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DISPERSAL TIMING, DISTANCES, AND RATES OF PENNSYLVANIA BLACK BEAR

A Thesis in

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by

Wendy C. Vreeland

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The thesis of Wendy C. Vreeland was reviewed and approved* by the following:

Duane Diefenbach
Adjunct Professor of Wildlife Ecology
Leader, PA Cooperative Fish & Wildlife Research Unit
Thesis Advisor

Mark Ternent
Wildlife Biologist, Pennsylvania Game Commission
Special Signatory

Matt Marshall
Adjunct Assistant Professor of Wildlife Conservation
National Park Service Program Manager

Walter Tzilkowski
Associate Professor Emeritus of Wildlife Science

Michael Messina
Professor
Head of the Department of Ecosystem Science and Management

*Signatures are on file in the Graduate School

ABSTRACT

In Pennsylvania, the black bear (*Ursus americanus*) population has expanded its range since the early 1980s. I investigated if dispersal timing, distance, and rates changed compared to previous research, and if those changes corresponded with range expansion and increasing population density. I used records of bears captured and ear-tagged <16 months of age with specific locations of tagging and recapture or dead recovery encounters (n = 466). I classified bears as dispersed if the measured distance between initial capture and final recovery was ≥13 km, which was the greatest linear distance across the average female bear home range in Pennsylvania. Based on this criterion, I classified <5% of bears as dispersing <16 months of age and dispersal occurred at 16–19 months of age. I estimated dispersal rates using logistic regression models, to investigate if dispersal differed by region or decade for males and females. Median distance dispersed was greater for males (47.03 km, n = 98) than females (25.84 km, n = 70). Region of Pennsylvania and decade were not related to the distance bears dispersed. Overall, male dispersal rate was 0.67 (SE = 0.06) and female dispersal rate was 0.28 (SE = 0.06). For males, I found that dispersal rates were 0.48 in the 1980s and increased to >0.75 in the 1990s and 2000s but did not vary by region of Pennsylvania. No single logistic regression model best explained female dispersal so I used model averaging to estimate dispersal rates by decade and region. The greatest increase in female dispersal rates occurred between the 1990s and 2000s in all regions. My results indicated a greater dispersal rate, at greater distances, for female bears than previous research in Pennsylvania but dispersal characteristics of males were similar to previous research. My results indicated that dispersal by females, especially at the edge of the species range in Pennsylvania, was likely important to the rate of range expansion of bears in Pennsylvania.

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Chapter 1

Introduction

The black bear (*Ursus americanus*) is one of the most studied animals in North America. In Pennsylvania, research has been ongoing since the 1970s and the ensuing decades of research have provided a wealth of information. A literature review revealed >100 articles published that focused on some aspect of Pennsylvania black bear ecology (Ternent 2007). Since the hunting season was re-opened following closure for two years in the late 1970s, the Pennsylvania Game Commission (PGC) has collected harvest and life-history information on black bears.

Through the use of population models, the PGC has been monitoring the size of the population over time, but not bear dispersal. However, dispersal data are important for predicting the spread of genes, pattern of species invasions, success of reintroductions, and species persistence and evolution (Clobert et al. 2001, Kenward et al. 2002).

Dispersal has been defined as the permanent departure of an animal from its natal range to its adult range (Clobert et al. 2001, Bullock et al. 2002). Multiple other authors in Clobert et al. (2001) define dispersal events differently depending on the questions being addressed but, Andreassen et al. (2002) suggest one of the simplest descriptions of the process of dispersal being emigration from the natal range, transfer through multiple areas searching for an adult range, and immigration for establishment of an adult home range. The definition of dispersal that best fits the data available for this study was that dispersal was movement from a natal site to settlement at a new site.

Timing of departure of yearling bears from their mothers has been documented throughout the range of black bear in North America (Jonkel and Cowan 1971, Alt 1977, Lindzey and Meslow 1977, Alt 1978, 1980*b*, Reynolds et al. 1980, Garshelis and Pelton 1981, Rogers

1987, Schwartz and Franzmann 1992, Lee and Vaughan 2003, 2004). All of these studies documented separation of yearlings from the adult female from mid-May through early July. A few of these studies documented departure of yearlings from natal ranges as late as October after separation from their mother in early summer. In Pennsylvania, female bears typically are receptive every other summer if they are successful at raising young to the yearling stage of life. Females that lose cubs shortly after birth are capable of breeding in two consecutive summers.

Strong philopatry by one sex increases relatedness among nearby individuals, and dispersal theory predicts that such philopatry should result in greater dispersal rates in the other sex as an inbreeding avoidance mechanism (Perrin and Goudet 2001). Also polygynous mating systems are associated with female investment in raising young, and thus females are more likely to benefit from the defense of an acquired territory (Perrin and Goudet 2001). Thus, rates of dispersal for black bears, which have a polygynous mating system, should follow a similar pattern of greater male dispersal and limited female dispersal.

Black bears in the western United States have similar timing of separation from mothers, but complete departures from natal ranges vary, when compared to bears in eastern states. Family breakup is more or less the permanent separation of a mother from the close company of her offspring (Rogers 1987). Schwartz and Franzmann (1992) documented that timing of family breakup in Alaska was similar to Minnesota, but dispersal occurred when most male bears were 2 years of age. In western Idaho, Reynolds et al. (1980) documented yearling bears remaining with their mothers until early June. Following family breakup, mean distance between yearling bears and their mother increased as the season progressed. Reynolds et al. (1980) also documented most bears never recaptured (56%) were dispersing bears <4 years of age. In Minnesota, Rogers (1987) documented yearlings remained with their mothers until they were 16–17 months of age and breakup of the family was probably prompted by the mother simply leaving the young. Rogers (1987) also documented yearlings living alone in a small portion of their mother's home range after family breakup. After 1–2 years, the males dispersed, but females remained and expanded their ranges as they grew to maturity. Lindzey and Meslow (1977) documented dispersal by 4-year-old males on Long Island in southwestern Washington. Although males did not leave Long Island until this age, the distance between females and their cubs began increasing during the first week of June, coinciding with the beginning of the breeding season. In Montana, Jonkel and Cowen (1971) documented family breakup at the beginning of the breeding season that began in late June. Most young bears left their mother's home range, but typically female cubs remained and were tolerated.

Garshelis and Pelton (1981) documented home range use in Great Smoky Mountains National Park (GSMNP) in North Carolina and Tennessee. While following a mother-daughter pair, mutual avoidance was documented after family breakup in the spring of the daughter's second year. Most yearling-adult avoidance in the GSMNP was documented as temporal avoidance compared to departures creating exclusive spatial avoidance documented in other studies. Lee and Vaughan (2004) reported family breakup and departures in Virginia occurred from mid-May to mid-June, and no yearlings remained in their natal range or with siblings after breakup occurred. A previous study by Lee and Vaughan (2003) documented males departing their mother's home ranges from June through September. Two male bears remained in their mother's home range which the authors attributed to finding suitable habitat left vacant by the death of an adult male.

In Pennsylvania, Alt (1977) first documented the departure of yearlings from the adult females during late June or July, and no yearlings remained with the females after the breeding season. Following that research, Alt (1978) documented a change in the separation of yearlings and adult females. He documented the departure began in early May through late May, instead of June and July. Several female yearlings remained in part of their natal range while male yearlings dispersed from May through October. Dispersal was primarily by males as yearlings and 2-yearolds, with one reported as having dispersed as a 3-year-old. Annual progress reports by Alt (1979*b*, 1980*b*) continued to monitor dispersal and recoveries of yearlings. No male yearlings were recovered in their natal ranges after 18 months of age, and few dispersed prior to 17 months of age. Most female yearlings did not depart, and either remained completely within or continued to use a portion of their natal range. Only one female was recovered away from her natal range after 18 months of age. These results suggest a rapid departure of the male yearlings, but little to no departure of females, in Pennsylvania.

Wolff (1994) compared dispersal distances across multiple taxonomic groups and suggested distances moved by juveniles may be due to an opposite sex adult in the natal range or overlapping ranges. Individuals of several species have been documented to remain in a natal range if the opposite sex parent or nearby adult were eliminated and no longer present in their former home range, and no examples of parental aggression as the cause of juvenile dispersal were located (Wolff 1993). Bowman et al. (2002) calculated that distances moved by juveniles could be based on the linear dimension of a home range when body size was ignored; they inferred that median distance moved was 7 times the linear dimension of a home range.

In other areas of North America, Garshelis and Pelton (1981), Clevenger and Pelton (1989), Elowe and Dodge (1989), Wooding et al. (1992), Lee and Vaughan (2003, 2004) and Dobey et al. (2005) reported distance information for cubs, yearlings or subadult black bears as short as 0.2 km into habitat adjoining the mother's home range, but unoccupied by another adult (Appendix A). Both sexes were reported to make maximum dispersal movements 100–200 km (Rogers 1987, Elowe and Dodge 1989). After family breakup average separation distances from mothers for females ranged from 0.5 – 3.5 km and males ranged from 0.8 – 15.7 km. Clevenger and Pelton (1989) and Lee and Vaughan (2004) documented increasing distances through the summer with greatest distances recorded in early fall. During extensive research with black bears in New Mexico, through radio telemetry and genetic analysis, Costello (2008, 2010) and Costello et al. (2008) were able to document emigration distances of both sexes of yearlings. Female yearlings were found overlapping annual ranges with natal ranges although distances between natal and adult ranges varied from 0–5 km. Male bear emigration distances were 22–62 km, which were 2–6 average home-range diameters.

In north-central Pennsylvania, Wakefield (1969) was the first to record movements of wild captured and nuisance bears in Pennsylvania. Wakefield (1969) documented a 42 km movement by a non-nuisance bear. Eveland (1973), Kordek (1973), and Alt (1977, 1978) provided insight into bear dispersal in northeastern Pennsylvania when population abundance was lower than today. Eveland (1973) documented males averaging 11.7–13.4 km (depending on age) while average movement by females was 6.3 km. Kordek (1973) reported similar distances to Eveland (1973) for females ($\bar{x}$ = 5 km) and males ($\bar{x}$ = 13.7 km). Alt (1978) found yearling males dispersed up to 53 km from their mother's home range, whereas females established adult home ranges near their natal range (≤ 6.5 km). Based on concurrent information on breeding status of adult females (Alt 1983), dispersal movements in these studies overlapped with the peak of the breeding season from mid-June to mid-July. Recording movement distances continued in Pennsylvania while relocating female black bear to southwestern counties of Pennsylvania (Alt 1979*a*, 1980*a*, Ternent 2007). The longest movement recorded during research in Pennsylvania was a female over 2 years of age that moved 172.8 km (Alt 1995).

In Virginia, Lee and Vaughn (2003) reported dispersal movements similar to Pennsylvania but surmised that their definition of a dispersal event was too strict to identify all dispersal movements. They defined dispersal as a movement of a male bear (>18 km) or female (>8 km) from their natal home range when the two home range areas did not overlap. They recorded female movements ranging from 0.3 – 13.9 km, but did not consider any of their females as dispersed. The male movements were 0.9 – 80.0 km and dispersal was limited due to early loss of transmitters before most males may have finished dispersing. More recently, Costello (2010), working in New Mexico, documented female yearlings overlapping their natal and adult ranges that averaged 3 km between central points. She also documented yearling male dispersal distances of 22–61 km. She surmised that the >20 km male dispersal distances typically observed would serve to minimize encounters between males and closely related females.

