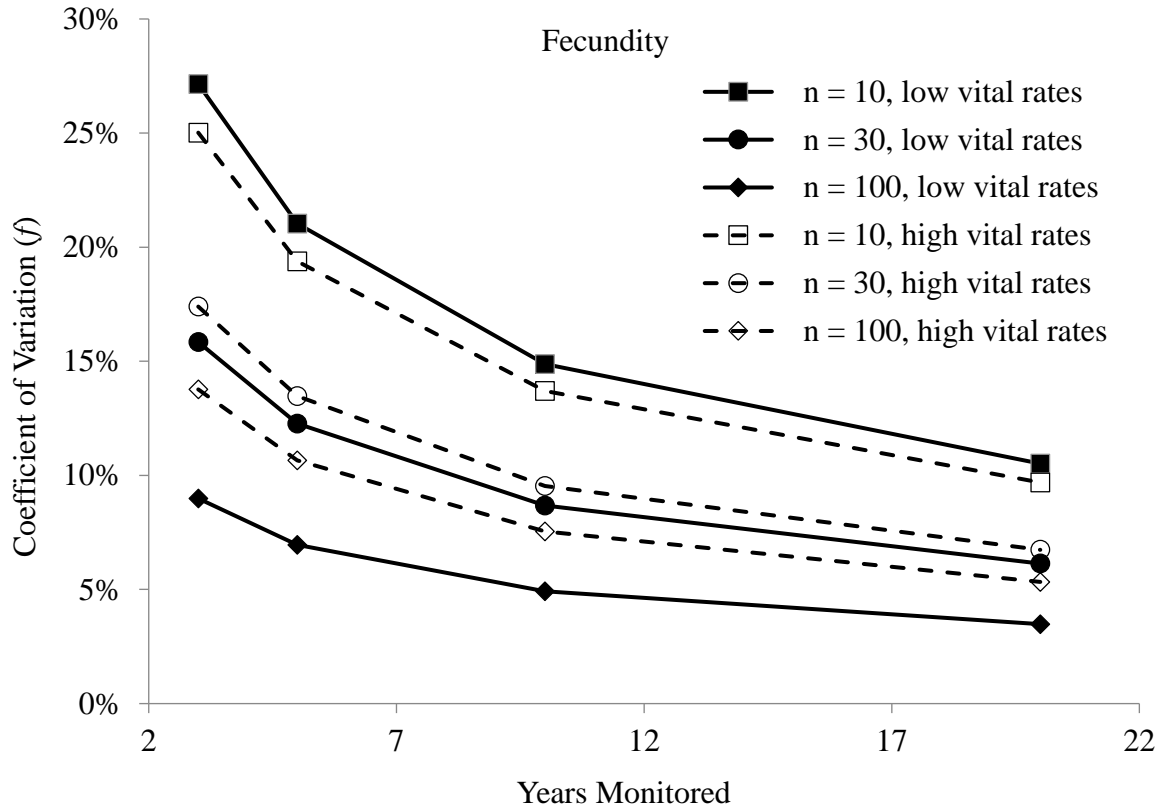


Figure 4-4. Age class-specific estimates of precision for fecundity estimates from radiotelemetry data of American black bears (*Ursus americanus*) as a function of sample size and number of years monitored (3, 5, 10, or 20). “Low” vital rates are from Ontario (Kolenosky 1990); “high” vital rates are a composite from Virginia populations (see citations in Table 5).

