

Summer 8-21-2015

Reproductive Ecology of Black Bears in Maine: Maternal Effect, Philopatry, and Primiparity

Alyssa A. Vitale

University of Maine - Main, alyssa.vitale@umit.maine.edu

Follow this and additional works at: <http://digitalcommons.library.umaine.edu/etd>



Part of the [Behavior and Ethology Commons](#)

Recommended Citation

Vitale, Alyssa A., "Reproductive Ecology of Black Bears in Maine: Maternal Effect, Philopatry, and Primiparity" (2015). *Electronic Theses and Dissertations*. 2305.

<http://digitalcommons.library.umaine.edu/etd/2305>

This Open-Access Thesis is brought to you for free and open access by DigitalCommons@UMaine. It has been accepted for inclusion in Electronic Theses and Dissertations by an authorized administrator of DigitalCommons@UMaine.

**REPRODUCTIVE ECOLOGY OF BLACK BEARS IN MAINE:
MATERNAL EFFECT, PHILOPATRY,
AND PRIMIPARITY**

By

Alyssa A. Vitale

B.S. University of Maine, 2012

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Wildlife Ecology)

The Graduate School

The University of Maine

August 2015

Advisory Committee:

Shawn T. McKinney, Assistant Unit Leader, U.S. Geological Survey Maine
Cooperative Fish and Wildlife Research Unit, Assistant Professor of Wildlife
Ecology, Co-Advisor

Daniel W. Linden, Post-doctoral Research Associate, Maine Cooperative Fish and
Wildlife Research Unit, Co-Advisor

Mary S. Tyler, Professor of Zoology

THESIS ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Alyssa Vitale, we affirm that this manuscript is the final and accepted thesis. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

Dr. Shawn T. McKinney, Assistant Professor

June 19th, 2015

Dr. Daniel W. Linden, Post-doctoral Research Associate

June 19th, 2015

© 2015 Alyssa A. Vitale
All Rights Reserved

LIBRARY RIGHTS STATEMENT

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at The University of Maine, I agree that the Library shall make it freely available for inspection. I further agree that permission for “fair use” copying of this thesis for scholarly purposes may be granted by the Librarian. It is understood that any copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Signature:

Date:

**REPRODUCTIVE ECOLOGY OF BLACK BEARS IN MAINE:
MATERNAL EFFECT, PHILOPATRY,
AND PRIMIPARITY**

By Alyssa A. Vitale

Thesis Co-Advisors: Dr. Shawn T. McKinney

Dr. Daniel W. Linden

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Master of Science
(in Wildlife Ecology)
August 2015

The American black bear (*Ursus americanus*) relies upon dens in order to successfully reproduce and protect their offspring. Black bears utilize a variety of den types, each providing a different degree of protection. Black bears also exhibit an extended maternal care period in which offspring stay with their mother for 18 months. Maine's black bear population is one of the largest in the U.S. (>30,000 bears) and since 1975, the Maine Department of Inland Fisheries and Wildlife has conducted research and monitoring to manage the population. This unique dataset allowed for examination of several generations of multiple maternal lineages which was ideal for assessing both den type selection and primiparity (age of first reproduction).

My objectives for this study were to determine 1) whether subadult females chose the same den type as their mother (maternal effect) or if they selected a den near their yearling den, regardless of den type (philopatric effect); 2) whether differences among

study areas explained observed differences in den site selection, 3) if there was regional variation in the age of primiparity of Maine black bears; 4) the relationship between the age of primiparity and the probability of recruitment from the primiparous litter; 5) the relationship between the age of primiparity and lifetime productivity; and 6) the relationship between the age of primiparity and body condition.

I analyzed den selection data of 168 subadult females and primiparity data of 85 females from 1981-2013 at four study sites in Maine using GIS, generalized linear modeling, model selection, and analysis of variance (ANOVA). The top den selection model, which included maternal effect and study area, accounted for 85% of the den type selection model likelihood. Maternal effect models were more strongly supported than philopatric effect models and regional variation in den type use was observed. These results suggest that not only is a behavioral maternal effect present in black bears and that this maternal effect combined with regional variation in den type availability influences den type selection, but also that the protection afforded by den type may be an important factor in selection decisions.

I found regional variation in age of primiparity among the study areas ($p = <0.001$). Multiple comparison testing indicated age of primiparity differences between Spectacle Pond – Bradford ($p = <0.001$) and Stacyville – Bradford ($p = 0.009$). Logistic regression indicated there was a difference in the successful recruitment of at least one offspring from the primiparous den among the primiparous ages ($p = 0.002$). Probability of successful recruitment increased with increasing age of primiparity. I found no difference in lifetime productivity among the primiparous ages ($p = 0.532$). I also found no difference in primiparous body condition among the primiparous ages ($p = 0.591$).

These results suggest that regional differences in food quality and abundance may influence regional variation in age of primiparity. Understanding factors that influence den type selection as well as the influence of age of primiparity on other reproductive life history traits can help guide wildlife and habitat management decisions.

ACKNOWLEDGEMENTS

I would like to thank my co-advisors, Shawn McKinney and Daniel Linden for their support, direction, and assistance with this project. From initial development to final product, their ideas, comments and statistical recommendations have been invaluable. I would also like to thank my committee member, Mary Tyler, for her years of guidance and encouragement. Without her, this project would not have been possible. I also thank the late William Glanz for his mammalian expertise and the crucial role he played in the beginning of my graduate career.

I am grateful for the expertise and assistance I have received from employees and volunteers of the Maine Department of Inland Fisheries and Wildlife. I thank Randy Cross for his ideas during the development phase of this project, his continued assistance with data throughout, and for allowing me to join him and the Bear Crew in the field both during the winter and summer. His knowledge of bear ecology and memory of individual Maine black bears is remarkable and unmatched. I also thank Jennifer Vashon for her guidance and insight regarding management aspects of this project. Her support and mentorship, both for this project and beyond, have been invaluable and I greatly appreciate her assistance and the opportunities she has made available to me. I also thank the Bear Crew, including Lisa Bates, Jake Feener, Mitch Jackman, Ethan Lamb, and Kirk Michaud. Their accommodation and expertise during den and trap line visits was most helpful.

I thank several additional people from the Maine Cooperative Fish and Wildlife Research Unit. Cynthia Loftin's knowledge of GIS and assistance with ArcGIS were vital

to this project, as were her suggestions. I would also like to thank the other members of the McKinney lab including John Clare, Aly McKnight, and Connor Wood. Their ideas, suggestions, and camaraderie throughout this project were much appreciated.

Finally, I thank several fellow graduate student colleagues who have been essential to my progress. I thank Adrienne Leppold for her guidance, advice, and friendship. Her help during my first semester of graduate school was indispensable and she always made the office a welcoming place. I thank Nikko Shaidani for his ideas, assistance, and encouragement. His intelligence and pragmatism helped move this project forward and his friendship was unparalleled. I also thank Justin Lewin for his support, ideas, and humor. His encouragement throughout this project and unwavering optimism were inspiring and I am grateful to have shared an office with him.

Black bear denning and capture data were provided by the Maine Department of Inland Fisheries and Wildlife. Financial support for this project was provided by the Maine Department of Inland Fisheries and Wildlife, U.S. Geological Survey Maine Cooperative Fish and Wildlife Research Unit, and the University of Maine School of Biology and Ecology.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS	iv
LIST OF TABLES	x
LIST OF FIGURES	xi
CHAPTER ONE: THE INFLUENCE OF MATERNAL EFFECT AND PHILOPATRY ON SUBADULT FEMALE BLACK BEAR DEN SELECTION IN MAINE	
Abstract	1
Introduction.....	2
Black Bear Denning.....	4
Research Objectives.....	7
Justification.....	7
Methods.....	8
Study Areas.....	8
Data Collection	11
Data Acquisition and Pre-Processing.....	11
ArcGIS Processing.....	12
Den Selections	12
Distance Parameterization	13
Den Type Classification.....	13

Data Organization and Classification	14
Data Analysis	15
Models.....	15
Candidate Models	16
Model Selection	16
Results.....	19
Den Type Selection.....	19
Den Type Use by Study Area	20
Den Type Consistency from Yearling Den to Subadult Den.....	23
Discussion.....	24
Den Type Selection.....	24
Den Type Use by Study Area	28
Den Type Consistency from Yearling Den to Subadult Den.....	29
Conclusions.....	31
Implications.....	33
CHAPTER TWO: THE INFLUENCE OF PRIMIPARITY ON BLACK BEAR RECRUITMENT AND LIFETIME PRODUCTIVITY IN MAINE	35
Abstract.....	35