Research Justification

Currently in Pennsylvania, 300–700 bears are ear-tagged annually and approximately 20% of these tagged bears are recovered during the hunting season (Diefenbach et al. 2004, Ternent 2010). Because thousands of bears have been tagged and recovered in Pennsylvania since the 1980s, sufficient data exist to assess dispersal movements (Kenward et al. 2002). Although radio-collaring allows near 100% tracking of dispersal movements, generally only adult females have been radio-collared in Pennsylvania and this age class has dispersed prior to radio-collaring (Ternent and Sittler 2007). In Pennsylvania, data were available on more than 65,000 individual bears handled since the mid-1970s, with approximately 9,600 having been marked with ear tags. Most early data were collected through intensive live-animal research conducted in the northeastern and north-central regions of Pennsylvania. The recent data contain captures across the range of bears in Pennsylvania.

Knowing when and how dispersal occurs and its role in the maintenance and expansion of a bear population is important for maintaining a viable population, and has implications for estimating abundance for models assuming population closure (Diefenbach et al. 2004). Characteristics of dispersal in male and female black bears are poorly understood in Pennsylvania. Limited research following individual bears, some wearing radio-collars, was performed before the bear population reached the higher population level currently in

Pennsylvania. When Pennsylvania bear numbers were at historic lows, two areas in the north-central and northeastern regions were the primary range of black bears in the state. From these two areas, population density has increased and distribution has expanded across two-thirds of the state (Ternent 2007). Overall bear density increased from 8.24 bears/100km^2 in 1980 to 18.8 bears/100km^2 in 2008 (Figure 1-1; M. Ternent, PGC, unpublished data). The average annual increase in density from 1980–2008 averaged 0.38 bears/100km^2 but annual change by year varied. Average annual increase in density was 0.23 bears/100km^2 during the 1980s, 0.35 bears/100km^2 during the 1990s, and 0.56 bears/100km^2 during the 2000s. The overall increase in bear density occurred in both the core and non-core areas and in all regions of Pennsylvania (Appendices C and D).

My research questions addressed implications of how dispersal patterns vary spatially and temporally in Pennsylvania. Understanding changes in dispersal, as the bear population increased in Pennsylvania, may help managers identify successful strategies for reducing bear-human conflicts and understanding effects of the population on re-colonization and continued expansion. I used decade as a surrogate for population density because the abundance of bears had been increasing with regulated management of the Pennsylvania population (Figure 1-1). Increasing densities and the range expansion of bears has resulted in more bear-human conflicts. The number of bears being captured and moved due to nuisance complaints has been increasing each year (Ternent 2007). Understanding dispersal rates and distances, and the factors that influence dispersal, will help identify the scale at which bear populations need to be managed to minimize bear-human conflicts.

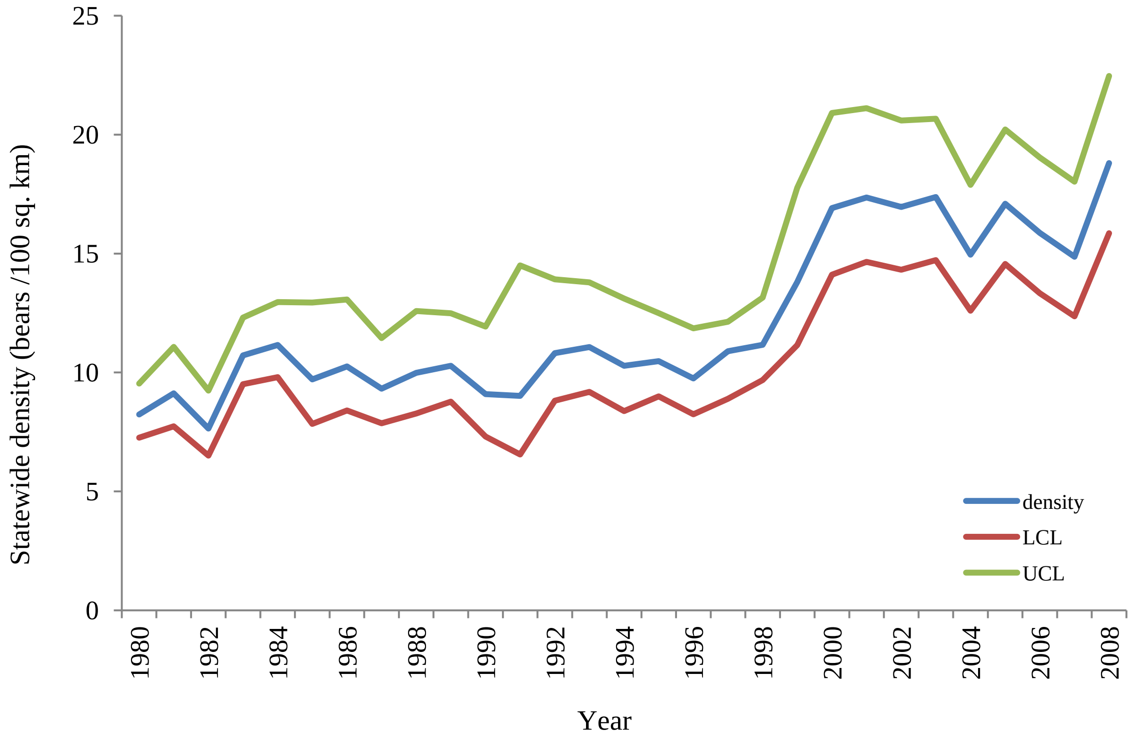

Figure **1-1**: Density of black bears (bears/100km^2) and 95% confidence limits based on estimated population size and the area of counties where harvests occurred in Pennsylvania, 1980–2008.

Objectives and Hypotheses

My objectives were to (1) describe timing of dispersal of yearling bears by calculating dispersal probabilities by age of bears, (2) quantify dispersal distances of yearling bears and assess whether the distance of dispersal was greater in the historic core bear population area compared to newly established area of the bear range, and (3) estimate dispersal rates for yearling bears across Pennsylvania and estimate dispersal rates in the core bear population area compared to the newly established area of the bear range. I analyzed recapture and dead recovery data obtained when bears were ≥16 months of age from bears tagged before dispersal is known to occur (≤15 months of age).

Timing of departure of yearling bears from natal ranges is known to occur as breeding season begins and continues through fall. I hypothesized timing of dispersal in Pennsylvania overlapped the onset of breeding season and yearling departures from their mother peaked in May and June. I predicted dispersal was completed by the time male and female bears reached 24 months of age. Male bears are known to disperse before females; therefore, timing in Pennsylvania should indicate that yearling males depart before yearling females.

Dispersal theory predicts that strong philopatry by one sex should result in greater dispersal rates in the other sex as an inbreeding avoidance mechanism (Perrin and Goudet 2001). Previous research has found a greater proportion of males than females dispersed and males disperse farther distances. However, documented increasing population densities since the 1980s suggest more suitable habitat has become occupied, and dispersing juveniles may have to travel greater distances to find unoccupied suitable habitat. Bear densities are greater in the north-central and northeastern regions of Pennsylvania, which contain the historic bear range, and more intraspecific competition for resources may be occurring (Appendices C and D). I hypothesized female bears dispersed shorter distances about 0.5 – 1 times the greatest linear distance across an average female home range in Pennsylvania (approx. 6–15 km), and male black bears dispersed over 20 km, or the equivalent of 1.5 – 15 times the greatest linear distance across an average female home range in Pennsylvania (approx. 20–200 km). I expected dispersal distance increased for both sexes across the decades as bear density increased. I predicted dispersal distance was greater in the north-central and northeastern regions of the state compared to the regions of lower densities (western, south-central and southeastern). For distances moved by bears in the historic core area, I predicted both sex moved greater distances in the core area than the non-core area due to already existing higher densities of bears.

Dispersal in black bears is male dominated but limited female dispersal has been observed. Home ranges of female offspring tend to overlap the mother's range via short-distance dispersals, which over time will create a slowly expanding central population. Newly established populations exist at lower densities resulting in less competition for resources and mates. Higher population densities create increased competition for available space and mating opportunities. I hypothesized that dispersal rate increased since the 1980s as a result of increasing population densities and increased competition for unoccupied suitable habitat. Previous Pennsylvania research documented dispersal rates for male were 0.85 – 1.00 and female rates were 0.0 – 0.20; therefore, I expected male black bear dispersal rate was near 1.00 whereas the dispersal rate for females was <0.20. For males, I predicted an increase in the dispersal rate each decade as population densities increased, with the greatest increase during the 2000s when the greatest average annual rate of change in density occurred. For females, I predicted dispersal rates were similar across decades because of observed limited female dispersal. If an increase occurred, I expected to see the change from the 1990s to the 2000s due to the highest population densities being most recent. In the north-central and northeastern regions of Pennsylvania, I predicted dispersal rates were greater compared to the other 3 regions. I predicted greater overall dispersal rates for both sexes from the core area. Across all decades, I expected both sexes to exhibit greater dispersal rates in the core area compared to the non-core area. I predicted that more males in the core area of the north-central and northwestern regions dispersed when compared to the non-core area in those regions, and males in the south-central and western regions did not differ in dispersal rates between the core area and the non-core area. I also predicted that females in the core area had greater dispersal rates than in the non-core area for all regions.

Chapter 2

Methods

The data I used for analysis were obtained from the PGC and contained all bears handled within the state from 1969–2008. Handling events occurred throughout the year related to hunting seasons, research efforts, collection of roadkills, response to nuisance complaints, or tagging efforts by agency personnel. Pennsylvania Game Commission employees and researchers captured bears using culvert traps, foot snares, dart guns, and locating cubs in dens associated with radio-collared females (Wakefield 1969, Kordek 1973, Alt 1977, 1990, Ternent and Sittler 2007). Annually, 300–700 bears were ear-tagged throughout the state where uniquely numbered metal ear tags were attached to each ear (National Band and Tag Company, Newport, Kentucky, USA or Hasco Tag Company, Dayton, Kentucky, USA). Also, some bears received a unique tattoo to ensure recovery information was documented if ear tags were lost.

The PGC database of bear captures, recaptures and dead recoveries included date of capture, age at capture (or recapture), capture location, and recovery location (Appendix B). I selected bears initially tagged at <16 months of age that had subsequent recaptures or dead recoveries at all ages. After retaining these encounters, I verified each capture history for consistency of sex; age (in months) from initial capture to subsequent recoveries; township, county, and wildlife management unit (WMU) of capture; and a description of locations for each encounter. If I was unable to identify capture, recapture, or dead recovery sites on a map, I excluded the data from analysis. The database used for analysis contained a capture record and a final recapture or dead recovery record for bears with identifiable locations. Several bears were only recaptured at <16 months of age, or recaptured both <16 months and when they were ≥16 months of age.

For all bears, I assumed a birth month of January and the age of a bear handled that month was labeled as 0 (cub) or 12 months (yearling) of age. I used the bear age at date of initial tagging for determining the age at subsequent recoveries. If comments or weight information suggested that bear age at initial tagging was unlikely to be ≤15 months old, the data were not used. Ages estimated from extracted teeth were performed by Matson's Laboratories (Missoula, Montana) via counting cementum annuli. Compared to estimated ages calculated from initial captures, there were several estimated ages from extracted teeth showing discrepancies. For consistency in situations when the known age and the tooth age differed, I aged the bears based on the initial capture information instead of the tooth data.