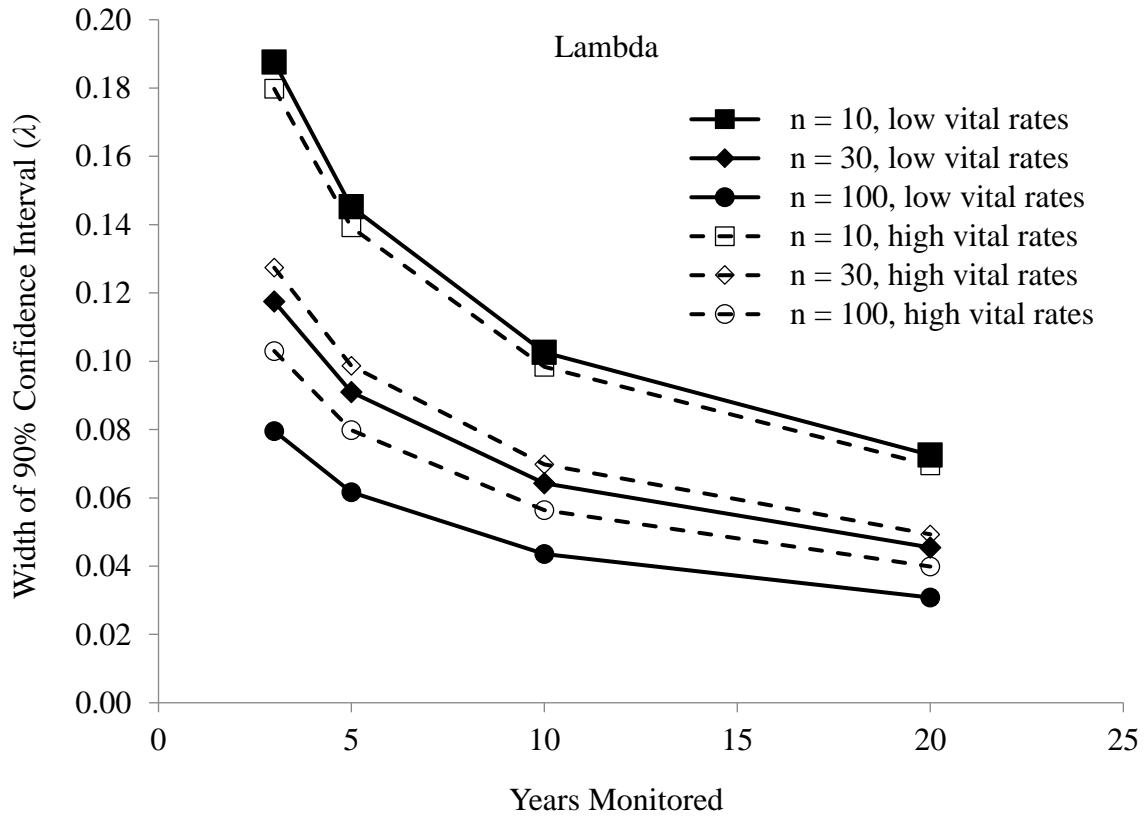


Figure 4-5. Width of 90% confidence intervals on lambda estimates for population growth rate simulations of American black bears (*Ursus americanus*) as a function of years monitored, sample size, and vital rates. “Low” vital rates are from Ontario (Kolenosky 1990); “high” vital rates are a composite from Virginia populations (see citations in Table 5).

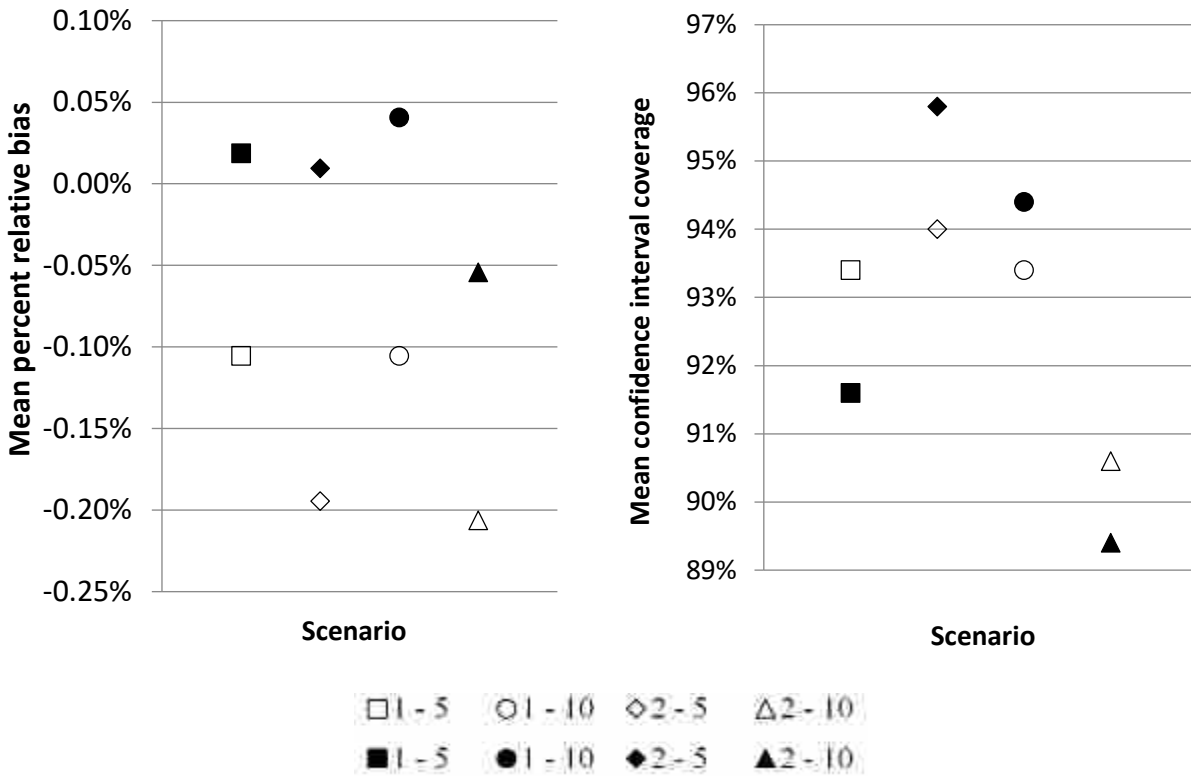


Figure 4-6. Selected results of program MARK population growth rate simulations for American black bears (*Ursus americanus*). Scenario numbers are the same as in Table 7; e.g., “Scenario 1–5” corresponds to a declining population with high apparent survival and low detection rates with 5 years of monitoring. Open symbols represent populations of N = 100 and closed symbols N = 500.

APPENDIX C. SUPPLEMENTAL MATERIAL

Table 4-S1. Noninvasive genetic sampling literature summary.

Summary of publications related to the use of noninvasive genetic sampling methods to estimate black bear population parameters and model capture probabilities.

Reference	Site name	Year	State/Province	Area (km ²)
Coster et al. (2011)	Pittsburg	2006	NH	196
Coster et al. (2011)	Milan	2006	NH	223
Coster et al. (2011)	Pittsburg	2007	NH	196
Coster et al. (2011)	Milan	2007	NH	223
Tredick and Vaugahn (2009)	Great Dismal Swamp NWR	2001	VA	175
Tredick and Vaugahn (2009)	Pocosin Lakes NWR	2002	NC	115
Tredick and Vaugahn (2009)	Alligator River NWR	2003	NC	150
Tredick and Vaugahn (2009)	Great Dismal Swamp NWR	2002	VA	175
Tredick and Vaugahn (2009)	Pocosin Lakes NWR	2003	NC	115
Tredick and Vaugahn (2009)	Alligator River NWR	2004	NC	150
Dreher et al. (2007)	Northern Lower Peninsula	2003	MI	36,848
Mowat et al. (2005)	Sout-central Selkirks	1996	BC	5,226
Mowat et al. (2005)	North-central Selkirks	1996	BC	4,640
Poole et al. (2002)	Prophet Plateau	1998	BC	5,413
Poole et al. (2001)	Prophet Mountains	1998	BC	3,114
Mowat et al. (2005)	Yellowhead	1999	BC	5,352
Mowat et al. (2005)	Parsnip Plateau	2000	BC	3,016
Mowat et al. (2005)	Parsnip Mountains	2000	BC	3,636
Mowat et al. (2005)	Bowron	2001	BC	2,494
Tredick et al. (2007)	Pungo Unit of Pocosin Lakes, NWR	2002	NC	50