Introduction.....	36
Black Bear Reproductive Strategy.....	38
Maine Black Bears.....	40
Research Objectives.....	41
Justification.....	41
Methods.....	42
Study Areas.....	42
Data Collection.....	45
Data Acquisition and Pre-Processing.....	45
Primiparity and Recruitment Classifications.....	46
Data Organization.....	47
Data Analysis.....	47
Regional Variation in Age of Primiparity.....	47
Age of Primiparity and Primiparous Recruitment.....	48
Age of Primiparity and Lifetime Productivity.....	49
Age of Primiparity and Body Condition.....	49

Results.....	50
Regional Variation in Primiparity.....	50
Age of Primiparity and Recruitment.....	53
Age of Primiparity and Lifetime Productivity	56
Age of Primiparity and Body Condition.....	57
Discussion.....	58
Regional Variation in Primiparity.....	58
Age of Primiparity and Recruitment.....	61
Age of Primiparity and Lifetime Productivity	63
Age of Primiparity and Body Condition.....	66
Conclusions.....	67
Management Implications.....	69
REFERENCES	71
BIOGRAPHY OF THE AUTHOR.....	78

LIST OF TABLES

Table 1.1. Revised black bear den type classification system	14
Table 1.2. Candidate models selected to evaluate competing hypotheses on the relative support of a philopatric effect or maternal effect on subadult female black bear den type selection in Maine.....	18
Table 1.3. AIC _c results of 12 <i>a priori</i> multinomial logistic models for 168 subadult female black bears in Maine..	20
Table 2.1. Mean age of primiparity results for 85 observed primiparous female black bears by study area..	52

LIST OF FIGURES

Figure 1.1. Approximate locations of the four Maine Department of Inland Fisheries and Wildlife (MDIFW) black bear study areas.....	10
Figure 1.2. Count of subadult female black bear dens by study area and den type in Maine.....	21
Figure 1.3. Den type frequency of subadult female black bear dens by study area in Maine.....	22
Figure 1.4. Count and percentage of 168 female black bear yearling — first principle identification den (PID) den type pairings in Maine.....	24
Figure 2.1. Approximate locations of the four Maine Department of Inland Fisheries and Wildlife (MDIFW) black bear study areas.....	44
Figure 2.2. Count of 85 observed primiparous female black bears by age in Maine	51
Figure 2.3. Mean age of primiparity of female black bears in four Maine study areas	53
Figure 2.4. Count of 164 recruited and not recruited offspring from the primiparous den by age of primiparity of mother.....	54
Figure 2.5. Primiparous recruitment frequency of 64 observed primiparous dens by age of primiparity of mother	55

Figure 2.6. Probability of a successfully recruited offspring from the primiparous litter by age of primiparity derived from 64 female black bears with known recruitment..... 56

Figure 2.7. Boxplots of the lifetime combined litter mass of 85 observed primiparous female black bears by age of primiparity..... 57

Figure 2.8. Boxplots of the calculated primiparous body condition of 74 observed primiparous female black bears by age of primiparity 58

CHAPTER ONE:
THE INFLUENCE OF MATERNAL EFFECT AND PHILOPATRY ON
SUBADULT FEMALE BLACK BEAR DEN SELECTION IN MAINE

ABSTRACT

The American black bear (*Ursus americanus*) relies upon dens in order to successfully reproduce and protect their offspring. Black bears utilize a variety of den types, each providing a different degree of protection. Maine's black bear population is one of the largest in the U.S. (>30,000 bears) and since 1975, the Maine Department of Inland Fisheries and Wildlife has conducted research and monitoring to manage the population. This unique dataset allowed for examination of several generations of multiple maternal lineages. My objectives for this study were to 1) determine whether subadult females, during their first solo denning experience, chose the same den type as their mother (maternal effect) or if they were more prone to select a den near their yearling den, regardless of den type (philopatric effect); and 2) assess whether differences among study areas explained observed differences in den site selection.

I analyzed den selection data of 168 subadult females from 1981-2013 at four study sites in Maine using GIS, multinomial logistic regression, and model selection to determine which hypothesis (maternal effect or philopatric effect) had more support. The top model, which included maternal effect and study area, accounted for 85% of the den type selection model likelihood. Maternal effect models were all more strongly supported than philopatric effect models. Moderate protection den types were the most frequently

used in all four study areas. Spectacle Pond had the highest proportion of the most protective den types (37%), while Bradford had the highest proportion of the least protective den types (19%). Ninety-six subadult females (57%) used the same den type as their mother. Of the 72 females (43%) that transitioned to a different den type, 57 (79%) involved a transition from a lower protection den to a higher protection den. These results suggest that not only is a behavioral maternal effect present in black bears and that this maternal effect combined with regional variation in den type availability influences den type selection, but also that the protection afforded by den type may be an important factor in selection decisions. Understanding these factors that influence den type selection can help guide wildlife and habitat management decisions.

INTRODUCTION

Selection of birth sites is an important and well-documented process across many animal taxa. Nest site selection, for example, is important for predator avoidance and nest success of many species of birds (Joern and Jackson 1983; Wesolowski 2002; Davis 2005), embryonic development, offspring survival and behavior, and temperature-dependent sex determination influencing sex ratios of reptiles (Schwarzkopf and Brooks 1987; Burger 1993; Wilson 1998), offspring growth and population structure of amphibians (Petranka 1990), and survival and growth of embryonic and juvenile fish (Scott et al. 2005; Phelps et al. 2009). Likewise, den site selection is equally important for predation protection, energy conservation during gestation and lactation, offspring survival, and successful recruitment of many mammal species (Henner et al. 2004; Person and Russell 2009; Ross et al. 2010). Because they contribute to the increased chance of survival of developing offspring, the ability to select appropriate birth sites

should be adaptive and favored by natural selection (Schwarzkopf and Brooks 1987). Birth site selection allows species to cope with risky environments and provides protection from both predation pressures and environmental pressures (Wilson 1998; Bowyer et al. 1999; Wesolowski 2002). In addition to using these sites for giving birth to offspring, many species with altricial young utilize these same sites during offspring growth and development. In these circumstances that require parental care of young, selection of the birth site may also influence the amount and type of maternal care given to the offspring (Bowyer et al. 1999).

Two frequently observed factors that influence birth site selection are philopatry and maternal behavior (Skeel 1983; Waser and Jones 1983; Bowyer et al. 1998; Benson and Chamberlain 2007). Philopatry is defined as an individual's continued use of its natal home range past the age of independence from its parents (Waser and Jones 1983). As a result of this philopatric influence, females of many species select birth sites near their own birth place (Skeel 1983; Ramsay and Stirling 1990; Hepp and Kennamer 1992).

Maternal behavior can be influenced by many things including gene expression (Meaney 2001), epigenetics (Champagne 2008), and past experiences (White et al. 2001). Maternal behavior can also result from a maternal effect on behavior. Maternal effects can result from a non-genetic transfer of phenotypes from a mother to her offspring, including behavioral phenotypes (Rödel et al 2008). To differentiate the concept from other similar, broader concepts such as maternal inheritance, maternal effects can be viewed as the causal influence of maternal behavioral phenotypes on the offspring's behavioral phenotype (Wolf and Wade 2009). Rather than simply passing a behavior on through teaching or social learning (Caro and Hauser 1992; Heyes 1994; Laland 2004;

Thornton and Raihani 2010), behavioral maternal effects are mediated by both the mother's phenotype and her environment, allowing for transgenerational phenotypic plasticity with regard to the behavior (Maestripieri and Mateo 2009; Wolf and Wade 2009).

While the importance of birth site location has been demonstrated at both an individual and population level across several taxa of animals, the factors that largely contribute to site selection are less well understood. This information is a crucial component for understanding a species, its life history, and its management needs. In this study, I address the relative importance of philopatric effects and maternal effects using a long term data set of den site selection in American black bears (*Ursus americanus*).

Black Bear Denning

The American black bear is an omnivorous mammal that ranges across much of North America. They are found in large expanses of Canada and Alaska, many forested areas in the lower 48 states, and even northern Mexico (Doan-Crider and Hellgren 1996). Within dens, black bears undergo a period of annual winter dormancy known as torpor, which is characterized by increased lethargy, decreased body temperature, slowed heart rate, and reduced metabolism (Johnson 1978). Torpor is believed to be a mechanism by which black bears avoid periods of extreme cold, heavy snowfall, and low food supplies. (Johnson and Pelton 1980).