To evaluate the effects of population increase on changes in dispersal patterns, I assigned each bear to a decade of dispersal based on the year the bear became 12 months old. Previous research in Pennsylvania reported most dispersal occurred by 24 months of age (Alt 1978, 1980*b*). I labeled all dispersal years from 1980–1989 as being the decade 1980s, 1990–1999 as the decade 1990s, and 2000–2008 as the decade 2000s.

I estimated dispersal distance by calculating the distance between initial capture and the final recapture or dead recovery location. In northeastern Pennsylvania, Alt (1977) estimated average home range was 41 km^2 for females and 173 km^2 for males. A study of female home range size in north-central Pennsylvania showed an average of 24.8 km^2 (McLaughlin 1981). Alt et al. (1980: 133) noted "…another parameter occasionally used for home range comparisons is the greatest linear distance across the home range". In northeastern Pennsylvania, the greatest distance across home ranges of male was ≤26 km and female bears was ≤13 km (Alt et al. 1980, Ternent 2007). Although my data did not track specific bears using telemetry and did not determine if initial capture was within a mother's home range, I assumed the initial capture locations to be within the natal range because most bears were captured with their mothers. I assumed calculated distances ≥13 kilometers represented dispersal events based on the research from Alt (1977). I investigated whether dispersal occurred for bears recaptured ≤15 months of age. If distance moved by a cub indicated the bear had dispersed, I reviewed the database comments to determine if the cubs were with their mother and siblings. Recaptures with mothers were identified as non-dispersers even though the calculated distance suggested otherwise for several cubs (n = 23).

I delineated 5 regions of Pennsylvania representing differing landscape and bear population characteristics (Figure 2-1). These regions were based on combinations of WMUs containing similar bear habitat and densities (Table 2-1). The western (W) region consisted of counties in northwestern and southwestern Pennsylvania, and combined WMUs that historically had low bear densities. The north-central (NC) region encompassed the Allegheny Plateau, merging WMUs that have consistently maintained high bear densities. The south-central (SC) region contained the state's ridge-and-valley topography, and combined areas of high and low bear densities although the high densities occurred in the most recent decade. The northeastern (NE) region included the northeastern counties of the state where bear densities varied from medium to high and were part of the historic range continually occupied by bears. Few bears occurred and no data were available in the southeastern (SE) region. The SE region was not included in further analysis.

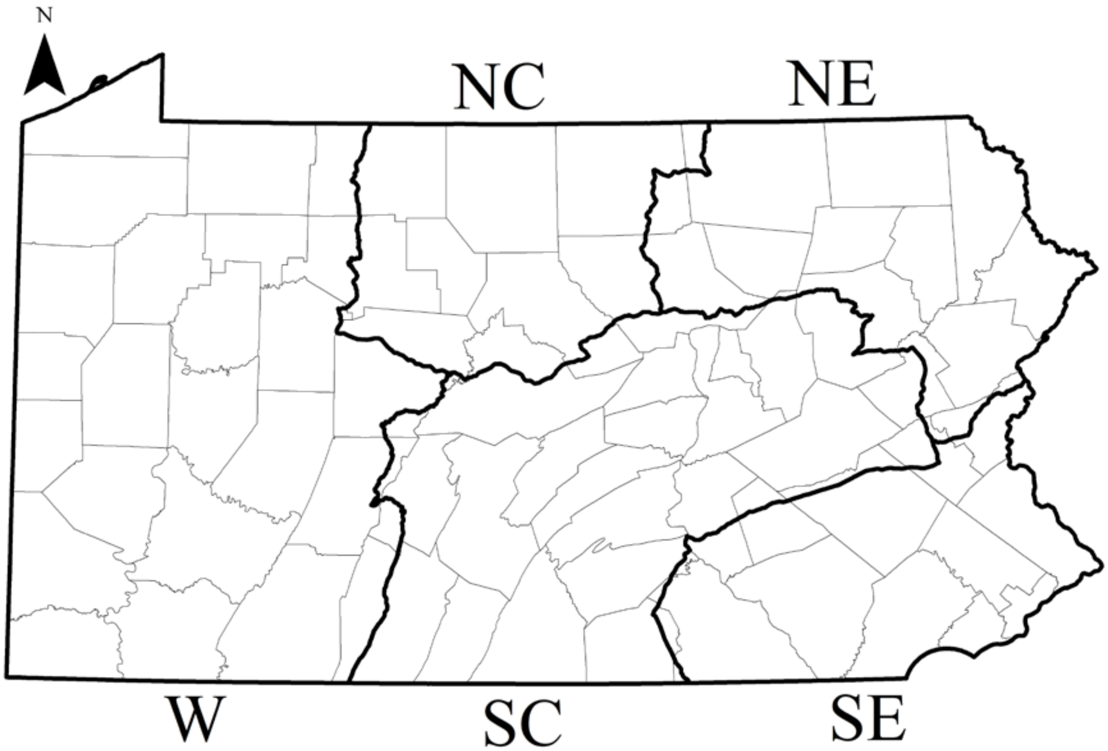

Figure **2-1**: Five regions of Pennsylvania merged from Pennsylvania Game Commission Wildlife Management Units to assess dispersal patterns of bears.

Table **2-1**: Estimated mean annual black bear density (bears / 100km^2) and standard deviation for each decade, by region in Pennsylvania, 1980–2008. Density was the estimated abundance divided by the total area of counties within a region where harvests occurred (M. Ternent, PGC, unpublished data).

	Western		North-central		South-central		Northeastern	
Decade	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
1980s	1.93	0.46	3.64	0.51	1.52	0.30	2.60	0.39
1990s	2.82	0.69	3.18	0.47	2.09	0.30	2.56	0.38
2000s	3.98	0.51	4.74	0.58	3.55	0.34	4.40	0.46

I assigned areas similar to the historic core areas in the north-central and northeastern regions (Ternent 2007) to represent the core area of the newly expanded population. I defined the core population area as townships where bears were harvested and research was conducted in the 1970s. To determine the townships associated with the core population area, I created 3 polygons in ArcGIS (ESRI Inc., Redlands, CA) around locations where harvest occurred and designated the townships within or intersected by these polygons as the core population area. Each bear was assigned to the core or non-core area of the current range based on the township of capture (Figure 2-2). The average annual bear densities in the core area and the non-core area increased each decade (Table 2-2).

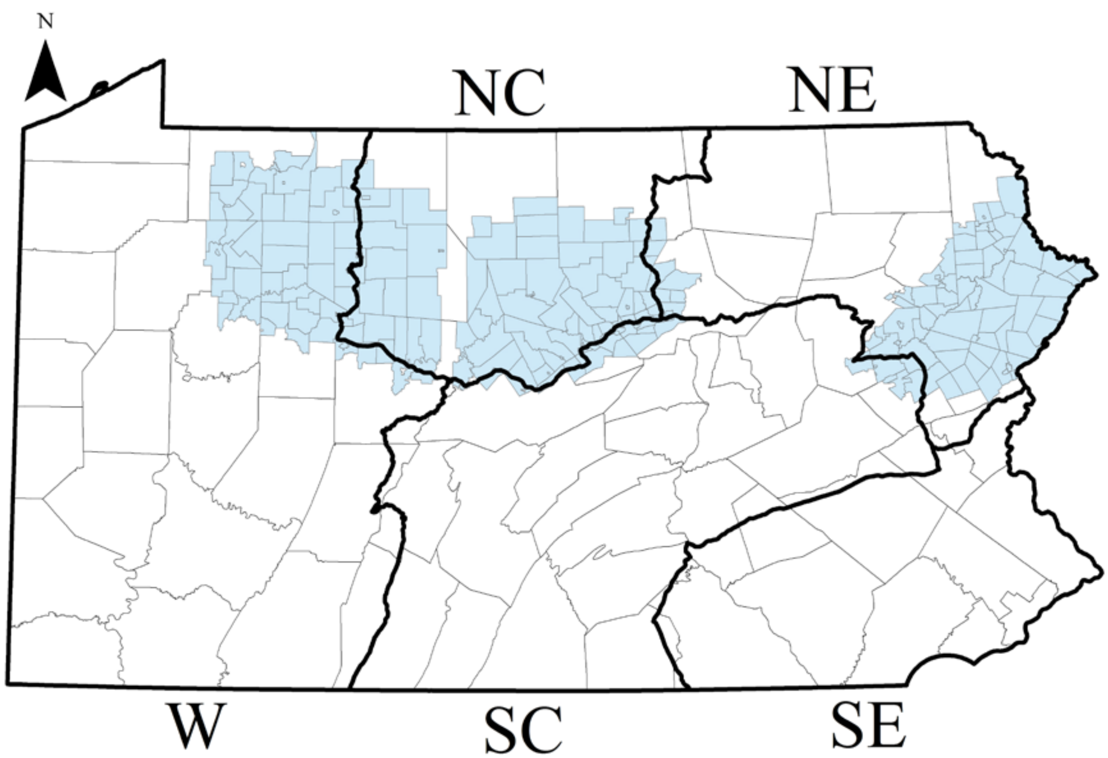

Figure **2-2**: Three groups of townships representing the core population area of the current bear range in Pennsylvania defined as areas where bear harvest and research occurred in the 1970s.

Table **2-2**: Estimated mean annual black bear density (bears / 100km^2) and standard deviation for each decade within the core and non-core areas of Pennsylvania, 1980–2008. Density was the estimated abundance divided by the total area of counties within a region where harvests occurred (M. Ternent, PGC, unpublished data).

	Core Area		Non-Core Area	
Decade	$\bar{x}$	SD	$\bar{x}$	SD
1980s	25.60	4.42	1.38	0.47
1990s	31.40	4.35	3.17	0.95
2000s	47.96	4.51	7.11	1.16

I used topographic maps of each county and descriptions of captures, recaptures, and dead recovery locations for each bear to assign x–y coordinates to locations. I projected all maps in Pennsylvania Albers projection and obtained coordinates in meters using the geographic coordinate system of North American Datum 1927. I calculated distances in kilometers between initial capture location and the final recapture or dead recovery for each bear. A dispersal event was determined based on the distance moved, and I classified both sexes as a disperser if distance was ≥13km or a non-disperser if distance was <13km. I assumed a dispersal event occurred prior to a recapture or dead recovery.

Timing of Dispersal

I estimated when dispersal occurred by calculating dispersal rates for each sex by grouped months over which dispersal could have occurred based on age at recapture or dead recovery (≤15, 16–19, 20–23, 24–27, 28–31, and 32+ months of age). For example, bears recaptured or dead recovered at 20–23 months of age could have dispersed at any age prior to or at the age at recovery. Therefore, the age groups provide estimates of cumulative dispersal rate by age. When dispersal rates between ages at recovery no longer increased then I assumed dispersal to be completed by the first age class where dispersal rates became constant. For example, if dispersal rates for the ≤15, 16–19, and 16–23 month of age groups increased but older age groups did not change, then I assumed dispersal was completed by 23 months of age.

Dispersal Distances

I developed a state-wide dispersal-distance function (Wiens 2001) separately for males and females using all distances. I binned calculated distances into 5 kilometer intervals for bears ≥16 months of age, only for the dispersal-distance functions due to reduced numbers of bears located at the longer distances. I used analysis of variance (ANOVA) to test for differences in dispersal distances for each sex between the regions, decades, and between the core area and the non-core area.