Tredick et al. (2007)	St. Johns	2001	FL	967
Gardner et al. (2010)	Fort Drum	2006	NY	157
Belant et al. (2005)	Stockton Island	2002	WI	41
Belant et al. (2005)	Sand Island	2002	WI	12
Bittner et al. (2013)	Alleghany/Garrett County	2000	MD	2152
Settlage et al. (2008), Laufenberg et al. (2013)	Great Smoky Mountains NP	2003	TN	200
Boersen et al. (2003)	Tensas River Tract	1999	LA	329
Immell and Anthony (2008)	Steamboat	2003	OR	112
Immell and Anthony (2008)	Toketee	2003	OR	155
Immell and Anthony (2008)	Steamboat	2004	OR	138
Immell and Anthony (2008)	Toketee	2004	OR	145
Settlage et al. (2008)	Great Smoky Mountains NP	2003	TN	160
Settlage et al. (2008)	3 National Forests	2003	NC, SC, GA	329
Triant et al. (2004)	Inland	1999	LA	208
Triant et al. (2004)	Coastal	1999	LA	142
Stetz et al. 2014	Glacier NP	2004	MT	4,100
Stetz et al. 2014	Glacier NP	2005	MT	4,100
Obbard et al. (2010)	11 WMUs	2004, 2005	ON	
Sawaya et al. (2012)	Banff NP	2006	AB	2,246
Sawaya et al. (2012)	Banff NP	2008	AB	2,247

4-S2. R Code for Closed Population Abundance Simulations

```
## NEBBTC Simulation of closed population abundance estimation using routines in ## the R
package 'WiSP'. Modified by Jeff Stetz and Mike Sawaya

## WiSP is not on CRAN - must be downloaded from developer website: ##
http://www.ruwpa.st-and.ac.uk/estimating.abundance/WiSP/index.html

## I had to extract files to a folder not in C:\Program Files, then copy/paste to C:\Program
Files\R\R-2.15.1\library

## ---- set working directory -----
setwd('C:\..\'); getwd()
require(wisp); require(rgl); require(xlsx)
x.len <- c(100,200) study region
y.len <- c(100,200) study region
ngroups <- seq(400,900,by=100) this is the number of individuals
occ <- c(5,7,10) occasions
for(x in 1:length(x.len)) { for(y in 1:length(y.len)) {
for(n in 1:length(ngroups)) { for(o in 1:length(occ)) {
for(repl in 1:50){
my.region <- generate.region(x.length=x.len[x], y.width=y.len[y])
dimensions (aka survey region)
my.density <- generate.density(my.region, southwest=1, (simple plane in this case)
southeast=1, northwest=1) #plot.density.population(my.density)
resolution plots can slow things down
my.pop.pars <- setpars.population(my.density, number.groups=ngroups[n],
population (here, #groups=#individuals) size.method="user",
#
# x-dimension values for # y-dimension values for Number of groups; for us # Number of
sampling
# Creates population
# Defines density surface # 3D wire plot; high
# Number of animal groups in
# Method of how animal group
sizes are determined;
size.min=1, size.max=1, size.mean=1,
size values - if 'size.method' has been set to user.
only active if 'size.method' set to 'poisson'
reflecting individuals are independently detected exposure.method="beta",
# 'size.method = "user"' allows the user to enter possible group size values and their probabilities.
# Method of how group exposure is determined. 'method = beta' for Poisson-distributed group
exposure values;
user provides possible group exposure values and their probabilities.
exposure.min=0, exposure.max=1,
```

```

exposure values (only used when 'exposure.method = user'.
exposure.mean=0.5, (only if 'exposure.method = beta').
exposure.shape=0.1,
Beta distribution (only if 'exposure.method = beta').
type.values = c("Male","Female"), properties for animal groups.
# If 'method = user' the

# Lower and upper bounds of # Mean group exposure value # Shape parameter of the
# Vector of possible type
# Vector of possible group # min, max, and mean size
# I've set group size to 1,type.prob = c(0.45,0.55)) # Vector of respective type my.pop <-
generate.population(my.pop.pars)
# summary(my.pop)
#plot.population(my.pop, type='details', show.sizes=T, show.exp=T, dsf=0.75, title='my.pop')
my.cr.design.pars <- generate.design.cr(my.region, # Capture-recapture design parameters;
n.occ=occ[o], effort=rep(1,occ[o])) # number of occasions; relative effort across occasions
"effort=c(1,1,1,1,1)"
my.sample.cr.pars <- min/max values
my.point.est.crMh <- point.est.crMh(my.cr.sample,num.mix =2,init.N =-1) # Currently set to
model Mh with 2 mixtures
#summary(my.point.est.crMh) # Currently have summaries turned off to limit clutter
my.interval.est.crMh <- int.est.crMh(my.cr.sample,num.mix =2,init.N =-1, # Nonparametric
bootstrap CIs with 99 runs
ci.type='boot.nonpar', nboot=99, plot=F) #summary(my.interval.est.crMh)
##---- A new row for a dataframe with each element, for instance -----
if(my.pop.pars$size.method=="user"){ groupsize=mean(my.pop.pars$size.values)
} if(my.pop.pars$size.method!="user"){
groupsize=my.pop.pars$size.mean }
#A single row of the table
new.row <- data.frame(Nhat.ind=my.interval.est.crMh$boot.mean$Nhat.ind,
effort=my.cr.design.pars$effort[1],
occasions=my.cr.design.pars$number.occasions,