The onset and duration of denning varies spatially as a function of latitude. Black bears in more northern latitudes den earlier and for longer periods of time, whereas southern bears den later in the year and for shorter time periods (Kolonesky and

Strathearn 1987). Bears in the Alaskan interior have been reported to den for up to seven months, from early October to early May (Schwartz et al. 1987). Pregnant females in northern Mexico den for only four months, from late December to late April. Males and non-pregnant females in Mexico may den for only a few days or weeks, and some do not den at all (Doan-Crider and Hellgren 1996).

Regardless of the climate or latitude, female black bears need to den for several months in order to successfully reproduce (Wooding and Hardisky 1992; Davis 1996). Dens not only serve as birthing locations for cubs, but are also relied upon by female black bears to keep themselves and their offspring protected during torpor, and to provide thermal buffering from the external environment (Davis 1996; Crook and Chamberlain 2010). Consequently, concealment and protection from thermal exposure are key attributes of a den site (Beecham et al. 1983). These denning requirements do not end after the cubs are born because cubs stay with their mother through their first summer and den with her once again as a yearling, so protection benefits extend to the yearling den as well (Miller 1994; Hopkins III 2013).

Philopatry plays an important role in black bear home range selection, or second-order selection, and therefore may also play an important role in eventual den selection or third-order selection (Johnson 1980). Shortly after the yearling denning period, when offspring are about 18 months of age, family groups separate (Ryan 1997). Male offspring typically disperse as subadults whereas females are philopatric. Females rarely disperse far from their natal home range and often inherit portions of their mother's home range (Davis 1996). After inheriting portions of this range, females tend to gradually expand their home range beyond its original extent (Elowe 1987; Rogers 1987). The age

of first reproduction of black bears can vary greatly among regions, however most females produce their first litter between 3 and 7 years of age (Jonkel and Cowan 1971; Kordek and Lindzey 1980; Schooley et al. 1994).

Maternal effects may also play an important role in black bear den selection. Maternal effects can influence the physiological traits of offspring, such as weight or growth rate, but can also affect behavioral traits. This is often evident in species that exhibit phenotypic plasticity in response to environmental variability. By adjusting to environmental change, a mother can affect her offspring's phenotype if that offspring is likely to encounter or inherit a similar environment (Maestriperi and Mateo 2009). Due to the extended period of parental care in many mammals, this taxon shows the largest and most significant influence of maternal effects (Reinhold 2002). Since black bears exhibit both phenotypic plasticity and extended maternal care, maternal effects may be evident in the species.

Experimental studies on mice (*Mus musculus*) showed female transgenerational transmission of behavioral phenotypes related to maternal care (Curley et al. 2008). Few studies of non-nutritional behavioral maternal effects on mammals have been conducted; however natal experiences and maternal effect on habitat selection were shown to influence the behavioral phenotypes of female cactus bugs (*Chelinidea vittiger aequoris*) (Miller et al. 2012). Maternal effects may, however, also influence behavioral phenotypes of black bears. As discussed above, dens and their selection are a large component of maternal care in black bears. Therefore, the maternal effects shown in the mouse maternal care experiment by Curley et al. (2008) can be extended to black bear maternal care, specifically den selection. As such, den type selection may be a behavioral

phenotype passed from a mother black bear to its female offspring in the form of a maternal effect. This may lead to a similarity in den type selection of females as subadults, although the influence of maternal effects has been observed to diminish with increasing offspring age (Reinhold 2002).

Research Objectives

Black bears exist throughout most of the state of Maine, with the greatest density in the northern half of the state. The current Maine black bear population is estimated to be greater than 30,000, making it one of the largest populations in the United States (MDIFW 2014). The Maine Department of Inland Fisheries and Wildlife (MDIFW) has conducted a research and monitoring program of the state's bears since 1975, resulting in 40 years of population and denning data, the only large, long-term black bear dataset of its kind. These data allow for the unique opportunity to study multiple maternal lineages that extend back for several generations. Additionally, these data allow for the monitoring of many individual bears from birth through adulthood, a rare and important aspect of studying both philopatric effects and maternal effects (Waser and Jones 1983). My primary objective in this study was to determine whether there is more support for a philopatric effect or a maternal effect on subadult female black bear den type selection for a first solo subadult den. My second objective was to assess whether differences among study areas explained observed differences in den site selection.

Justification

Denning site is an important aspect of many species' natural histories (Schwarzkopf and Brooks 1987; Davis 2005; Baldwin and Bender 2008). Understanding

the factors that contribute to den site selection can provide insight into denning ecology. This information can be used by both wildlife and habitat managers to better understand the species they interact with in order to inform management decisions, regardless of the ultimate goals of those decisions. Whether for conservation purposes, hunting regulations, or forest management practices, information on the denning habits of any species of interest can be extremely useful (Wilson 1998; White et al. 2001; Immel et al. 2013).

With regard to black bears, a better understanding of denning ecology, as well as if and how den selection decisions relate to maternal lineages, may allow for more precise and directed management of bear populations by providing wildlife managers with more information on the likely denning locations of specific bears or maternal lines. This would be useful for informing harvest regulations, increasing the accuracy of state black bear population models, and improving land use management in association with habitat managers. Additionally, black bears have never been examined from a maternal effect standpoint. This particular dataset may be the largest and best dataset to accomplish the task of exploring such a novel aspect of black bear ecology.

METHODS

Study Areas

The MDIFW black bear monitoring program is an ongoing program that has been conducted in four study areas across Maine: Spectacle Pond, Stacyville, Bradford, and Downeast (Figure 1.1). The Spectacle Pond study area has been in use since 1975 and is located in northern Maine, making it the northernmost study area. The landcover in this

study area is predominantly deciduous forest and the land is used for commercial logging. There are no paved roads or permanent human structures (Schooley et al. 1994). Spectacle Pond has historically contained the least diverse and dependable food supplies of all the study areas, with bears utilizing hard mast such as beech nuts (*Fagus grandifolia*) during mast years. Some soft mast, such as raspberries (*Rubus spp.*), is available along old logging roads (Seger et al. 2013).

The Stacyville study area was active from 1975 to 2004, when the last radiocollared bear's signal was lost. It is located in north-central Maine and is divided by a branch of the Penobscot River. One half of the study area is composed of deciduous forest while the other half contains agricultural fields and several small towns (Schooley et al. 1994).

The Bradford study area has been active since 1982 and is located in central Maine. The landcover in this study area is predominantly coniferous forest, however, there are also several bogs and swamps, and it is bordered by the Penobscot River. Bradford has the most abundant and reliable food supplies with high densities of soft mast, beaver (*Castor canadensis*), and white-tailed deer (*Odocoileus virginianus*) (R.A. Cross, MDIFW, personal communication, 2012). The study area contains small towns and several agricultural areas, including farms and apple (*Malus domestica*) orchards (Schooley et al. 1994).