Rates of Dispersal

I defined dispersal rate as the proportion of bears that moved ≥13 km between their capture and final recapture or dead recovery location. To estimate dispersal rate (D), I developed a sex-specific set of candidate logistic regression models (SAS 9.3, SAS Inc. Cary, NC) examining all possible combinations and interactions of the variables region and decade. I modeled dispersal rate (1 = dispersed; 0 = non-dispersed) separately for males and females because I expected dispersal rates to differ for each sex. For all models, the reference decade was the 1990s and the reference region was the northeastern (NE). I used an intercept-only (null) model to estimate an overall dispersal rate (D) for each sex. I used Akaike's Information Criterion, adjusted for small sample size ((Burnham and Anderson 2002), to select the best model of dispersal. I used model averaging if no single best model was evident.

To test differences in dispersal proportions for each sex between the core area and non-core area, I performed a chi-square test of independence using contingency tables for statewide, decade, and region data.

Chapter 3

Results

Timing

Dispersal first became evident when yearling female bears were 16–19 months of age. The estimated dispersal rate ($\hat{D}$) for females recovered at 16–19 months of age was 0.28 (SE = 0.06). All other female age groups indicated similar dispersal rates as bears recovered at 16–19 months of age (Figure 3-1). Similar to females, male dispersal was first evident when they were 16–19 months of age ($\hat{D}$ = 0.61 SE = 0.18; Figure 3-2). Male bears recovered when older than 19 months of age had similar dispersal rates as those recovered at 16–19 months of age, which indicated that most dispersal occurred when they were 16–19 months of age.

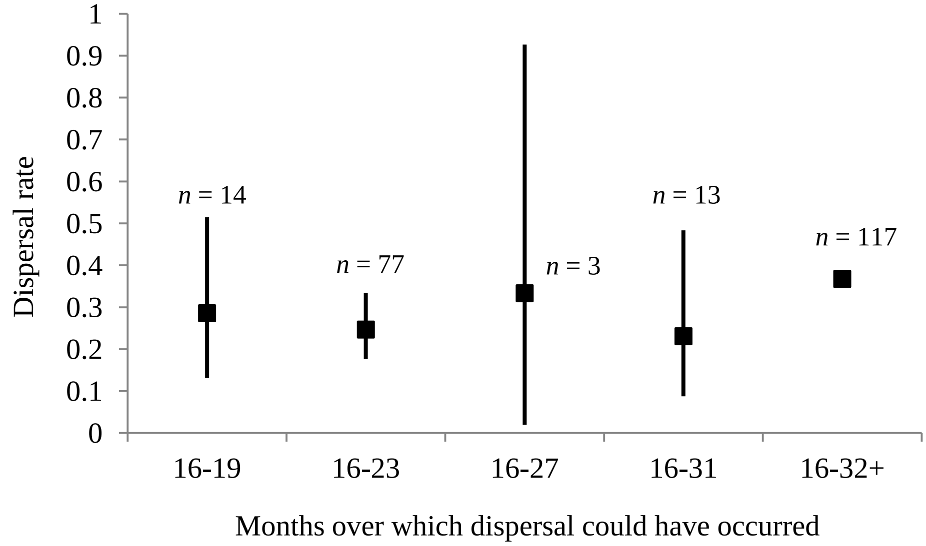

Figure **3-1**: Estimated dispersal rate grouped by age in months over which dispersal could have occurred (and 95% CI) for female black bears based on age at recapture or dead recovery when ≥16 months of age in Pennsylvania, 1980–2008.

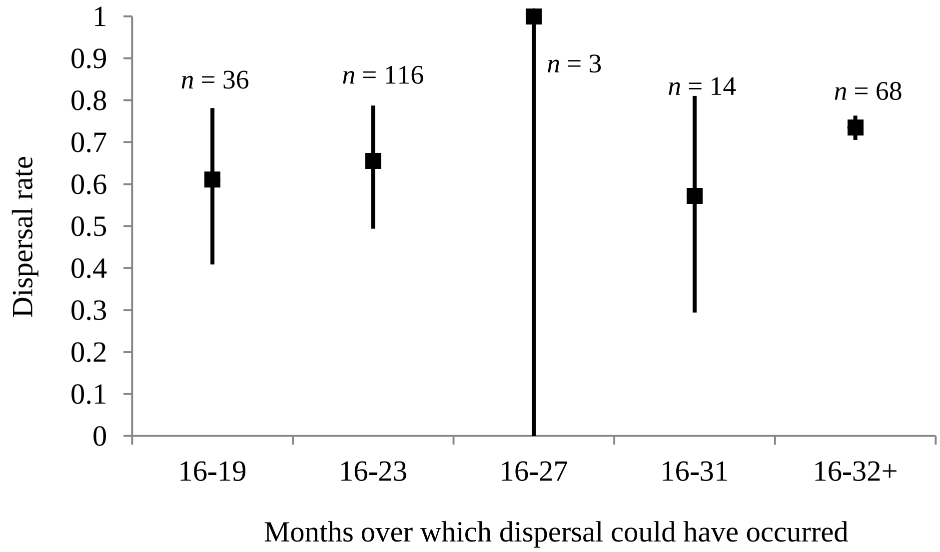

Figure **3-2**: Estimated dispersal rate grouped by age in months over which dispersal could have occurred (and 95% CI) for male black bears based on age at recapture or dead recovery when ≥16 months of age in Pennsylvania, 1980–2008.

Distances

Median distance dispersed was greater for males (47.03 km, *n* = 98) than females (25.84 km, *n* = 70). Female bears ≥16 months of age dispersed an average distance of 31.28 km (SE = 2.18 km), which was about 2 times the greatest linear distance across an average female home range in Pennsylvania. The average dispersal distance moved by male bears ≥16 months of age was 54.12 km (SE = 2.49 km), about 4 times the linear distance across an average female home range.

All average male dispersal distances were greater than female dispersal distances for each of the regions and decades (Table 3-1, 3-2). I failed to detect a difference for dispersal distances among regions for males ($F_{3, 155}$ = 1.25, P = 0.29) and females ($F_{3, 66}$ = 2.74, P = 0.11). Also, I failed to detect differences for distance dispersed across decades for males ($F_{2, 132}$ = 0.66, P = 0.52) or females ($F_{2, 67}$ = 3.13, P = 0.39). For both sex, the dispersal distance functions indicated that most bears did not move far beyond an average home range size (Figures 3-3 and 3-4).

Table **3-1**: Summary statistics of dispersal distances (km) by region for Pennsylvania black bears ≥16 months of age at recapture or dead recovery, 1980–2008.

	Males					Females				
Region	n	$\bar{x}$	SE	95%LCL	95%UCL	n	$\bar{x}$	SE	95%LCL	95%UCL
W	42	54.56	3.35	47.79	61.34	19	29.82	2.90	23.72	35.92
NC	14	55.50	9.22	35.59	75.42	17	40.42	6.01	27.67	53.16
SC	16	51.42	5.77	39.11	63.72	5	30.49	6.99	11.08	49.89
NE	26	54.31	4.96	44.10	64.52	29	27.02	3.00	20.88	33.15

Table **3-2**: Summary statistics of dispersal distances (km) by decade for Pennsylvania black bears ≥16 months of age at recapture or dead recovery, 1980–2008.

	Males					Females				
Decade	n	$\bar{x}$	SE	95%LCL	95%UCL	n	$\bar{x}$	SE	95%LCL	95%UCL
1980s	21	55.42	5.72	43.49	67.34	17	26.00	2.81	20.05	31.96
1990s	20	46.05	4.78	36.06	56.05	13	32.43	3.84	24.06	40.79
2000s	57	56.47	3.31	49.84	63.09	40	33.15	3.39	26.30	40.00

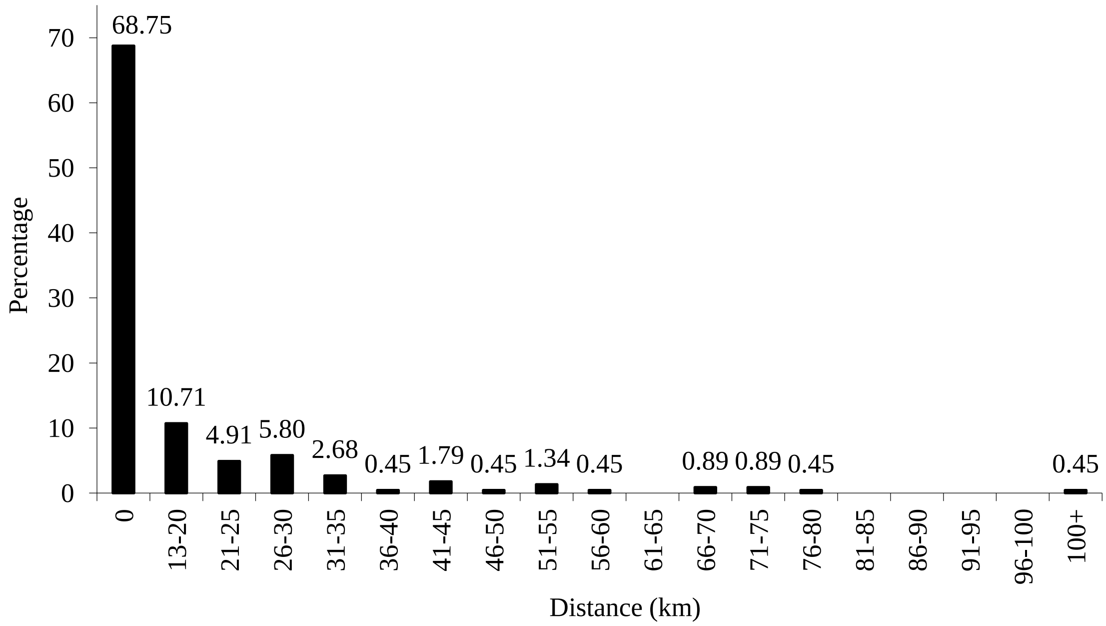

Figure **3-3**: Dispersal distance function for female black bears ≥16 months of age based on distance moved (km) from capture to final recapture or dead recovery in Pennsylvania, 1980–2008. Movements of ≤12 km were combined in the initial distance group as non-dispersing bears.