```

```

SE=my.interval.est.crMh$se$Nhat.ind, replicate=repl,x=x.len[x],y=y.len[y],ngroup=ngroups[n],
nindivid=ngroups[n]*groupsize,occ=occ[o],

min.cp.mark=my.sample.cr.pars$theta0.marked,
max.cp.mark=my.sample.cr.pars$theta0.marked,
min.cp.unmark=my.sample.cr.pars$theta1.unmarked, max.cp.unmark=my.sample.cr.pars
$theta1.unmarked )

##---- Within a loop, you do the following to add the new row to your table (or create a table)
if(exists("out.table")){
out.table <- rbind(out.table,new.row)
} if(!exists("out.table")){
out.table <- new.row
probabilities.
# was pmin.unmarked=0.01, pmax.unmarked=0.25, # Re/capture probability
setpars.survey.cr(my.pop, my.cr.design.pars, pmin.marked=0.01, pmax.marked=0.25,
improvement=0) # Improvement in detection my.cr.sample <-
generate.sample.cr(my.sample.cr.pars)
across sessions #summary(my.cr.sample)
}
}#end repl

##---- Save output to .xlsx file; static destination file name -----
##---- Destination .xlsx has to be created first (one time); worksheets added after that -----
filespot <- ("C:/.../NEBB.wisp.sims.output.xlsx")

##---- Dynamic worksheet name; worksheet added to common destination file -----
-----

##---- R will return an error if worksheet with same name exists or if file is open -----

SaveExcel <- write.xlsx(out.table, filespot,
sheetName=paste("XY",x.len[x],y.len[y],"N",ngroups[n],"Occ",occ[o],
"Mh.005.5",sep="."), col.names=T, row.names=F, append=T)

rm(out.table)
}#end o
}#end n }#end y

```

```

}#end x
### ---- Simulations based on conditions defined above ----- #
#my.Mh.cr.sim <- point.sim.crMt(pop.spec=my.pop.pars,
'mypop' and 'mydens' allows randomization
# design.spec=my.cr.design.pars,
# survey.spec=my.sample.cr.pars, B=99, seed=123456)
replicates; setting seed makes it reproducible #
# using user defined # B=num
#save(out.table,file=paste("wisp.X",x,"Y",y,"N",n,"Occ",o,"Mh.005.5.RData", sep=".")) #
#summary(my.Mh.cr.sim)
##plot(my.Mh.cr.sim)
#
#
## Suggested citation:
## Zucchini, W., Borchers, D.L., Erdelmeier, M., Rexstad, E. and Bishop, J. 2007.
## WiSP 1.2.4. Institut fur Statistik und Okonometrie, Geror-August-Universitat Gottingen, ##
Platz der Gottinger Seiben 5, Gottingen, Germany.

```

4-S3: R Code for Spatially-Explicit Capture-Recapture Simulations

An R function to run a suite of SECR simulations

Modified from Murray Efford's 2012-05-31 code by J.Stetz and A.Mynsberge

Set working directory

```
setwd('C:/.../Simulations/secr/Results');
```

```
require(secr)
```

```
runsim <- function(nrepl = 25, outputfile = 'sim.output.RData') {
```

```
## ---- Parameter values -----
```

```
  D <- c(0.001, 0.005, 0.01, 0.015)
```

```
  g0 <- c(0.05, 0.01, 0.15)
```

```
  sigma <- c(400,1000, 2000, 3000)
```

```
## ---- Design variables -----
```

```
  spacing <- c(1000, 2000, 3000)
```

```
  occasions <- c(5,7,10)
```

```
  nspacing <- length(spacing)
```

```
  noccasions <- length(occasions)
```

```
## ---- Grid dimensions -----
```

```
  nx <- 25; ny <- 25
```

```
## ---- Simulation variables -----
```

```
  buff <- 15000
```

```
## ---- array to hold results -----
```

```

output <- array(dim = c(nspacing, noccasions, 3, nrepl))
# output.SE <- array(dim = c(nspacing, noccasions, nrepl))
# output.CV <- array(dim = c(nspacing, noccasions, nrepl))
dimnames(output) <- list(spacing, occasions, c("est", "se", "cv"), NULL)
# dimnames(output.SE) <- list(spacing, occasions, NULL)
# dimnames(output.CV) <- list(spacing, occasions, NULL)

cat('Starting simulations', date(), '\n')
flush.console()
## ---- loop over replicates, spacing, and noccasions -----
for (r in 1:nrepl) {
  for (sp in 1:nspacing) {
    grid <- make.grid (nx = nx, ny = ny, spacing = spacing[sp])
    for (nocc in 1:noccasions) {
      temppop <- sim.popn (grid, D = D, buffer = buff)
      tempCH <- sim.caphist (grid, popn = temppop,
        detectfn = 0, noccasions = occasions[nocc],
        detectpar = list(g0 = g0, sigma = sigma))

## bracketing with try() allows us to continue if there is an error in secr.fit
      tempfit <- try (secr.fit (tempCH, detectfn = 0, buffer = buff,
        trace = FALSE, verify = FALSE,
        start = log(c(D,g0,sigma))), silent = TRUE)
      if (!inherits(tempfit, 'try-error')) {
        temppred <- unlist(predict(tempfit)['D',])
## here we save only the relative SE of D-hat...replace as desired
        output[sp,nocc,"est",r] <- temppred['estimate']
        output[sp,nocc,"se",r] <- temppred['SE.estimate']
        output[sp,nocc,"cv",r] <- temppred['SE.estimate'] / temppred['estimate']