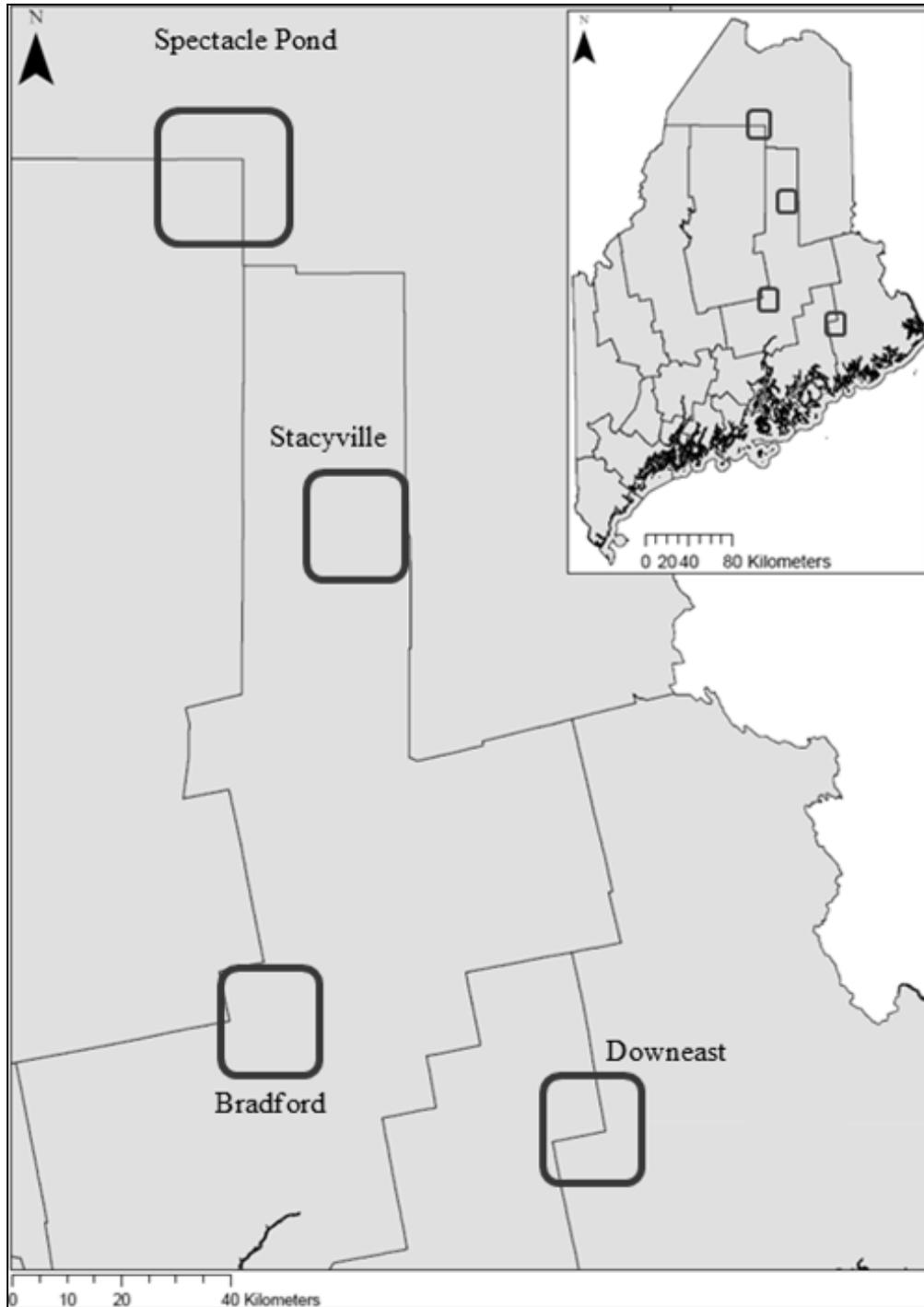


Figure 1.1. Approximate locations of the four Maine Department of Inland Fisheries and Wildlife (MDIFW) black bear study areas. Study areas are indicated by black boxes. Inset shows the approximate location of the four study areas within the entire state of Maine.

The Downeast study area is located in east-central Maine and has been active since 2004 as a replacement for the defunct Stacyville study area. This study area's landcover was dominated by deciduous forests, but now also contains regenerating coniferous and mixed-species forests. The Downeast study area contains abundant soft mast, including several nearby lowbush blueberry (*Vaccinium angustifolium*) fields. Hard mast is also available during mast years (Seger et al. 2013).

Data Collection

This study utilized several decades of previously collected black bear denning data. Each summer, MDIFW biologists trapped, measured, and radiocollared female black bears using the protocols and methods described by Schooley et al. (1994). Biologists then visited the dens of radiocollared bears each winter to collect data on the female, any offspring she may have had, and the den itself. All cubs received an ear tag for identification and yearling females were fitted with their own radiocollars, so they could be tracked to their own dens in the future (MDIFW 2011).

Data Acquisition and Pre-Processing

Denning data collected from February 10, 1981 to March 22, 2013 were acquired from MDIFW in the form of several Microsoft Excel spreadsheets. These raw field data contained fields for each den including study area, bear identification number, den date, x and y UTM coordinates, and den type. If any offspring were present in the den, the offspring identification number, age class, and sex were also included.

The dataset contained den locations recorded in two different datums. All dens from February 10, 1981 to February 8, 2004 were recorded in North American Datum of

1927 (NAD27). All dens from February 9, 2004 to March 22, 2013 were recorded in North American Datum of 1983 (NAD83). As a result of this mid-season datum change, I used ESRI ArcGIS 10.1 mapping software to convert the NAD27 dens to NAD83 using the Project tool (ESRI 2012). This successfully projected the entire dataset in NAD83 and I combined the two files using the Merge tool in order to create a single, continuous 1981-2013 denning dataset. This denning dataset was used for all den type selection analyses.

ArcGIS Processing

Den Selections

Prior to analysis, I used ArcGIS 10.1 to identify specific dens for each study bear. A total of 477 individual females were identified using their principle identification (PID) numbers. Separating the females by PID numbers allowed for the selection of each individual bear's principle identification dens, or PID dens. A PID den was defined as any den an adult or subadult bear used without the presence of its mother. PID den use generally began when the bear reached independence at two years of age, when den selection was done by that bear, not the mother. Each bear in the study had at least 1 PID den (range = 1-22, median = 3) and I created shapefiles for each bear to identify its PID den locations. Provided such information was known, the yearling den was also identified for each study bear (n = 195), and I created individual shapefiles for each yearling den. It was for these 195 females that further GIS analysis was performed.

Distance Parameterization

Because the denning dataset contained no preexisting distance attribute by which to analyze philopatry, I used ArcGIS 10.1 to create one. This was done using the Generate Near Table tool for each of the 195 females. This tool calculated the distance between each of a bear's PID dens and its yearling den. For each bear, the PID dens were used as the input feature and its yearling den was used as the near feature. I joined the near table output to the overall PID den table using a simple tabular join. This tabular join appended all of the den information to the distance attribute of the near table, effectively pairing den type and distance from yearling den.

Den Type Classification

MDIFW uses a seven den type classification system: excavations, blowdowns, brushpiles, rock cavities, ground nests, tree dens, and other (a broad category for dens not characterized by one of the other six den types). This extensive classification system was not designed for the purpose of den type analysis. Certain den types, such as blowdowns, are broadly used to describe a variety of den structures, each offering a different level of protection to the denning bear (R.A. Cross, MDIFW, personal communication, 2013). To help account for discrepancies caused by coarse classification in some den types, den types were reclassified into a four-den-type system based on the degree of protection they afford to the bears (Wathen et al. 1986) (Table 1.1). Den type 1 was composed of dens that provided the least amount of protection and included only ground nests. Den type 2 afforded moderate protection and included excavations, blowdowns, and brushpiles. Den type 3 provided the most protection and included rock cavities and tree dens. Due to the

variety of den structures utilized by bears in the original other category, this category was maintained in the reclassified system, but was not included in subsequent analyses.

Table 1.1. Revised black bear den type classification system. The original Maine Department of Inland Fisheries and Wildlife (MDIFW) den types included in each new den classification and the protection level afforded by each classification are outlined.

Revised Den Type	Protection Level	Original Den Type
1	Least	Ground Nest
2	Moderate	Excavation, Blowdown, Brushpile
3	Most	Rock, Tree
Other	Varied	Other

Data Organization and Classification

The data from each bear’s near table were consolidated into one Excel spreadsheet for analysis. Bear age at each PID den was calculated based on the known year of birth and added as an additional field. Following this, a separate Excel spreadsheet was created, containing only the first PID den for each bear, representative of a bear’s first solo subadult den.

The den type of each bear’s yearling den and first PID den were paired and classified as either “Same” or “Different”, based upon the reclassified den type system. Bears without known yearling or PID den types, or those classified in the catch-all “other” category, were removed. The remaining subadult females (n=168) were used in analysis for this component of the study.

Data Analysis

All analyses were performed using R version 2.15.1 (R Core Team 2012).

Models

To approach the question of whether female subadult den selection is more influenced by a maternal effect or a philopatric effect, I constructed multiple models representing competing hypotheses under these two primary effects. Female subadult den type served as the response variable for the black bear den site selection analysis.

Because den type was a categorically distributed dependent variable (Table 1.1), I used multinomial logistic regression to predict the probabilities of den type selection given multiple combinations of the four following independent variables.

This first independent variable was the yearling den type, or YD Type—first PID den type pairing (coded 1 if it was the same as the subadult den type and 0 if it was different). YD Type was used to represent the influence of maternal effect on den type selection. The distance from the yearling den to the first solo den (Distance from YD, km) was a continuous variable used to represent the influence of philopatry on den type selection. Distance from YD was natural log transformed. Study Area (1, 2, 3, or 4) was included to identify any regional variation in den type selection that may be present and to provide some coarse insight into the den type availability of each study area, given the lack of such availability data. Finally, Year represented den year of each bear's first solo den (1984-2013). Year was used to measure any temporal variation in den type selection and to provide some insight into the influence of changes to forest management practices over the last 30 years.