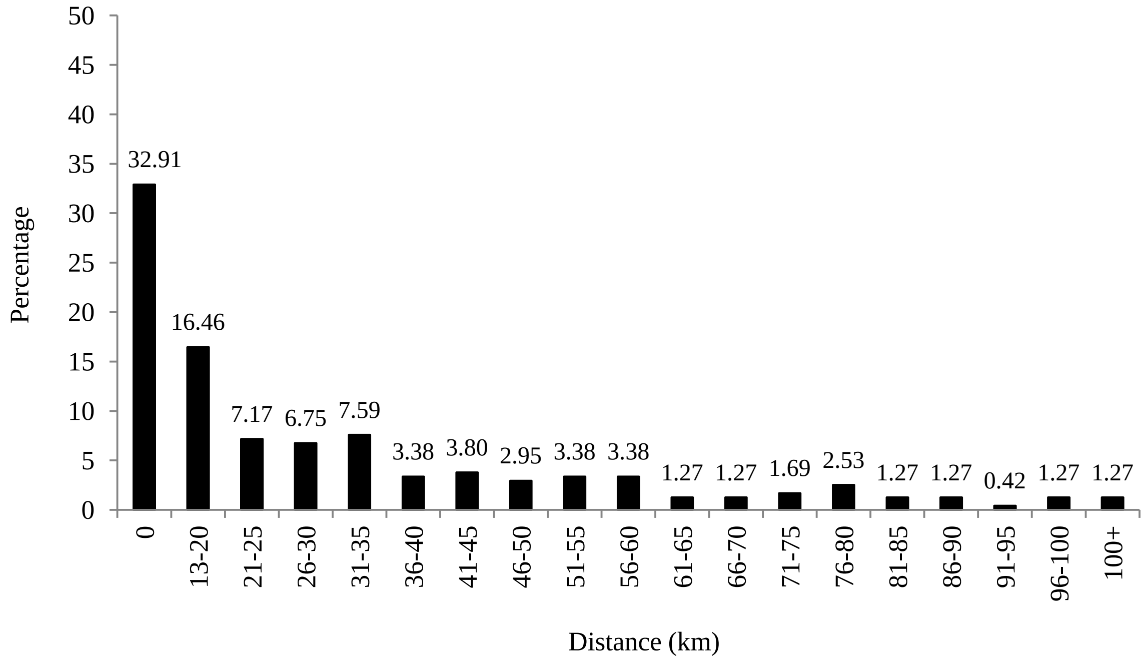

Figure **3-4**: Dispersal distance function for male black bears ≥16 months of age based on distance moved (km) from capture to final recapture or dead recovery in Pennsylvania, 1980–2008. Movements of ≤12 km were combined in the initial distance group as non-dispersing bears.

Rates

Bears recovered <16 months of age were unlikely to disperse. Dispersal rate for female cubs was 0.04 (SE = 0.026, *n* = 57) and for male cubs was 0.02 (SE = 0.018, *n* = 62). Only 2 female cubs dispersed during the 1980s with no dispersals during the 1990s and 2000s. Only 1 male cub dispersed during the 2000s. Dispersal rates for bears recovered ≥16 months of age was 0.28 for females (SE = 0.06, *n* = 224) and 0.67 for males (SE = 0.06, *n* = 237). Overall dispersal rates for males were lower than I had predicted near 1.0, and overall rates for females were higher than I predicted at <0.20.

No single logistic regression model best explained female dispersal so I used model averaging to estimate dispersal rates by decade and region (Figure 3-7, Tables 3-3 and 3-5). Some maximum likelihood estimates for parameters in the full model could not be calculated, so I did not use the full model in calculating the averaged model. The decade-only model had the highest model weight (w_i = 0.45) but the null model was also competitive with the second highest model weight (w_i = 0.22). The other variable combinations were also influential (w_i = 0.08–0.15) in my decision to use model averaging. The decade-only logistic regression model best explained male dispersal (w_i = 0.87; Tables 3-4 and 3-5). There was not strong enough evidence to use any of the additional models (w_i = 0.00–0.12).

Table **3-3**: Logistic regression models estimating dispersal rate for female black bears recovered ≥16 months of age in Pennsylvania, 1980–2008.

Model variables	No. parameters	ΔAIC_c	Model weights	Model likelihood
decade	2	0.000	0.4505	1.0000
null	1	1.454	0.2178	0.4834
region	3	2.251	0.1462	0.3245
decade+region+decade*region	5	2.885	0.1065	0.2363
decade+region	5	3.481	0.0790	0.1754

Table **3-4**: Logistic regression models estimating dispersal rate for male black bears recovered ≥16 months of age in Pennsylvania, 1980–2008.

Model variables	No. parameters	ΔAIC_c	Model weights	Model likelihood
decade	2	0.000	0.8707	1.0000
decade+region	5	3.975	0.1193	0.1370
decade+region+decade*region	5	9.438	0.0078	0.0089
region	3	12.244	0.0019	0.0022
null	1	15.806	0.0003	0.0004

Table **3-5**: Coefficients from best logistic regression model for female and male black bears recovered ≥16 months of age in Pennsylvania, 1980–2008. Parameter estimates and SE were model averaged for females. The reference level was 1990s for decade and NE for region.

	Female		Male	
Model variables	Estimate	SE	Estimate	SE
Intercept	-1.1683	0.3129	1.0116	0.3371
Decade(1980s)	-0.3822	0.5552	-1.1488	0.4107
Decade(2000s)	0.2187	0.4932	0.2144	0.4019
Region(W)	-0.1978	0.2437		
Region(NC)	-0.2699	0.4524		
Region(SC)	0.1511	0.2817		

My results of dispersal rates for the decades and regions did not match predictions. Dispersal rates for females ($\hat{D}$ = 0.16–0.38) were influenced by decade (Figure 3-5). I had predicted similar female dispersal rates across the 1980s and 1990s with a possible increase between the 1990s and 2000s. Dispersal rates for females ($\hat{D}$ = 0.22–0.43) were not strongly influenced by region (Figure 3-6) even though I expected the NC and NE regions to have greater rates. For female bears within all regions, the dispersal rate was similar in the 1980s and 1990s and increased in the 2000s (Figure 3-7). Females in the NC region had greater dispersal rates ($\hat{D}$ = 0.24–0.36) than females in all other regions every decade. During the 2000s, dispersal rate was similar among all regions ($\hat{D}$ = 0.32–0.36). Females in the NC region had the largest increase in dispersal rate from the 1990s ($\hat{D}$ = 0.21) to the 2000s ($\hat{D}$ = 0.36).

For males, dispersal rates across decades almost matched my predictions but dispersal rates by regions were different than predicted. Dispersal rates for males ($\hat{D}$ = 0.47–0.77) were influenced by decade (Figure 3-5) and it almost matched the increase I had predicted. I failed to detect differences in dispersal rates for males ($\hat{D}$ = 0.56–0.79) by region (Figure 3-6) even though I expected the NC and NE regions to have higher rates than the rest of Pennsylvania.

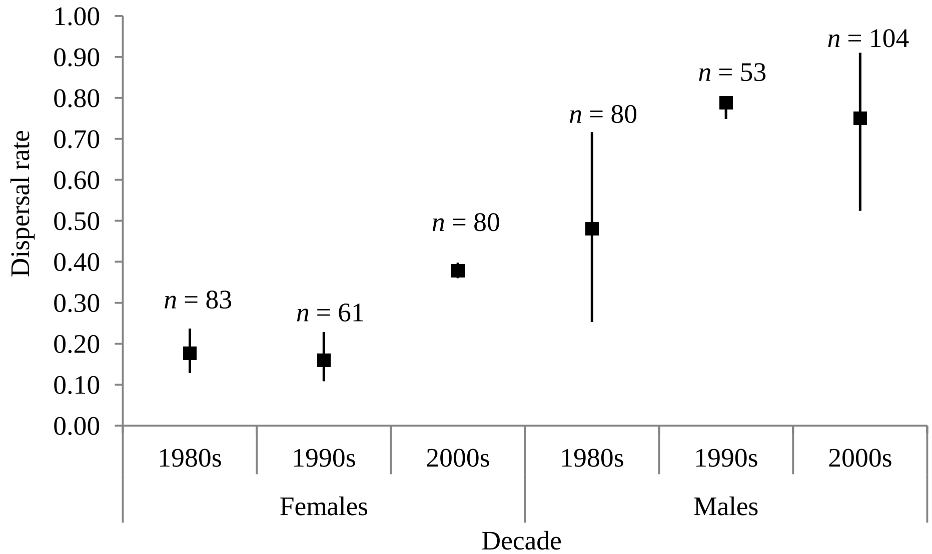

Figure **3-5**: Estimated dispersal rate during 3 decades (and 95% CI) of female and male black bears recaptured or dead recovered when ≥16 months of age in Pennsylvania, 1980–2008. Sample size for each decade included.

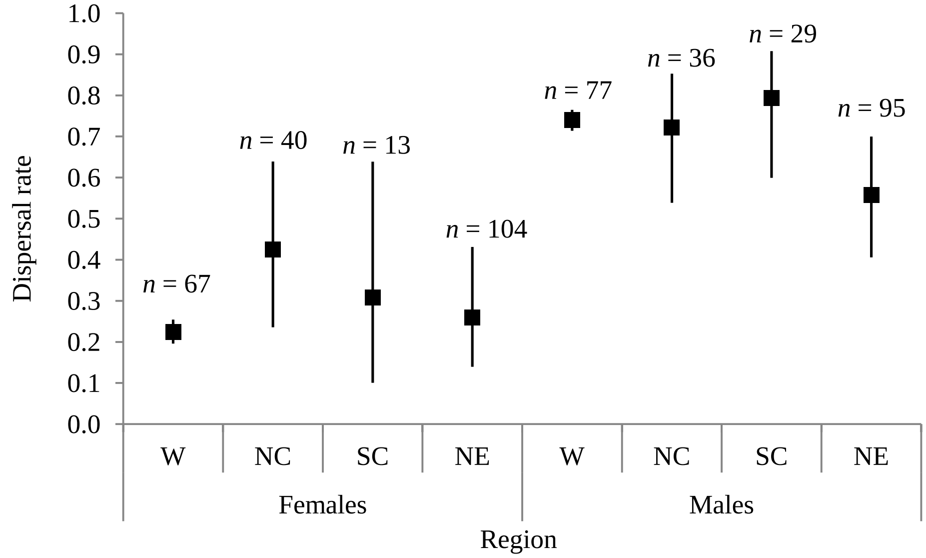

Figure **3-6**: Estimated dispersal rate in 4 regions of Pennsylvania (and 95% CI) of female and male black bears recaptured or dead recovered when ≥16 months of age, 1980–2008. Sample size for each region included.

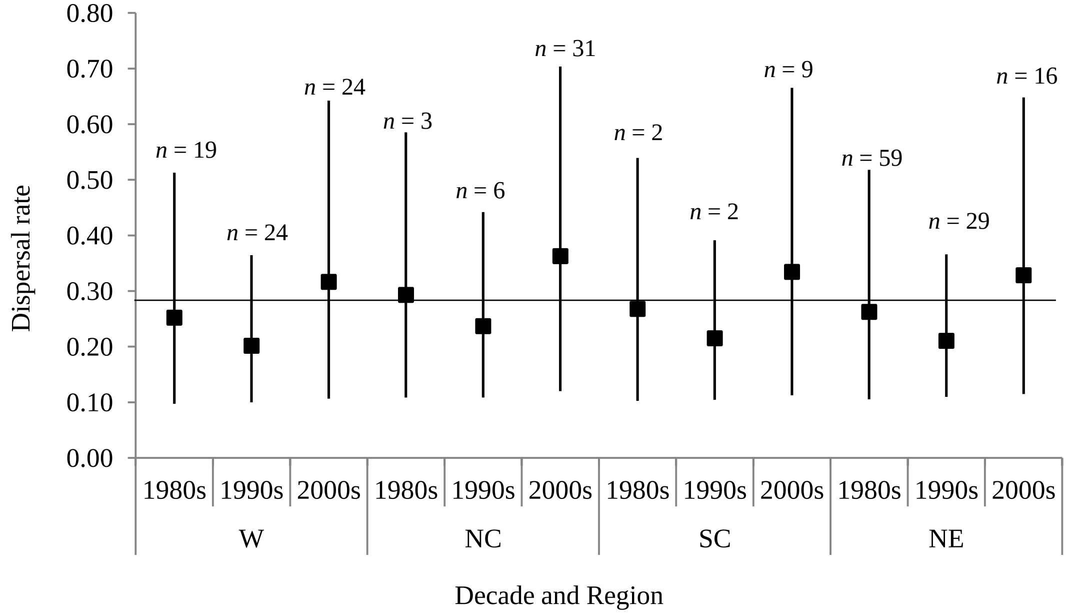

Figure **3-7**: Estimated dispersal rate (and 95% CI) of female black bears, for each decade among regions within Pennsylvania, based on coefficients of a model-averaged logistic regression model (Table 3-4), 1980–2008. Bears were recaptured or dead recovered when ≥16 months of age. Sample size for each decade-region combination included. The black horizontal line represents the overall dispersal rate ($\hat{D}$ = 0.28) for female bears based on the same combined data.