```



```

    }
    else{
    cat("!\n")
    }
}
}
cat('Completed replicate', r, date(), '\n')
flush.console()
save(output, file = outputfile)
#save(output.SE, file = gsub("output","output.SE.",outputfile))
#save(output.CV, file = gsub("output","output.CV.",outputfile))
}
output
}

## ---- Output filename is NOT dynamic -----
runsim (nrepl = 25, outputfile = 'sim.output.D.005.g0.15.sigma.3000.25b.RData')

##---- Convert sigma to home range in km2 -----
for (hr in 1:length(sigs)) {
  homerange = ((sigs*(qchisq(0.95,2)^0.5))^2)*3.1415}
homerange/1000000
##---- NEBBTC secr simulation output extraction, formatting, and analysis -----
##---- Manual file selection; mix of static and dynamic outputs -----
##---- J. Stetz and M. Sawaya - last modified 05 August 2012 -----

require(xlsx)

```

```

setwd('C:/.../Simulations/secr/Results');

##---- Provide filename within parantheses; influde suffix ".RData" -----

filename="sim.output.D.001.g0.05.sigma.1000.10.RData"
load(filename)
dim(output)
dimnames(output)
id<-dimnames(output)
spacing=id[[1]]
occ=id[[2]]
rep=dim(output)[3]
for(i in 1:length(spacing)){
  for(j in 1:length(occ)){

      new.rows=data.frame(spacing=spacing[i],occasions=occ[j],
      rep=1:25,estimate=output[spacing[i],occ[j],"est"],
      SE=output[spacing[i],occ[j], "se"],
      CV=output[spacing[i],occ[j], "cv"],)
    if(exists("out.table")){
      out.table=rbind(out.table,new.rows)
    }
    else{
      out.table=new.rows
    }
  }
}
}

```

```
##---- Name components coming from file name -----
##---- Requires that the naming convention stays the same -----
##---- The "\\" are to take the special meaning out of the period -----
##---- Note that there are some factors (vs. numeric); changed later -----
```

```
out.table$D=unlist(strsplit(filename,"\\.")[4])
out.table$g0=unlist(strsplit(filename,"\\.")[6])
out.table$sigma=unlist(strsplit(filename,"\\.")[8])
out.table$gridsize=unlist(strsplit(filename, "\\.[0-9]")[9])
out.table$filename=(filename)
d = unlist(strsplit(filename,"\\.")[4])
g = unlist(strsplit(filename,"\\.")[6])
sig = unlist(strsplit(filename,"\\.")[8])
gr = unlist(strsplit(filename, "\\.[0-9]")[9])
strsplit(filename,"\\."); sapply(out.table,"class")
```

```
##---- Converting whole columns, hence use of sapply function -----
```

```
#formatC(out.table$est, digits=4, format="f", flag=0, ignoreNA=T, zero.print=T)
```

```
out.table[,sapply(out.table,"class")==="factor"] <-
sapply(out.table[,sapply(out.table,"class")==="factor"],"as.character")
out.table[, c(7:10)] <- sapply(out.table[, c(7:10)], as.numeric)
out.table$D=(out.table$D/1000); out.table$g0=(out.table$g0/100)
```

```
##---- Convert 'Inf' SE's to 'NA' for calculating CIs and/or confidence interval coverage ('CIC') --
is.na(out.table$SE)=!is.finite(out.table$SE)
out.table$PRB=((out.table$estimate-out.table$D)/out.table$D)
```

```

out.table$lowCI=(out.table$estimate-
(1.96*out.table$SE));out.table$upperCI=(out.table$estimate+(1.96*out.table$SE))

#out.table$CIC=ifelse((out.table$estimate<out.table$upperCI)&(out.table$estimate>out.table$lowCI), 1, 0)

out.table$CIC2=ifelse(((out.table$estimate-
(1.96*out.table$SE))&(out.table$estimate+(1.96*out.table$SE))),1,0)

#out.table

##---- First save output as RData file, then .xlsx -----

save(out.table, file=paste("D",d,"g0",g,"sigma",sig,"grid",gr,"frmtd.RData",sep="."))

##---- Save output to .xlsx file; static destination file name -----
##---- Destination .xlsx has to be created first (one time); worksheets added after that -----

filespot <- ("C:/.../Simulations/secr/Results/NEBB.secr.sims.output.summary.10b.xlsx")

##---- Dynamic worksheet name; worksheet added to common destination file -----
##---- R will return an error if worksheet with same name exists or if file is open -----

SaveExcel          <-          write.xlsx(out.table,          filespot,
sheetName=paste("D",d,"g0",g,"sigma",sig,"grid",gr,sep="."),
          col.names=T, row.names=F, append=T)

```

4-S4: MATLAB Code for Demographic Analysis Simulations

```
% Lamvaresti.m: a program to estimate the sampling variance in log stochastic lambda
% using approximation formulae from Doak et al. 2005 (equation numbers refer to this
% paper and its appendix 3).
% Further modified from code provided by R. Harris for NEBBTC Technical Report
% J.Stetz and M.Sawaya - last modified 24 Feb 2013

% You must have the symbolic math toolbox of Matlab to use this program.
% This program uses two functions (secder.m and eigenall.m) from the website of
% programs that accompany Morris and Doak (2002): www.sinauer.com/PVA/
% The general form of data entry used here is quite similar to other, simpler
% programs also on this website, including Vitalsens.m and Stochsens.m; reading
% through these programs may help you understand the structures used here if you
% having trouble.

% One warning: the symbolic logic routines and the simulations to estimate correlations
% in beta variable means and variances are time-consuming, with one to several minutes
% between different steps. Be patient.

% 25 age classes; 6 vital rates (4 survival, 1 fecundity) - zero correlation throughout

clear all;
global yrsam kknms mmnms % global variables used by called functions
randn('state',sum(100*clock)); % seeding random numbers
rand('state',sum(100*clock)); % seeding random numbers
warning off % MATLAB:divideByZero

%***** Parameters that must be input by user *****
```

% First, give symbolic names for each vital rate to be used in this program. For the desert tortoise,

% these are: first, six survival rates (for stages 2-7); next, 5 growth rates (stages 2-6);

% and, finally, three fecundities (stages 5-7).