Candidate Models

Models were designed in an effort to avoid spurious variables and relationships in order to limit the number of candidate models (Burnham and Anderson 2002). A total of twelve candidate models were chosen *a priori* for analysis (Table 1.2). A null model (model 1) was used to represent the relationship between subadult den type and the lack of independent variables, in order to determine which models performed the poorest. Conversely, a global model (model 2) was used to represent the relationship between subadult den type and all four identified variables in order to determine if the complexities of the system warranted the inclusion of all variables, despite the associated penalty included to enforce parsimony. A model including only study area (model 3) was used to represent the relationship between subadult den type and regional variation. A model including only year (model 4) was used to represent the relationship between subadult den type and temporal variation. Models 5-8 (Table 1.2) represented scenarios in which the hypothesis of the influence of maternal effect on subadult den type selection was supported. Models 9-12 (Table 1.2) represented scenarios in which the hypothesis of the influence of a philopatric effect on subadult den type selection was supported.

Model Selection

I used an information-theoretic approach to rank models based on Akaike's Information Criterion (AIC). AIC balances the goodness of fit with model complexity to attempt to identify the best model (i.e., the model with the most support from the data), order models from best to worst, and calculate the weight of evidence for each model (Burnham and Anderson 2002). In order to determine which candidate models fit the

best, AIC corrected for small sample sizes (AIC_c) was used. AIC_c was calculated for the twelve candidate models using the `AICctab` function within the `bbmle` package in R version 2.15.1 (Bolker and R Development Core Team 2012, R Core Team 2012).

Table 1.2. Candidate models selected to evaluate competing hypotheses on the relative support of a philopatric effect or maternal effect on subadult female black bear den type selection in Maine. Model name, variables incorporated in each model, and the scenario represented by each model are included. YD Type is the yearling den-first solo adult den pairing, SA is study area, Year is the den year of the first solo adult den, and Distance is the distance between a bear's yearling den and first solo adult den. Data collected from 1981-2013 in Maine, USA.

Model	Variables	Representation
1	1	Null model
2	YD Type + log(Distance from YD) + Study Area + Year	Global model
3	Study Area	Regional variation/den type availability
4	Year	Temporal variation
5	YD Type	Maternal effect
6	YD Type + Study Area	Maternal effect and regional variation/den type availability
7	YD Type + Year	Maternal effect and temporal variation
8	YD Type + Study Area + Year	Maternal effect, regional variation/den type availability, and temporal variation
9	log(Distance from YD)	Philopatry
10	log(Distance from YD) + Study Area	Philopatry and regional variation/den type availability
11	log(Distance from YD) + Year	Philopatry and temporal variation
12	log(Distance from YD) + Study Area + Year	Philopatry, regional variation/den type availability, and temporal variation

RESULTS

Den Type Selection

A total of 168 subadult female black bears with known yearling and first solo dens were used in the model selection analysis (Table 1.3). The maternal effect hypothesis was overwhelmingly supported by these data. Model 6 was the top model and included both den type pairing and study area. Model 8 was the next best supported model and included den type pairing, study area, and den year (Table 1.3). Together, the top two models accounted for 98% of the den type selection model likelihood, and were the only models with more support than the global model. Models 5-8, which included den type pairing (i.e., maternal effect), were all more strongly supported than models 9-12, which included distance (i.e., philopatric effect). These data provided extremely little support for the philopatric effect hypothesis. Within the hypothesis model groupings (models 5-8 and models 9-12), models that included study area were more strongly supported than models that did not. The model that contained study area alone (model 3) was not well supported, accounting for less than 0.1% of the den type selection model likelihood (Table 1.3). Similarly, the model that contained year alone (model 4) was not well supported (Table 1.3). Model 4 and model 11 were the only models less supported than the null model.

Table 1.3. AIC_c results of 12 *a priori* multinomial logistic models for 168 subadult female black bears in Maine. Model name, model components, number of parameters (K), Akaike's Information Criterion values corrected for small sample sizes (AIC_c), differences in AIC values (Δ_i), and model weights (w_i) given for all candidate models. YD Type is the yearling den-first solo adult den pairing, SA is study area, Year is the den year of the first solo adult den, and Distance is the distance between a bear's yearling den and first solo adult den. Data were collected from 1981-2013 in Maine, USA.

Model	Model Components	K	AIC_c	Δ_i	w_i
6	YD Type + SA	10	221.2	0.0	0.8527
8	YD Type + SA + Year	12	225.0	3.8	0.1278
2	YD Type + log(Distance) + SA + Year	14	228.7	7.6	0.0195
5	YD Type	4	243.0	21.8	<0.001
7	YD Type + Year	6	245.8	24.6	<0.001
3	SA	8	274.5	53.4	<0.001
10	log(Distance) + SA	10	274.7	53.5	<0.001
12	log(Distance) + SA + Year	12	279.2	58.0	<0.001
9	log (Distance)	4	289.7	68.5	<0.001
1		2	289.9	68.8	<0.001
4	Year	4	292.6	71.5	<0.001
11	log(Distance) + Year	6	293.4	72.2	<0.001

Den Type Use by Study Area

The sample included 168 subadult females, with 83 (49%) from Spectacle Pond, 13 (8%) from Stacyville, 59 (35%) from Bradford, and 13 (8%) from Downeast.

Sampled females used all three den types, however the proportion of use varied by study area (Figure 1.2).

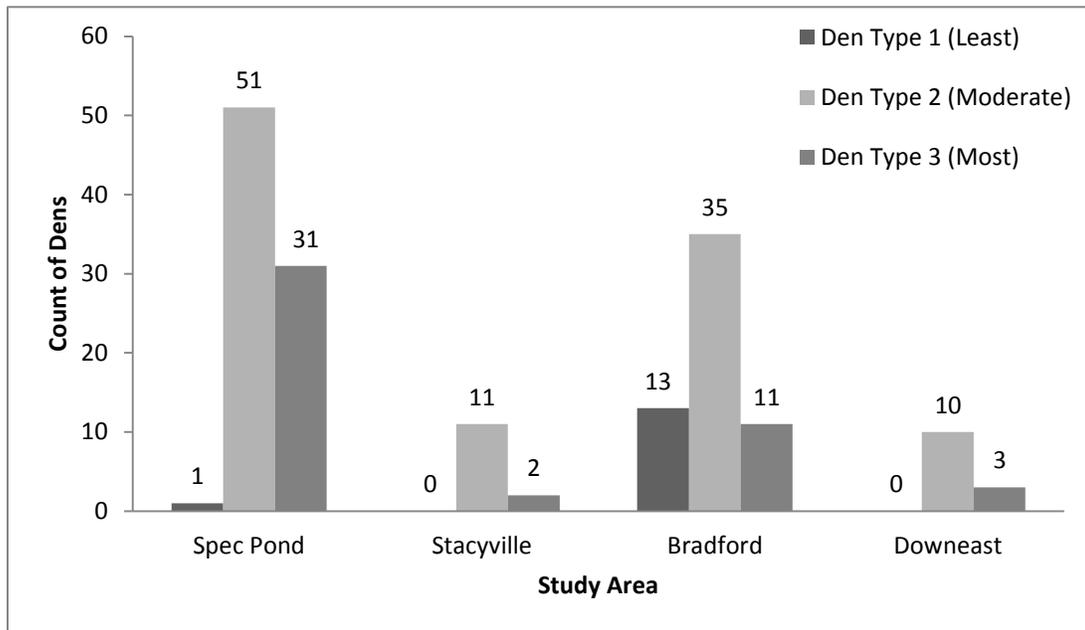


Figure 1.2. Count of subadult female black bear dens by study area and den type in Maine. Only subadults with known yearling and first solo dens included. Data were collected from 1981-2013 in Maine, USA.

Den type 2 (moderate protection) was the most frequently used den type, regardless of study area (range = 59% - 85% of total study area den type use, Figure 1.3). Den type 1 (least protection) was the least frequently used den type in three of the four study areas, being non-existent in the Stacyville and Downeast study areas and representing the lowest percentage of den type use in Spectacle Pond (1%, Figure 1.3). In Bradford, den type 1 (least protection) was the second most frequently used den type with 13 occurrences (22%). There were only a few den type 3 (most protection) dens used in Stacyville, with 2 occurrences (15%) and Downeast, with 3 occurrences (23%). Den type 3 was the least frequently used den type in Bradford with only 11 occurrences (19%); however it was the second most frequently used den type in Spectacle Pond with 31 occurrences (37%, Figure 1.2). Den type 2 use was fairly consistent across study areas,

taking into account the number of bears from each area. Spectacle Pond females used den type 3 proportionally more than bears from any other study area and Bradford females used den type 1 proportionally more than bears from any other study area (Figure 1.3).