Core Area

Mean and median dispersal distances for both sexes were greater in the non-core area (Table 3-5); however, I found no statistical difference for males ($F_{1,\,134}$ = 1.00, P = 0.31) or females ($F_{1,\,58}$ = 0.30, P = 0.58). Overall dispersal rates did not differ between the core area and non-core area for males (χ_1^2 = 0.83, 0.90 > P > 0.75) or females (χ_1^2 = 1.80, 0.25 > P > 0.10). I predicted higher bear density in the core area would have resulted in bears dispersing greater distances.

I detected a difference in dispersal rates between the core area and non-core area for females during the 1980s (χ_1^2 = 3.96, $P < 0.05$; Figure 3-8). However, I failed to detect differences of dispersal rates for females during the 1990s (χ_1^2 = 0.81, $0.50 > P > 0.30$) and 2000s (χ_1^2 = 0.10, $P = 0.75$). My prediction of female dispersal rates being greater in the core area during every decade was not supported. For males, I failed to detect a difference in dispersal rates for any decade between the core and non-core areas ($P > 0.05$; Figure 3-9). These results did not match my prediction for males in the core area having greater dispersal rates than bears in the non-core area.

Within regions dispersal rates differ from what I predicted for both females and males (Figures 3-10 and 3-11). For females, I detected a difference between the core and non-core areas in the NC region (χ_1^2 = 6.93, $P = 0.01$) and NE region (χ_1^2 = 4.82, $0.01 < P < 0.05$); and failed to detect a difference in the W region (χ_1^2 = 0.07, $P = 0.80$) and SC region (χ_1^2 = 0.043, $0.90 > P > 0.80$). I had predicted that region would not influence female dispersal rates and all rates from the core area would have been greater than the non-core area. For the males, I failed to detect a difference for any of the regions between the core and non-core areas ($P > 0.05$). I had predicted that dispersal rates would be greater for the core area males in the NC and NE regions.

Table **3-5**: Summary statistics of dispersal distances (km) for Pennsylvania black bears recaptured or dead recovered ≥16 months of age in the core and non-core areas of the bear range in Pennsylvania, 1980–2008.

	n	$\bar{x}$	SE	Median	Maximum
Females					
Core Area	76	12.07	2.18	4.90	106.71
Non-Core Area	105	14.39	1.58	7.34	77.60
Males					
Core Area	66	27.04	3.31	19.16	130.67
Non-Core Area	123	32.02	2.27	26.83	100.81

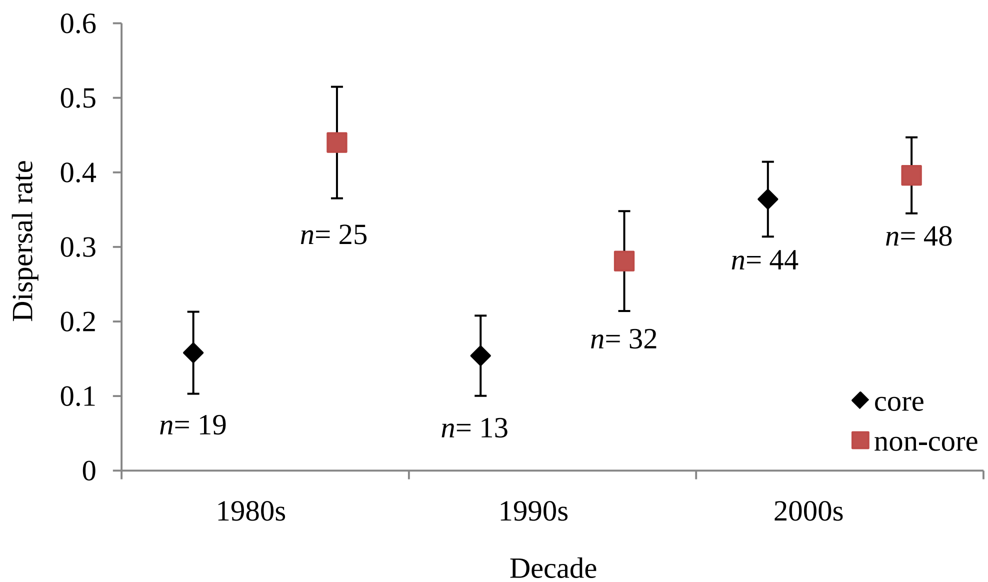

Figure **3-8**: Dispersal rates by decade (and SE bars), of female black bear recaptures or dead recoveries ≥16 months of age, in the core and non-core areas of the bear range in Pennsylvania, 1980–2008. Sample size for the decade included for each area.

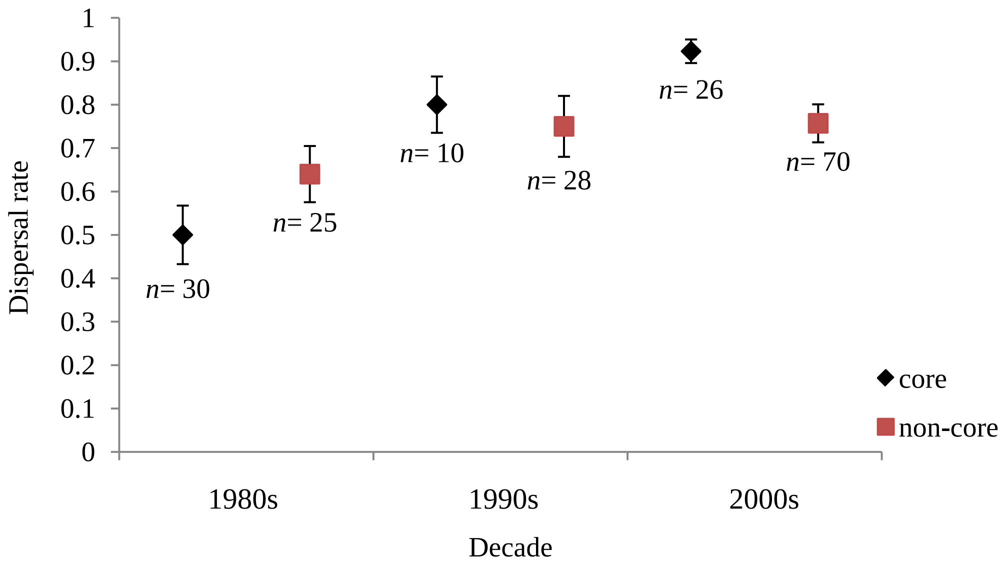

Figure **3-9**: Dispersal rates by decade (and SE bars), of male black bear recaptures or dead recoveries ≥16 months of age, in core and non-core areas of the bear range in Pennsylvania, 1980–2008. Sample size for the decade included for each area.

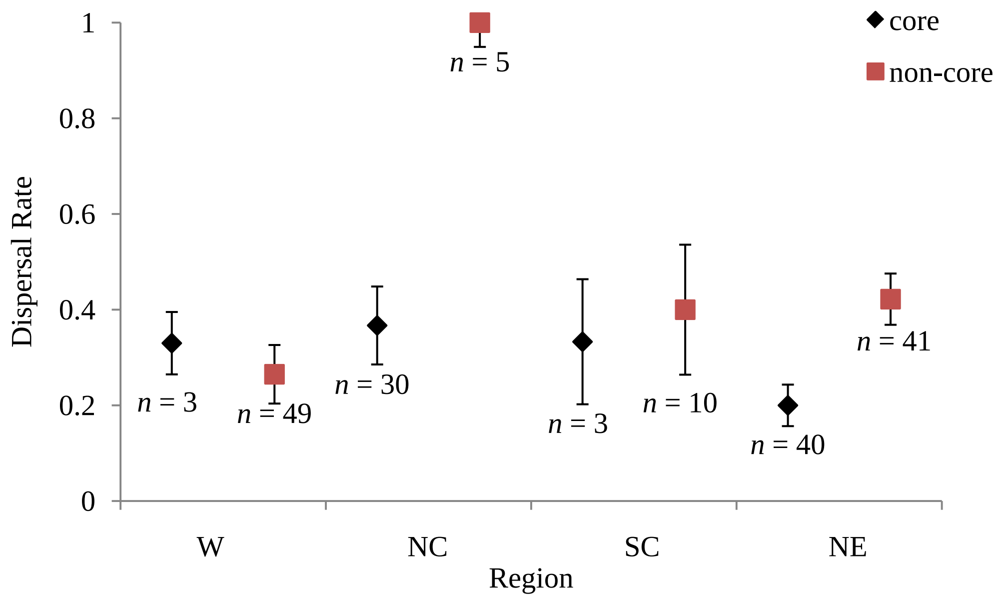

Figure **3-10**: Dispersal rates (and SE bars) by region, of female black bear recaptures or dead recoveries ≥16 months of age, in the core and non-core areas of the bear range in Pennsylvania, 1980–2008. Sample size for the region included for each area.

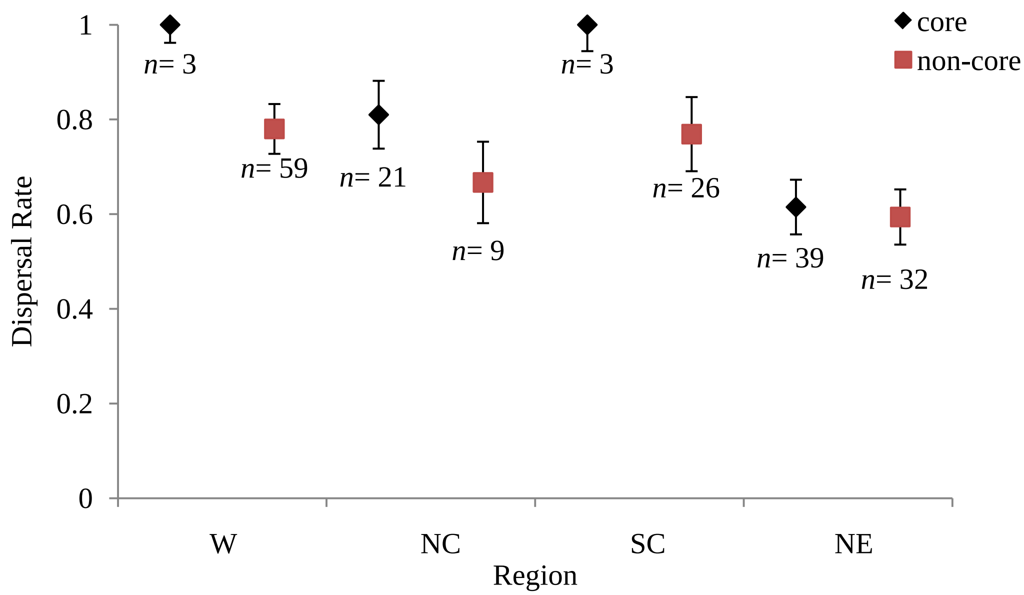

Figure **3-11**: Dispersal rates (and SE bars) by region, of male black bear recaptures or dead recoveries ≥16 months of age, in the core and non-core areas of the bear range in Pennsylvania, 1980–2008. Sample size for the region included for each area.