% These symbolic definitions are given below, and then the vector of these names (Svr) is defined.

syms v1 v2 v3 v4 v5 % vital rates as symbolic variables

Svr = [v1 v2 v3 v4 v5]; % vector of symbolic vital rates

% Next, give the mean Vital rate values:

% CUB surv(v1)=0.87; YEARLING surv(v2)=0.9; SUBADULT (2-3yr) surv(v3)=0.82;

% ADULT (4+) surv(v4)= 0.92; fecALL(v5)= 0.312 [; fec6+(v5) = 0.350] (note these are

% fx, not mx values)

% NOTE! INCLUDES ONLY ONE FECUNDITY!!

%Fx = total # offspring produced during x.

%mx = fecundity: mean # offspring produced

realvrmeans = [0.73 0.87 0.933 0.93 0.6875];

% Then estimated true temporal variances (not standard deviations) of the Vital Rates:

realvrvars = [0.00493 0.00435 0.0036 0.00271 0.020];

% Next, you must say what the distribution is for each vital rate: this program only distinguishes

% between beta-distributed variables (coded as 1) and all others, assumed to be fecundities

% or similarly distributed parameters (coded 2).

% I interpret this as survival rates (n=4) are betas, whereas fx (n=2) are

% fecundities

vrtypes = [ones(1,4),2];

% Then, you must give a the full estimated matrix of temporal correlations between the vital rates.


```

0 0 00 0 0 0 0 0 0 0 0 0 0 0 0 v4 0 0 0 0 0 0 0 0 0 0
0 0 00 0 0 0 0 0 0 0 0 0 0 0 0 0 v4 0 0 0 0 0 0 0 0 0
0 0 00 0 0 0 0 0 0 0 0 0 0 0 0 0 0 v4 0 0 0 0 0 0 0 0
0 0 00 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 v4 0 0 0 0 0 0 0
0 0 00 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 v4 0 0 0 0 0 0
0 0 00 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 v4 0 0 0 0 0
0 0 00 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 v4 0 0 0 0
0 0 00 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 v4 0 0 0
0 0 00 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 v4 0 0
0 0 00 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 v4 0 ];

```

```

% Now, what are the sampling intensities for each vital rate and the durations of sampling that
% you want to have run calculations for? insams is a matrix with columns of sampled number of
% individuals used to estimate each vital rate (in the same order as for the means and variances
% above) and rows for different sets of these samples to run. For example, the insams defined
% below has one set of sampling of 30 individuals for each vital rate, and one set of sampling
100
% individuals for each rate; remember that these sampling patterns can be those used or ones
you
% might want to consider.

```

```

insams = [10 10 10 10 10; 30 10 10 10 10; 10 30 10 10 10; 10 10 30 10 10; 10 10 10 30 10; 10
10 10 10 30; 30 30 10 10 30; 30 30 30 30 30];

```

```

% Then input each sampling duration that you want to consider: each number here is one
duration to try:

```

```

yrsams = [3 5 10 20];

```

```

% Rename output each time

```

```

outputfilename = 'NEBBTC_Var8.txt'; % The name of the file to save output data to

```



```
%***** End of Parameter inputs: Proceeding to calculations
*****
```

```
%First Step: Basic calculations and estimation of the deterministic vital rate sensitivities
```

```
estiouts=[]; % The variable to store output data
realmx = subs(symmx,Svr,realvrmeans); % Making a matrix of the mean numerical values
nmx = length(realmx); % Size of pop mx.
nvr = length(realvrvars); % Number of vital rates
```

```
[lambdas,lambda1,W,w,V,v]= eigenall(realmx); % Use eigenall.m to get eigenvalues
```

```
sensmx = v*w'/(v'*w); % Get sensitivities of matrix elements
```

```
vrsens = zeros(1,nvr); % Initialize vital rate sens.
```

```
for xx=1:nvr % A loop to calculate sensitivity for each vital rate
```

```
    % First get derivatives of elements with respect to vital rates:
```

```
    diffofvr = double(subs(diff(symmx,Svr(xx)),Svr,realvrmeans));
```

```
    vrsensbyelements(:,xx) = diffofvr;
```

```
    % Then, sum up to get row of total vital rate sensitivities:
```

```
    vrsens(xx) = double(sum(sum(sensmx.*diffofvr)));
```

```
end; % xx
```

```
% Second Step: Calculate stochastic lambda and its sensitivities to the matrix element means
```

```
mx = realmx; % Set mx equal to the name of stored pop'n matrix
```

```
vrcovmx = realcovmx.*(sqrt(realvrvars)*sqrt(realvrvars)); % Make a covariance matrix
```

```
tau=(vrsens)*vrcovmx*(vrsens'); % tau as in Tuljapurkar (1991), but estimated by vital rates
```

```
% Estimate log(lambda_S), the log of stochastic lambda:
```

```
loglamS = log(lambda1) - 0.5*(1/(lambda1^2))*tau;
```

```
squloglamderivs=[]; % Here, we are define the three storage variables for the final calcs:
```

```
squVarsums =[];
```

```

squCorrsums = [];

for ii=1:nvr % Loop to get the values needed to estimate the derivatives: d(log(lambda_S))/d(vi)
    kllsum=0;
    for kk=1:nvr
        for ll = 1:nvr
            dSldi =0;
            dSkdi =0;
            dSldi = sum(sum( sensmx.*double(subs(diff(diff(symmx,Svr(ll)),Svr(ii)),Svr,realvrmeans)) ));
            dSkdi = sum(sum( sensmx.*double(subs(diff(diff(symmx,Svr(kk)),Svr(ii)),Svr,realvrmeans)) ));
            for xx = 1:nmx
                for yy =1:nmx
                    dSldi = dSldi+vrsensbyelements(xx,yy,ii)*sum(sum(secder(mx,xx,yy).*vrsensbyelements(:,:,ll)
                    ));
                    dSkdi = dSkdi+vrsensbyelements(xx,yy,ii)*sum(sum(secder(mx,xx,yy).*vrsensbyelements(:,:,kk) ));
                end
            end
            kllsum= kllsum+vrcovmx(kk,ll)*(dSldi*vrsens(kk) +dSkdi*vrsens(ll));
        end
    end
end

% The derivatives of log(lambda_S) with respect to each vital rate:
loglamderivs(ii) = vrsens(ii)/lambda1+vrsens(ii)*tau/(lambda1^3) -
kllsum/(2*lambda1^2);

% The square of each derivative, which multiplies with the variance in each rate in equation 2.
squelamderivs(ii) = (loglamderivs(ii))^2;

% The sums that multiply with the variances of the variances terms in equation 2:
squVarsums(ii) = (1/lambda1^4)*( sum( vrsens(ii)*vrsens.*sqrt(realvrvars).*realcorrmx(ii,:))
)^2;