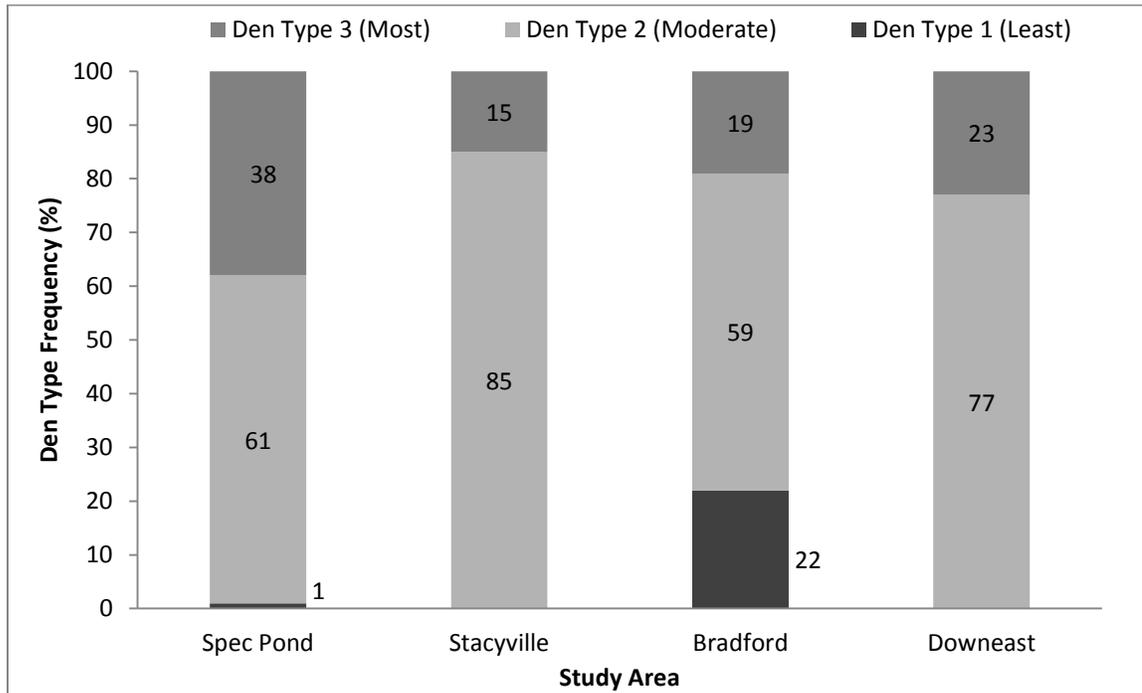


Figure 1.3. Den type frequency of subadult female black bear dens by study area in Maine. Only subadults with known yearling and first solo dens included. Data were collected from 1981-2013 in Maine, USA.

These results were further supported by interpretation of the multinomial logistic regression for the best supported model (model 6). The multinomial logit for Bradford relative to Spectacle Pond had 0.02 times odds for den type 3 (most protection) relative to den type 1 (least protection). The relative probability of a subadult den being den type 3 (most protection) rather than den type 1 (least protection) was 100% lower when at Bradford than when at Spectacle Pond, regardless of YD—PID den type pairing.

Den Type Consistency from Yearling Den to Subadult Den

During their first solo denning experience, 57% of the 168 females analyzed chose to use the same den type as the yearling den they shared with their mother the previous year, while 43% used a different den type. When broken down by den type pairing, den type consistency from yearling den to subadult den is further explained (Figure 1.4). The majority (85%) of same den type pairings occur with den type 2 (moderate protection) dens. Most different den type pairings result from transitions from a den type 2 (moderate protection) yearling den to a den type 3 (most protection) subadult den (30 transitions, 38% of different den type pairings). Of all different den type pairings ($n = 72$), 57 (79%) involved a transition from a lower protection level yearling den to a higher protection level subadult den. Only 15 (21%) pairings involved a transition from a higher protection level yearling den to a lower protection level subadult den. The only den type pairing that did not occur was a transition from a den type 3 (most protection) yearling den to a den type 1 (least protection) subadult den.

These results were further supported by interpretation of the multinomial logistic regression for the best supported model (model 6). The multinomial logit for same YD—PID den type pairings relative to different YD—PID den type pairings had 4.27 times greater odds for den type 2 (moderate protection) relative to den type 1 (least protection). The relative probability of a subadult den being den type 2 (moderate protection) rather than den type 1 (least protection) was 327% higher when YD—PID den type pairing was the same than when it was different, holding study areas constant. Conversely, the multinomial logit for same YD—PID den type pairings relative to different YD—PID den type pairings had 0.18 times odds for den type 3 (most protection) relative to den

type 1 (least protection). The relative probability of a subadult den being den type 3 (most protection) rather than den type 1 (least protection) was 81% lower when YD—PID den type pairing was the same than when it was different, holding study areas constant.

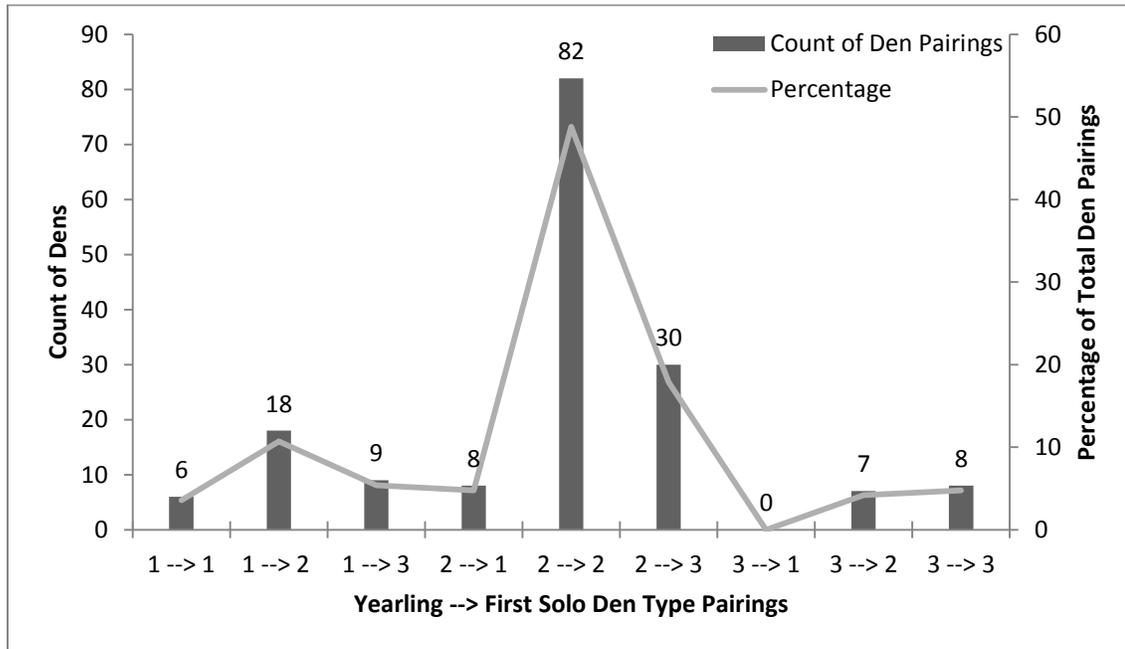


Figure 1.4. Count and percentage of 168 female black bear yearling — first principle identification den (PID) den type pairings in Maine. A PID den was defined as any den an adult or subadult bear used without the presence of its mother. Den types based upon reclassification system in which den type 1 offers the least protection, den type 2 offers moderate protection, and den type 3 offers the most protection. Arrows represent the transition from yearling den type to first solo subadult den type. Data were collected from 1981-2013 in Maine, USA.

DISCUSSION

Den Type Selection

Model selection indicated that model 6, which included both den type pairing and study area, was the best supported model of subadult female black bear den type selection (Table 1.3). This model represented the influence of a maternal effect on subadult den type selection as well as regional variation in den type selection among study areas. The

inclusion of maternal effect in the top model indicated that a subadult female's choice of den type was influenced by the behavioral den type phenotypes of its mother. While this particular analysis showed the presence of a maternal effect on den type selection of black bears, it did not indicate directional trends in this influence.

The inclusion of study area in the top model and the resulting regional variation was likely driven by differences in den type availability among the study areas. Black bear den selection is, at least in part, a function of den availability so in order to fully understand den selection, it is important to consider not only den use, but also den availability (Johnson and Pelton 1981; Garrison et al. 2012). The major limitation of this study was the lack of den type availability data. Random sampling of unused den sites did not occur during the multiple-decade sampling period. This was unfortunate because use and availability data are useful for determining if bears are selecting their den sites (Reynolds-Hogland et al. 2007).