Chapter 4

Discussion

My analyses indicated timing of departures did not change over a 30–year period, dispersal distances by females were greater than previous research reported, and dispersal rates overall differed from previous Pennsylvania research. About 20% fewer male bears dispersed compared to previous studies in Pennsylvania, but dispersal distances were similar (Alt 1978, 1979*b*, 1980*b*). Proportion of bears dispersing, depending on region, increased for females from 0.0–0.19 in the 1970s to 0.20–0.36 during 1980s – 2000s; and seemed to decrease for males from 0.85–1.00 in the 1970s to 0.48–0.79 depending on region and decade (Alt 1978, 1979*b*, 1980*b*). However, more records of dispersal were available for my research compared to previously published estimates of dispersal rates in Pennsylvania. Most previous Pennsylvania studies monitored and followed <60 bears over short time periods, whereas I used information from 466 individual bears over the span of 30 years. My results suggested that the documented greater dispersal distances and rates by females may partially explain the expansion of the bear population across Pennsylvania.

However, I agree with Alt (1978) that the use of tag returns for estimating dispersal movements has limitations because bears are known to make long, round trip excursions, of ≤40 km from their home range, during autumn. If these bears were recaptured or harvested while on an excursion, the tag return data would suggest the bear had dispersed when it actually had not (Alt 1978). I could not evaluate the effect of this type of error on my analysis, but most recoveries occurred during the hunting season when most bears should be within their normal home range.

The timing of dispersal for yearlings, inferred through using only ear tags, appeared to be similar to research that used radio telemetry to monitor the movement of bears. With the breeding season and related family break-up occurring in June and July (Alt 1977, 1978), yearlings would be 17 or 18 months of age. My results indicated dispersal rates of bears recaptured or dead-recovered when 16–19 months of age was not different from those recovered >20 months of age, which indicated most dispersal occurs during 16–19 months of age. My data did not show timing of departures from the natal home range to the week or month due to the lack of direct monitoring of individuals. Thus, the best evidence I had for timing of departures of yearlings was that almost no departures occurred before 14 months of age. The few yearling bears I identified as dispersed, from 13–15 months of age, suggested that the definition of yearling departure starting at 16 months of age was reasonable. I found no evidence that density of the bear population in Pennsylvania affected when yearlings dispersed. Increased bear densities do not affect the onset of estrus in female bears, which means the timing of dispersal of yearling bears should not have been affected.

My results of distances dispersed are important for explaining range expansion of bears in Pennsylvania. Recent research has documented that across taxonomic groups, distances moved by the sex that usually disperses is about 7 times the linear distance across the species home range (Bowman et al. 2002). For bears in Pennsylvania, my results showed longer distances dispersed by males compared to females, although distances I calculated did not suggest the male's movements are as extreme as Bowman et al. (2002) predicted. My results indicated that females dispersed greater distances compared to earlier research in eastern North America (Appendix A). Average female dispersal distances I calculated were about 3 times greater than expected from previous literature in Pennsylvania (Eveland 1973, Kordek 1973, Alt 1978, 1980*b*, Alt 1995). These distances indicated some females dispersed beyond their mother's home range and related females near or overlapping their mother's home range. Male average dispersal distances were different compared to previous Pennsylvania research (Eveland 1973, Kordek 1973, Alt 1978, 1980*b*). My results indicated males moved about 2 times greater than previously reported in

Pennsylvania which is about 4 times the linear distance across an average female home range. Males were moving well beyond any male or female relatives.

I predicted that dispersal distances would increase as population density increased, but I failed to detect any change over a 30–year period (Table 3-2). Lutz et al. (2015) documented dispersal distances of female white-tailed deer increased with increasing deer densities. If the dispersal behavior of female deer is to avoid dominant females (Lutz et al. 2015), female yearling bears in areas of higher bear densities may have to disperse farther to avoid dominant females. Even though yearling female bears have been documented overlapping newly established home ranges with a mother (Alt 1977; 1978; 1980, Rogers 1987, Costello 2008; 2010), multiple related females already overlapping a mother's home range could result in yearlings dispersing greater distances.

I failed to detect a difference for male dispersal distances, across decades, or among regions, suggesting that increased densities may not have affected distances moved by males. Young males are known to be the most mobile cohort of a bear population (Alt 1978, Elowe 1989). Being that males already disperse at high rates may help explain why I did not detect a change in a 30–year period. Therefore, males may disperse at similar rates and distances regardless of population density because this behavior likely evolved to minimize inbreeding.

As I predicted, dispersal rates for females increased over the decades as the population density increased in Pennsylvania. Even though dispersal in bears is male-biased, the greater dispersal rate exhibited by females in Pennsylvania compared to other research findings explains the expansion of the bear range in Pennsylvania that occurred over the past 30 years. The highest female dispersal rates occurred in the NC region of Pennsylvania, which had some of the highest densities every year. Rates in the NC region were higher each decade than all other regions that same decade. The increase in dispersal rates within the SC region compared to previous research may be related to the region's connectivity with the historic bear populations in the NC region, the highest bear densities, and the ease of movement along linear, forested ridges. Male white-tailed deer in central Pennsylvania, which is part of my defined SC region, tended to disperse in the same direction of the ridges (Long et al. 2010). The SC region also maintains connectivity with the SW region where female bears were introduced to expand the bear range in Pennsylvania (Alt 1979*a*, 1980*a*). As bear density increased in north-central Pennsylvania and bear density increased in the area where translocations occurred, it was possible female bears dispersed to unoccupied habitat throughout the SC region. As density of bears increases, competition for resources (food or space) should increase which could result in greater dispersal rates and distances by yearling females. Dispersal rates and distances determine the colonization rate of unoccupied, suitable habitat and thereby affecting nearby populations and the persistence of the primary population (Wiens 2001). The increased density of bears in the NC region may be the greatest influence on re-colonization of the SC region where suitable habitat is abundant.

The bears in Sproul State Forest, located in the NC region, exhibited different rates of dispersal than my study based on a joint analysis of dead recoveries and capture-recapture data (M. Ternent, unpublished data). Cubs of both sexes and yearling females exhibited strong site fidelity ($\hat{F}$ = 0.978), but male yearlings had lower levels of fidelity ($\hat{F}$ = 0.454). Poor food availability in reduced quality habitat is known to reduce litter size or create complete loss of pregnancies before implantation occurs (Ternent 2007). Females in the NC region produce smaller litters of cubs ($\bar{x}$ = 2 cubs/litter) than females in the NE region ($\bar{x}$ = 3 cubs/litter). Given what is known about the biology of bears in the NC region, and the potential of larger home ranges in poorer quality habitat, I may have over-estimated female dispersal rates for this region. There is a potential that movements by yearling females >13 km were still within a normal female home range. Given that potential, a yearling female moving just beyond 13 km may establish her new adult home range overlapping her mother's home range in the NC region. Understanding the sizes of adult home ranges in different regions of Pennsylvania might help better describe dispersal movements by more accurately defining when dispersal movement results in the bear leaving its natal home range.

Rates of dispersal for males by decade, increased as I predicted to be highest during the highest bear densities. With little overlap of home ranges among adult males, the need for yearlings to disperse farther to avoid male-male competition may explain increasing dispersal rates as density of bears increased. Male yearlings are unlikely to breed and adult females may exhibit aggressive behavior toward them. Young males are known to be the most mobile cohort (Alt 1978), because they are subordinate to adult males and females until they establish their own adult home range.

Dispersal distances within the core area were not greater than the non-core area, which is not what I predicted. Because little bear research (i.e., radio-collared bears) was conducted in W or SC regions of Pennsylvania during the early to mid–1970s, it is difficult to assess changes in dispersal rates and distances between the core and non-core areas. All information about bears in the non-core area comes from monitoring translocated, adult female bears that were solitary or with cubs or yearlings in the SW region (Alt 1995). These translocated females were in newly established regions outside the core area I defined, and because only a few were monitored (n = 22), I cannot make comparisons to my findings.

Rates and distances of dispersal by yearlings are important factors to expansion of a bear population along the periphery of the range. Dispersal rates and distances within the primary portion of the range are important for maintaining the population. As hunting removes individuals, long dispersal movements allow re-colonization of home range vacancies. Most variation in harvest rates of bears in Pennsylvania is explained by sex and age, where the overall harvest rate averages 20% of the population annually and similar numbers of each sex are harvested each year (Diefenbach et al. 2004, Ternent 2007). Lindzey et al. (1979) noted that typical sex structure in a well managed, hunted population will have females comprise 50% of the harvest. The timing of the Pennsylvania hunting season is late enough in the year to ensure that most females with cubs are in dens and less likely to be harvested (Ternent 2007). The vulnerability of younger males (1–3 years old) to harvest is greater than females and older males, and cubs and bears ≥4 years old are harvested at similar proportions (Diefenbach et al. 2004). Harvest rates are lower for females than males, but as hunter density increases so does harvest rate. Most bear hunting is still associated with the northern tier of Pennsylvania, which encompasses the core area I created, and has some of the highest harvest densities (Ternent 2014). Even though female yearlings are likely to overlap their home range with a mother, if there are related males in the area research has found females are more likely to disperse (Wolff 1993). I surmise that if hunting harvest rates of adults are too low, the high density of surviving adults may result in yearling bears seeking unoccupied territories away from related adults.

Consequently, the harvest rate for each sex in a region may influence dispersal behavior. High hunting harvest rates for a population can be considered similar to a population die-out in a local area. Dispersal ecology suggests that vacant areas can be re-colonized soon after unfavorable conditions improve, and for re-colonization to happen the locality must be accessible to individuals in surrounding areas (Hengeveld and Hemerik 2002). Newly established areas of the bear population in Pennsylvania can also be considered similar to vacated areas. At high population densities, interference experienced by an individual from another more competitive individual may have the consequence of the poorer competitor leaving (Sutherland et al. 2002). With lower harvest densities (0.1–1.3 bears/10mi^2; Ternent 2014) in regions of Pennsylvania, I suggest that the overlap of related adult males with a yearling female and her natal range could result in yearling females dispersing, due to adult males being more competitive for resources. Yearling males could also be affected by reduced harvest rates of females and their defense of territories. If harvest rates are high for an area, leaving open territories for re-colonization, my results suggested male yearlings may be taking advantage of accessible, nearby territories. Male dispersal rates lower than 1.00 may be due to establishing a territory fairly close to a natal range but avoiding related females.

Management Implications

Most bear-human complaints begin during April and May with a peak in June, during the breeding season (Ternent 2007). It is known that during these months adults are ranging widely in search of receptive partners and yearling males are dispersing to establish adult home ranges. My results indicate a substantial proportion of yearling males (>70%) and yearling females (>30%) disperse during this time, although female dispersal distances are not as far as males. Expansion of the bear population on the periphery of the current bear range into the more urbanized SW and SE regions of Pennsylvania is of concern to the PGC (Ternent 2010). Regulated hunting can be useful in suppressing and fragmenting portions of a population, causing lack of dispersal between the fragments, and leading to extinction at the margins of a range (Macdonald and Johnson 2001).