```

```

disp('The vital rate number and sensitivity of log(lambda_S) to this vital rate');
disp([ii,loglamderivs(ii)]);
end; %ii
% Finally, the matrix of values that multiple with the variances of correlations in equation 2:
squCorrsums = (1/lambda1^4)*((sqrt(realvrvars')*sqrt(realvrvars)).*(vrsens'*vrsens)).^2;
clear v1 v2 v3 v4 v5 Svr symmx; %making space in memory

% Third Step: estimate sampling variance in log(lambda_S)for different sampling patterns
for ii = 1:length(insams(:,1))% Loop through each set of sampling intensities
    SamNs = insams(ii,:); % The vector of within year sample sizes to use
    for jj=1:nvr          % A loop to use simulation to estimate the correlation of means and
        standard
            if vrtypes(jj) ==1 % deviations in sampled values for beta-distributed variables:
                mn = realvrmeans(jj);
                va = realvrvars(jj);
                vv = mn*((mn.*(1-mn)/(va))-1); % calculate the beta parameters
                ww = (1-mn).*((mn.*(1-mn)/(va))-1);
                aa = betarnd(vv,ww,SamNs(jj),10000); % Draw 10,000 sets of values
                aavars = var(aa);
                aaSD= sqrt(aavars);
                aameans=mean(aa);

                aacov=cov([aaSD',aameans']);
                vrvrvarcovs(jj) = aacov(1,2);
            else vrvrvarcovs(jj)=0;
        end;
        betacorrcontribut(jj) = 2*vrvrvarcovs(jj).*loglamderivs(jj).*(1/lambda1^2).*(sum( ...
            vrsens(jj)*vrsens.*sqrt(realvrvars(jj)).*realcorrmx(jj,:)) );
    disp('The vital rate number and, next line, beta-value correlation contribution to variance');
end;

```

```

disp(jj); disp(betacorrcontribut(jj));

end;

clear aa aavars aaSD aameans aacov; % making space in memory
for yy=1:length(yrsams); % Loop through the sampling durations
    yrs = yrsams(yy); % number of years of data

    for xx=1:nvr %loop to estimate within-year sampling variances of each vital rate:
        if vrtypes(xx) == 1;    inyrvar(xx) = realvrmeans(xx)*(1-realvrmeans(xx)); end; %
binomials
        if vrtypes(xx) == 2;    inyrvar(xx) = realvrmeans(xx); end; % using Poisson variance for
fecundities
    end

    % Next, estimate the total sampling variance for mean values (equation A6):
    meanvars = (1/yrs).*(realvrvars+inyrvar./SamNs);

    % Then, the variances for the corrected variance estimates (equation A9):
    correctedvarvars = (2*yrs/(yrs-1)^2)*realvrvars.*(realvrvars+2*(inyrvar./SamNs));

    SDvars = (correctedvarvars./(4.*realvrvars)); % Transform correctedvarvars to get
variances of SDs

    SDvars(isnan(SDvars)) = 0;

    correlvars = (yrs/(yrs-1)^2)*(realcorrmx.^2 -1).^2; % The variances of the correlations

    % At Last, get the outputs:

    % 1. The sampling variance in the estimate of deterministic log(lambda): this is also the
    % sampling variance in log(lambda_S) generated by sampling variance of the mean vital
rates:
    DeterLogLamVar = sum(squloglamderivs.*meanvars);

    % 2. Sampling variance of log(lambda_S) from just variance in means and variances of
vital rates:
    VarLogLamVar = sum(squloglamderivs.*meanvars+squVarsums.*SDvars );