Variations in den selection, such as those seen among different study areas, often occur as a result of variation in both environmental conditions and den site options available to bears in different areas (Hayes and Pelton 1994). Results from a Louisiana study indicated that female black bears from two populations in close proximity to each other exhibited significantly different habitat selection patterns, indicating that there is a high degree of behavioral plasticity in black bears (Benson and Chamberlain 2007). This population-level plasticity is likely present in other regions and could be seen among the four Maine study areas. These study areas varied not only geographically, but also by landcover type and anthropogenic influence (Schooley et al 1994). All of these factors could influence the availability of possible den types in each study area. Despite the lack

of historical den type availability data, the clear importance of study area and regional variation on den type selection, as shown in the model selection results, provided at least coarse insight into differences in den type availability among the study areas.

The poor performance of the study-area-alone model (model 3) further supported the lessened need for specific den type availability data. Previous black bear studies have indicated that in certain regions, den types were selected in proportion to den availability (Hayes and Pelton 1994). If this were true for Maine black bears, the model of study area alone (model 3) would have been much better supported because availability would have been the primary driving force behind den type selection. There have been observations of black bears in North Carolina selecting low protection ground dens when available high protection tree dens were present in a habitat within 100 m of ground dens (Brody 1984). This suggests that black bears may actively choose their den type, rather than simply being driven by den type availability and the model selection results indicated that this was likely the case for Maine black bears.

Models 5-8, which represented the influence of a maternal effect on den type selection, were all better supported than models 9-12, which represented the influence of philopatry (Table 1.3). This indicated that black bears were more likely to choose their den type based on the influence of their mother's behavioral phenotypes. Although philopatry was evident in the study females (mean distance between yearling den and first solo subadult den = 2.7 km, range = 0.1-53.8 km), bears were unlikely to choose a subadult den close to their yearling den site without regarding the den type.

After the primary variables of den type pairing and distance, study area was the next most important variable. The top models for each primary variable (model 6 and model 10) both included study area, indicating that regional variation and den type availability were important driving factors of subadult den type selection (Table 1.3). Year was representative of temporal variation in den type selection, primarily to account for changes in forest management practices over the course of the sampling period. Black bear habitat and den site availability is often influenced by land management practices, both historic and current (Immel et al. 2013). During the early years of the Maine black bear sampling period, extremely large, recent clearcuts were common in Maine's commercial forests (Sader et al. 2003). Forest management practices changed in 1991 when the Maine Forest Practices Act effectively banned large clearcuts and led to a rise in prevalence of partial harvest methods (Maine Forest Service 1999). This major forestry policy change could have potentially impacted black bear denning habitat.

The model of year alone (model 4) was one of the least supported models, indicating that at a state-wide scale, temporal variation in den type selection did not occur over the past four decades. When the year variable was paired with study area, such as in model 8, year slightly influenced subadult den type selection (Table 1.3). Spectacle Pond was the only study area primarily composed of commercially logged forest and may be the only study area that experienced the full impact of forestry changes as a result of the Maine Forest Practices Act. Year, and temporal variation on den type selection, was only an influencing factor as a function of study area.

Den Type Use by Study Area

Although model selection indicated that study area was an important factor in subadult den type selection, a more specific breakdown of den type by study area provided further insight. Den type use was not evenly distributed among study areas (Figure 1.2). Variation in den type distributions among the study areas may be explained, in part, by differences in den type availability (Hayes and Pelton 1994).

Den type 2 (moderate protection) was the most frequently used den type in all four study areas, being used at fairly consistent percentages among the study areas. This was not unexpected because den type 2 was the most inclusive den type category, containing the most frequently used original den type (blowdown) as well as two other less common types (excavation and brushpile). Distribution differences in den type 1 and 3 use began to show what could be interpreted as clear study area differences, likely due to regional den type availability differences.

Den type 3 (most protection) was primarily composed of tree dens, with a limited number of rock dens as well. Den type 3 use was fairly low in the four Maine study areas with the exception of Spectacle Pond (Figure 1.3). The mature forests of northern Maine, including those that comprise the Spectacle Pond study area, have been commercially logged for decades (Schooley et al. 1994). In order to develop cavities, trees must be of sufficient age and size (Davis 1996). In addition to the development of a cavity, this cavity must then be large enough to fit a black bear if it will be used as a tree den (Klenzendorf et al. 2002; Hersey et al. 2005). The prevalence of large, old trees in

Spectacle Pond compared to the other study areas could explain the disproportionately high den type 3 use in the study area.

Den type 1 (least protection) was composed entirely of ground nests and was not frequently used by subadult female black bears as a first solo den type (Figure 1.3).

Bradford was the only study area to exhibit high den type 1 use. This disproportionately high den type use may have been attributed to vegetational differences of the study areas. A negative relationship between vegetation density and den structure has been shown for black bear dens, with an increase in dependence on vegetation around a den attributed to a decrease in the structural security of a den (Hayes and Pelton 1994). For low protection dens, such as ground nests, an increase in vegetation around the den may act as compensation for the lack of structural security. When comparing the study areas with the most similarly sized populations, Bradford and Spectacle Pond, differences in vegetation density were apparent. Nearly 12% of Bradford dens had surrounding vegetation density classified as dense, whereas only 3% of Spectacle Pond dens had dense vegetation. This increase in vegetation density at Bradford may have contributed to an increase in low protection den type 1 use compared to the other three study areas.

Den Type Consistency from Yearling Den to Subadult Den

Model selection indicated the presence of a maternal effect on den type selection, however further investigation showed the trends in direction of this maternal effect (Figure 1.4). The majority of females (57%) used the same den type during their first solo denning experience as they used with their mothers the previous year in their yearling

den. Behavioral maternal effects are not well studied in black bears, but cub fidelity to maternal den type has been noted in prior black bear research.

As a lesser objective of a Virginia study analyzing den type selection, five cubs were followed from birth to adulthood and all five cubs showed the same den type preferences as their mothers (Klenzendorf et al. 2002). Although it was a very small sample size, these results seemed to indicate that a maternal den type preference, or maternal effect, may be passed on to offspring, though this is based on natal den rather than yearling den. An earlier study found that there was a greater tendency for black bears born in tree dens to use tree dens as an adult than bears born in ground dens (Wathen 1983). This suggested that previous experiences or a behavioral maternal effect may play a part in den selection, but once again focused on the natal den. During a black bear study in Louisiana, researchers found that reintroduced females exhibited similar denning behaviors as the females from the source population, indicating that a maternal effect may play a role in den selection, even in unfamiliar areas (Benson 2005). This evidence combined with the results from Maine black bears indicated that fidelity to maternal den type is common in black bears and likely due to the influence of a behavioral maternal effect.

Some females did use a different den type during their first solo denning experience and these differences indicated a key trend in maternal effect. Most females with a different den type pairing transitioned from a lower protection yearling den to a higher protection subadult den (Figure 1.4). Den site selection and the den protection benefits imparted to a bear by the den are important for black bears (Wathen et al. 1986; Davis 1996). Den concealment and protection from exposure assist with protecting

females and their offspring during winter dormancy (Beecham et al. 1983). Females select dens in order to reduce their total energy expenditure over the denning season and for this reason, females and subadults typically select dens more carefully than males, choosing more protective den types (Johnson 1978; Smith et al. 1994). This established trend supported why my results showed 57 (79%) subadult females with different den type pairings transitioned to more protective den types, including 9 bears (9% of different den type pairing bears) that transitioned from den type 1 (least protective) to den type 3 (most protective). Only 15 bears made a downward transition in den type protection level from yearling den to subadult den, and none of these transitions were from den type 3 (most protection) to den type 1 (least protection). These unlikely decisions may have, in part, been due to den type availability, both as a result of differences among study area as well as the presence of other bears already in more desirable den types in areas of high bear density.

CONCLUSIONS

A behavioral maternal effect on den type has been detected in black bears and shows more of an influence than a philopatric effect on subadult female black bear den type selection during the bear's first solo denning experience. The maternal effect on den type selection combined with regional variation in den type selection, indicative of differences in den type availability among study areas, best explains den type selection in Maine subadult female black bears. Year and associated temporal variation mildly influences den type selection, but only as a function of study area and only when also paired with the maternal effect on den type selection.

Den type use varies by study area, further indicating that regional variation in den type availability occurs among the four Maine study areas. The least protective den type 1 was most frequently used by Bradford subadults, most likely due to the higher vegetation density in the study area. The most protective den type 3 was most frequently used by Spectacle Pond subadults, most likely due to the prevalence of large trees in the mature, deciduous-dominated forests of this northern Maine study area.