The management plan for black bears in Pennsylvania manages populations by setting hunting seasons and bag limits for each wildlife management unit (WMU). However, as the bear population in Pennsylvania has increased, increased bear harvests around municipalities where bear-human conflicts increased was considered (M. Ternent, PGC, personal communication). Male dispersal distances averaged >50km and female distances averaged >30km with this study, and some bears have dispersed >100 kilometers (M. Ternent, personal communication). Based on these dispersal distances, it is likely that bear densities need to be reduced at the scale of a WMU if bear-human conflicts in a given community are to be reduced.

Currently the bear population in Pennsylvania does not appear to be near a biological carrying capacity (Ternent 2007). However, the cultural carrying capacity may have been exceeded in several communities where bear-human conflicts have increased (M. Ternent, personal communication). Adapting management strategies to the rapidly changing tolerances of a cultural carrying capacity may not be feasible for some managers. My research indicates that longer dispersal movements and high rates of dispersal by both sexes of bears will allow the bear range in Pennsylvania to continue to expand and allow bears to rapidly re-colonize local areas of reduced bear density if the surrounding area continues to support high bear densities.

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Appendix A

Documented movements or dispersal distances (km) across the United States for both male and female black bears, ages ranging from cubs to subadults less than 4 years of age.

State	Author	Sex-Age	minimum	maximum	average
PA	Wakefield (1969)	male cub (1 of 2)		12.8	
		male n=1		108.8	
	Eveland (1973) n=16	Male		28.8	11.7
		Female			6.3
		solitary cub	4.8		
		Yearling			7.2
		subadult male			13.4
	Kordek (1973)	male n=21	2.8	32.7	13.7
		female n=13	0.7	10.8	5
	Alt (1977)	male n=1	5	105	
	Alt (1978)	male (<4yrs, n=59)	1.2	53	13
		female (<4yrs, n=14)	0.2	6.5	2.4
	Alt (1979*b*)	male (≤yearling n=8)	14.4	67.2	30.4
		female (≤yearling, n=5)		1.6	
	Alt (1980*b*)	male (≤yearling n=8)	4.8	60.8	20.8
		female (≤yearling, n=16)	0	1.6	
	Alt (1995)	females (2+, n=22)	1.8	172.8	20.7
MN	Rogers (1987)	males n=20	13	219	61
		females n=3	3	11	
AK	Schwartz & Franzmann (1992)	male (n=18, 1-3yrs)	3	27	
		female n=1			
FL	Woodring (1994)	male n=4	22	56	
	Dobey (2005)	male (subad, n=2 of 18)		50	
VA	Garshelis & Pelton (1981)	male n=1	18	25	
		male n=11	1.6	63.6	15.7
	Lee and Vaughn (2003)	female n=20	0.3	13.9	3.5
NM	Costello (2008) n=22	male			34
		female			2.9
	Costello et al. (2008)	males n=290			20
MA	Elowe & Dodge (1989)	males n=8	30	200	
		female n=1		15	

Appendix B

Capture and recovery form used by the Pennsylvania Game Commission personnel for each bear handled within Pennsylvania.

PENNSYLVANIA GAME COMMISSION

❐ **CAPTURE REPORT** ← ← ← check one → → → ❐ **KILL REPORT**

Date of Capture/Kill: ______________ (Mo / Da / Yr) **Bear Seal #:** ____________ ❐ harvest ❐ illegal/nonseason

Had this bear been previously ear tagged? ⇑ YES ⇑ NO

Right ear tag # ____________ **Left ear tag #** ____________ **Tattoo #** ____________

Bear radio collared? ⇑ YES ⇑ NO **Radio frequency** (if known): ______________

	WMU	County (code)	Township (code)	Specific Location
Kill/ Capture				
Release				

Cause of Death or Reason for Capture:

⇑ LEGAL HARVEST
⇑ ILLEGAL HARVEST
⇑ HIGHWAY KILL
⇑ RESEARCH

⇑ DAMAGE/ NUISANCE – check type –
⇑ OTHER (specify in remarks)

❍ Corn
❍ Apiary
❍ Domestic Animals (specify in remarks)
❍ Property (specify in remarks)
❍ Other (specify in remarks)

Sex: ⇑ MALE ⇑ FEMALE ⇑ UNK **Age:** ⇑ CUB ⇑ YEARLING ⇑ ADULT

Parts collected: ⇑ TOOTH ⇑ GALL ⇑ OTHER ______________________

Symptoms of Mange: ⇑ YES ⇑ NO

Weight (lbs): ____________ circle one → Live wt / Dressed wt circle one → Actual / Estimated

Remarks:

CID #: ____________________ **Bear Harvest Tag #:** ____________________

Hunter's Phone Number: ____________________ **Time of Harvest:** __________

⇑ Rifle ⇑ Shotgun ⇑ Handgun ⇑ Muzzleloader ⇑ Bow/Compound Bow ⇑ Crossbow

Check Station ______________________________

Form Completed by: ______________________ (please print) **Date:** ____________

Form PGC-100A- WM 6/10

Appendix C

Estimated black bear density (bears / 100km^2) and 95% confidence intervals, by region in Pennsylvania, 1980–2008 (see Methods).

	Western			North-central			South-central			Northeastern		
Year	Density[a]	95% UCL	95% LCL	Density[a]	95% UCL	95% LCL	Density[a]	95% UCL	95% LCL	Density[a]	95% UCL	95% LCL
1980	1.36	1.58	1.20	3.62	4.19	3.19	0.81	0.94	0.72	2.47	2.86	2.18
1981	1.59	1.93	1.35	3.65	4.44	3.10	1.27	1.54	1.07	2.66	3.23	2.25
1982	1.75	2.12	1.49	2.84	3.43	2.42	1.07	1.29	0.91	2.01	2.43	1.71
1983	2.09	2.40	1.85	4.28	4.92	3.80	1.69	1.95	1.50	2.70	3.10	2.40
1984	1.82	2.11	1.60	4.44	5.15	3.90	1.79	2.08	1.57	3.17	3.68	2.78
1985	1.51	2.01	1.22	3.44	4.59	2.78	1.71	2.28	1.38	3.09	4.12	2.50
1986	1.68	2.14	1.38	4.14	5.28	3.40	1.53	1.96	1.26	2.94	3.75	2.41
1987	2.21	2.71	1.86	3.16	3.89	2.67	1.72	2.11	1.45	2.28	2.80	1.92
1988	2.47	3.11	2.04	3.35	4.22	2.77	1.83	2.30	1.52	2.38	3.00	1.98
1989	2.80	3.40	2.39	3.47	4.21	2.96	1.81	2.20	1.55	2.24	2.72	1.91
1990	2.30	3.02	1.85	2.53	3.33	2.04	1.93	2.53	1.55	2.37	3.10	1.90
1991	2.36	3.80	1.72	2.85	4.59	2.07	1.67	2.68	1.21	2.17	3.50	1.58
1992	2.43	3.13	1.98	3.64	4.68	2.97	1.97	2.54	1.61	2.81	3.62	2.29
1993	2.69	3.35	2.23	3.35	4.18	2.78	2.34	2.92	1.94	2.69	3.35	2.23
1994	2.61	3.32	2.12	2.69	3.43	2.19	2.13	2.71	1.73	2.89	3.69	2.36
1995	3.36	4.01	2.88	3.04	3.63	2.61	2.17	2.59	1.87	1.91	2.28	1.64
1996	2.63	3.20	2.22	2.89	3.51	2.44	1.77	2.15	1.49	2.48	3.02	2.10
1997	2.90	3.23	2.37	3.69	4.11	3.01	1.85	2.07	1.51	2.41	2.68	1.97
1998	2.36	2.78	2.05	3.14	3.70	2.72	2.44	2.87	2.11	3.23	3.81	2.80
1999	4.57	5.88	3.69	3.97	5.11	3.20	2.67	3.44	2.16	2.59	3.34	2.09
2000	3.75	4.64	3.13	5.47	6.77	4.57	3.27	4.04	2.73	4.44	5.49	3.70
2001	4.30	5.23	3.63	5.11	6.22	4.31	3.94	4.80	3.33	3.95	4.80	3.33
2002	3.97	4.82	3.35	4.45	5.40	3.76	3.75	4.56	3.17	4.80	5.83	4.05
2003	4.26	5.07	3.61	4.69	5.58	3.97	3.64	4.33	3.08	4.77	5.68	4.04
2004	3.07	3.67	2.59	3.72	4.45	3.13	3.35	4.01	2.82	4.66	5.57	3.92
2005	3.62	4.28	3.08	4.85	5.73	4.13	3.69	4.36	3.14	4.90	5.80	4.18
2006	3.81	4.57	3.20	4.52	5.43	3.80	3.22	3.86	2.70	4.31	5.18	3.62
2007	4.19	5.08	3.49	4.28	5.19	3.56	2.92	3.54	2.43	3.49	4.23	2.90
2008	4.86	5.81	4.10	5.54	6.62	4.67	4.16	4.97	3.51	4.27	5.10	3.60

[a]Density was the estimated abundance divided by the total area of counties within a region where harvests occurred (M. Ternent, PGC, unpublished data).

Appendix D

Estimated black bear density (bears / 100km^2) and 95% confidence intervals, for the core and non-core areas of Pennsylvania, 1980–2008 (see Methods).

	Core Area			Non-Core Area		
Year	Density[a]	95%UCL	95%LCL	Density[a]	95%UCL	95%LCL
1980	18.66	16.45	21.59	0.71	0.63	0.83
1981	22.10	18.74	26.83	1.20	1.02	1.46
1982	18.35	15.62	22.18	0.77	0.66	0.93
1983	26.79	23.77	30.77	0.96	0.85	1.10
1984	28.59	25.13	33.21	1.38	1.22	1.61
1985	26.70	21.57	35.59	1.75	1.41	2.33
1986	30.12	24.69	38.40	1.43	1.17	1.82
1987	25.91	21.87	31.84	1.77	1.49	2.18
1988	28.58	23.69	36.02	1.74	1.44	2.19
1989	30.28	25.83	36.78	2.12	1.81	2.58
1990	24.25	19.49	31.83	2.29	1.84	3.01
1991	26.92	19.56	43.28	1.85	1.34	2.97
1992	30.38	24.76	39.09	2.54	2.07	3.27
1993	33.20	27.55	41.35	2.59	2.15	3.22
1994	29.56	24.08	37.69	3.15	2.57	4.02
1995	29.93	25.69	35.69	4.07	3.49	4.85
1996	30.41	25.71	36.98	3.00	2.54	3.65
1997	35.74	29.19	39.82	3.46	2.83	3.86
1998	34.41	29.84	40.54	3.64	3.16	4.29
1999	39.15	31.63	50.41	5.09	4.11	6.55
2000	53.59	44.70	66.25	5.55	4.63	6.87
2001	51.29	43.30	62.40	6.29	5.31	7.65
2002	49.52	41.81	60.13	6.41	5.41	7.78
2003	50.93	43.15	60.58	7.32	6.20	8.70
2004	43.53	36.68	52.09	6.36	5.36	7.62
2005	48.31	41.16	57.14	7.86	6.69	9.29
2006	44.73	37.58	53.66	7.82	6.57	9.38
2007	39.43	32.79	47.80	6.94	5.77	8.41
2008	50.35	42.46	60.15	9.46	7.98	11.31

[a]Density was the estimated abundance divided by the total area of counties where harvests occurred within the core and non-core areas (M. Ternent, PGC, unpublished data).