```

```

% 3. Sampling variance of log(lambda_S) from variances of means, variances, and
correlations,
%   but without the effects of beta variable correlations
FullLogLamVar =
sum(squloglamderivs.*meanvars+squVarsums.*SDvars+0.5*sum(squCorrsums.*correlvars) );
% 4. The best of sampling variance of log(lambda_S) with the effects of beta variable
correlations
FullLogLamVarADDED = FullLogLamVar+sum(betacorrcontribut);

% Save the data: as now written, the outputs are one row for each combination of sampling
duration and
% intensity. The columns of data are: sampling intensity for the first vital rate; sampling
% duration; sampling variance (SV) for deterministic log(lambda); SV for log(lambda_S)
from SV in
% vital rate means and variances; SV for log(lambda_S) from SV in means, variances, and
correlations;
% SV for log(lambda_S) from all sources; estimated log(lambda_S) for the input
parameters; and,
% estimated log(deterministic lambda).
estiouts = [estiouts;[SamNs(1) yrs  DeterLogLamVar  VarLogLamVar  FullLogLamVar
FullLogLamVarADDED ...
loglamS log(lambda1) meanvars SDvars ]];
disp('The sampling intensity set, sampling duration set, and sampling variance in
log(lambda_S)');
disp([ii,yy, FullLogLamVarADDED]);
end; %yy
end; %ii
save(outputfilename, 'estiouts','-ASCII'); % This saves a file with the data in estiouts
disp('DONE!');

```

4-S5: Mark-Recapture Models

Black bear population parameters (e.g., abundance, density) can be estimated from a variety of mark-recapture models, each with their own ability to accommodate assumptions. Some of these assumptions apply to all models (e.g., demographic closure, marks are not lost), whereas other assumptions can only be relaxed with specific model types. Managers should examine the model assumptions and decide which ones would apply to their populations before finalizing their selections. Independent of which model type is chosen, managers should gain a thorough understanding of the assumptions that apply to their model before making management decisions based on its results. This is particularly important for interpreting density estimates based on models that relax the assumption of geographic closure.

Although there are many more mark-recapture models than we can possibly cover here, the models we presented (Table 4-S6) have the greatest potential to provide reliable estimates of population parameters for black bears in the Northeast. Of these, the Huggins closed-capture model (Huggins 1991) has been used most frequently to estimate black bear abundance because of its ability to incorporate individual covariates to model detection probabilities (i.e., increase estimate precision). Closed-population mixture models have also been used when individual capture heterogeneity is known to bias estimates because of differences in individual detection probabilities. Recently developed SECR models allow for precise estimates while addressing the geographic closure assumption, but these models have their own assumptions that may not be biologically feasible (e.g., home ranges that are stationary during sampling) or may be violated in real-world sampling scenarios (e.g., capture probability highest at home-range center). When demographic or geographic closure is known to be violated, we suggest that managers consider an open population model such as Pollock's robust design (Pollock et al. 1990), which requires multiple primary sampling periods (usually years).

Table 4-S6. Assumptions of mark-recapture models for estimating American black bear population parameters in jurisdictions of the Northeastern Black Bear Technical Committee.

Model suitability^a	Closed population	Closed pop w/ mixture	Huggins-closed	Spatially-explicit	Integrated	Mark-resight	Open population
<u>Parameter of interest</u>							
Abundance	+	+	++	+	+	+	+
Density	+	+	+	++	+	+	+
Survival					+		++
Reproduction					+		++
Population growth					+		++
<u>Model assumptions</u>							
Every animal has chance of being readably marked	+	+	+	+	+	+	+
Marks are read correctly and not lost	+	+	+	+	+	+	+
Every animal with equal capture probability	+					+	
Every animal has circular home range				+			
Detection probability highest at home range center				+			
Detection probability can be related to covariates			+	+	+	+	
Population has been representatively sampled	+	+	+	+	+	+	+
Population is demographically closed	+	+	+	+	+	+	
Population is geographically closed	+	+	+		+	+	
Study area boundaries do not change							+

^a “++” = most suitable or applicable, “+” = suitable or applicable, null = not suitable or applicable; based on synthesis of report findings.

4-S7: Statistical Analysis Software

Most of the mark-recapture model types presented in our review can be implemented with one or more freely available computer software packages. These software programs can estimate a range of population parameters and offer a number of appealing features (Table 4-S8). Some of the software programs have excellent graphic user interfaces (GUI) which makes obtaining parameter estimates easy for wildlife managers. Caution should always be applied when using these programs, however, because even somewhat cryptic settings can have profound effects on the reliability of population parameter estimates (e.g., different link functions in Program MARK).

Among the many software programs available to managers, Program MARK (White and Burnham 1999) stands out with the most proven track record of reliable use for estimating black bear abundance and population growth. Program MARK can accommodate a variety of data types (e.g., hair snares, bear rubs, telemetry, remote photographs, observations) and can implement most mark-recapture models that are commonly used by researchers and managers to estimate black bear population parameters (Table 4-S7).

Program R packages have particular appeal over stand-alone programs such as MARK because they generally offer greater versatility to estimate parameters of interest (Table 4-S8). Nonetheless, Program R requires an extensive time investment to adequately learn the programming language. Therefore, managers (or anyone else) may encounter the frustration of a steep learning curve to become proficient with producing reliable results. Advantages to R include that the program is free and open source, the programming language is consistent across many different packages, extensive online resources are available, and new packages are constantly being developed to accommodate new sampling methods and mark-recapture models.

Table 4-S8. Software packages for analyzing mark-recapture models for American black bear populations in jurisdictions of the Northeastern Black Bear Technical Committee.

Software suitability ^a	Program R packages					
	DENSITY	MARK	RISKMAN	SECR	RMARK	WiSP
<u>Parameter of interest</u>						
Abundance	+	++		+	+	+
Density	++	+		++	+	+
Survival		++			++	
Recruitment		++			++	
Population growth	^b	++	++	^b	++	
<u>Features</u>						
Open access software	+	+	+	+	+	+
Open-source code				+	+	+
Documentation	++	++	++	++	+	+
Graphic user interface	++	+	++			+
Individual covariates	+	+		+	+	+
Sex-specific parameter estimates	+	+	+	+	+	+
Simulations	++	++	++	+		++

^a”++” = most suitable or applicable, “+ = suitable or applicable, null = not suitable or applicable; based on synthesis of report findings.

^b = new models under development