A behavioral maternal effect is present in Maine black bears and may explain the prevalence of maternal den type fidelity. Most subadult females chose to use the same den type during their first solo denning experience as their mothers chose for the yearling den they shared the previous year. Bears that used a different den type during their first solo subadult denning experience were more likely to transition from a low protection yearling den to a higher protection subadult den rather than downgrade to a lower protection den.

Many factors may be influencing a female's selection of birth site, including maternal effect and philopatry. An understanding of these factors, as well as the importance they have with regard to birth site, is essential to understanding a species and its management needs. Regardless of taxa, the primary goal of animal birth site selection is to increase the chance of offspring survival, and this is done primarily through protection from predation pressures and environmental pressures (Wilson 1998; Bowyer et al. 1999).

Implications

The presence of a behavioral maternal effect on den type selection is a novel aspect of black bear ecology that has not previously been examined. The large, long-term MDIFW dataset allowed for exploration of the topic and facilitated the monitoring of many individual bears from birth through adulthood as well as an analysis of the behavioral aspects of maternal lineages.

In addition to contributing novel information to the field of black bear ecology, this research has several management applications. By evaluating the influence of philopatric effects and maternal effects on den type, this research has provided insight into black bear behavior as well as the factors that influence den type selection. This insight will help wildlife managers to better understand and predict black bear denning choices, allowing for better protection or more informed hunting regulations, depending on management goals.

This research can be applied to habitat and land use management as well. Recognizing patterns of black bear denning and understanding the driving forces and underlying significance of these patterns may be useful for determining the ideal land use practices for an area inhabited by black bears. For instance, imposing land use restrictions such as a moratorium on development or road construction in high-density black bear areas may help to protect cubs and mothers in dens, especially low protection den types. Similarly, if certain den types are particularly important to lineages or specific bears in an area, then logging practices or development could be altered to reflect the needs of the species, given an understanding of the influence of maternal effect on den type selection.

Future research could be conducted to evaluate the relationship between den type and offspring recruitment to examine whether this individual-level maternal effect is manifested at the population level. Insight into animal behavior and the factors that influence birth site selection are important not only for black bear management, but also more broadly for wildlife and habitat management of any species that exhibits birth site selection.

CHAPTER TWO:
THE INFLUENCE OF PRIMIPARITY ON BLACK BEAR RECRUITMENT
AND LIFETIME PRODUCTIVITY IN MAINE

ABSTRACT

The American black bear (*Ursus americanus*) exhibits an extended maternal care period, with cubs staying with their mother through their first summer and denning with her once again as a yearling. Age-specific life history traits including age of primiparity (first reproduction), frequency of reproduction, and recruitment can all affect black bear population dynamics. Maine's black bear population is one of the largest in the U.S. (~30,000 bears) and since 1975, the Maine Department of Inland Fisheries and Wildlife has conducted research and monitoring to manage the population. My objectives for this study were to determine 1) if there was regional variation in the age of primiparity of Maine black bears; 2) the relationship between the age of primiparity and the probability of recruitment from the primiparous litter; 3) the relationship between the age of primiparity and female lifetime productivity; and 4) the relationship between the age of primiparity and female body condition.

I analyzed primiparity data of 85 females from 1981-2013 at four study sites in Maine using generalized linear modeling, analysis of variance (ANOVA), and t-tests. I found regional variation in age of primiparity among the study areas ($p = <0.001$). Multiple comparison testing indicated age of primiparity differences between Spectacle Pond – Bradford ($p = <0.001$) and Stacyville – Bradford ($p = 0.009$). Logistic regression

indicated there was a difference in the successful recruitment of at least one offspring from the primiparous den among the primiparous ages ($p = 0.002$). Probability of successful recruitment increased with increasing age of primiparity. I found no difference in lifetime productivity among the primiparous ages ($p = 0.532$). I also found no difference in primiparous body condition among the primiparous ages ($p = 0.591$). These results suggest that regional differences in food quality and abundance may influence regional variation in age of primiparity. Food quality and abundance, along with a bear's life experience, may also influence recruitment rates. Understanding age of primiparity, and its influence on other reproductive life history traits, can help provide important insight for wildlife management decisions.

INTRODUCTION

The life history of a species can reflect variability in its reproductive strategies and may influence population dynamics (Saether et al. 2013). Life History Theory is derived from evolutionary theory, and strives to explain variation in an organism's life history, most notably their reproductive biology and related life history traits (Stearns 2000; Figueredo et al. 2005). This includes life history traits such as lifespan, rate of development, age of first reproduction, generation time, frequency of reproduction, number of offspring, level of parental investment, and survival (Pianka 1970; Leggett and Carscadden 1978). Based on these traits, organisms exhibit behaviors, or life history strategies, that further shape their ecological trajectories. In the most simplistic sense, the life history strategies of organisms can be viewed in terms of the theory of r- and K-selection, which is based primarily on the trade-off between reproductive timing and the number of offspring produced (MacArthur and Wilson 1967; Wilson 1975). R-selected

species inhabit variable or unpredictable environments and invest more heavily in reproductive efforts, typically having short lifespans, faster developmental rates, earlier reproduction, larger numbers of offspring, lower offspring survival, and lower parental investment. Conversely, K-selected species inhabit constant or predictable environments and invest more heavily in reproductive efficiency, typically having longer lifespans, slower developmental rates, later reproduction, lower numbers of offspring, higher offspring survival, and higher parental investment (Pianka 1970; Reznick et al. 2002; Figueredo et al. 2005).

Life history traits are shaped by both intrinsic genetic factors and extrinsic ecological factors (Stearns 2000). Due to these complexities and the inherent fluctuation of extrinsic factors, organisms are often viewed on an r-K continuum, rather than as purely r-selected or K-selected (Pianka 1970). This r-K continuum has traditionally allowed for relative comparisons among species based on life history strategies, however the continuum, and the Life History Theory, may also be applied to intraspecific variation in life history traits and the relative comparisons of individuals or populations of a particular species (Rushton 1985; Figueredo et al. 2005). This within-species variation is primarily driven by population adaptations to environmental condition and can result in variation of life history strategies along the r-K continuum, even for highly K-selected species (Rushton 1985). A study of five populations of American shad (*Alosa sapidissima*), all exposed to different environmental conditions, found that the reproductive life history traits exhibited by fish, including age of primiparity and frequency of reproduction, differed depending on the population as a function of

environmental harshness, primarily in the form of thermal variation (Leggett and Carscadden 1978).

The concept of population-specific reproductive strategies is indicative of within-species variation in life history traits as a function of extrinsic factors. Variation in age-specific life history traits such as lifespan, age of maturity, and recruitment can affect population dynamics (Heppel 1998; Saether et al. 2013). Another important age-specific life history trait is the age of primiparity, or age of first reproduction. The age of primiparity marks the beginning of a female's reproductive contribution to a population, making it an optimal life history trait to examine, both in terms of population dynamics and the Life History Theory. Understanding the reproductive biology and life history strategies of a population are critical for understanding population dynamics and the management strategies needed to maintain that population.

Black Bear Reproductive Strategy

The American black bear (*Ursus americanus*) is an omnivorous mammal that ranges across much of North America. They are found in large expanses of Canada and Alaska, many forested areas in the lower 48 states, and even northern Mexico (Doan-Crider and Hellgren 1996). Based on Pianka's r-K continuum, black bears fall along the K-selected side of the spectrum, with their long lifespans, late age of first reproduction, and long period of parental care (Kolenosky 1990; Samson and Huot 1995). Black bears also have one of the lowest rates of reproduction of any land mammal in North America (Jonkel and Cowan 1971). The black bear breeding season occurs during the summer,

after which males and females do not typically interact (Jonkel and Cowan 1971; Schwartz and Franzmann 1992; Ryan 1997; McLaughlin 1999).

Pregnant female black bears require a den in order to give birth (Wooding and Hardisky 1992; Davis 1996). Within dens, black bears undergo a period of annual winter dormancy known as torpor, which is characterized by increased lethargy, decreased body temperature, slowed heart rate, reduced metabolism, and a reliance on fat reserves (Johnson 1978). Torpor is believed to be a mechanism by which bears avoid periods of extreme cold, heavy snowfall, and low food supplies (Johnson and Pelton 1980). It is also during this torpor that female black bears give birth to a litter of one to six cubs every other year (Noyce and Garshelis 1994; Ryan 1997). Black bears exhibit an extended maternal care period, with cubs staying with their mother through their first summer and denning with her once again as a yearling. Shortly after the yearling denning period and prior to the breeding season, when the offspring are about 18 months of age, the family group separates (Ryan 1997). Although black bears typically breed every other year, females may breed and produce cubs in two consecutive years if they lose their entire first litter prior to the start of the breeding season during the second year (Garrison et al. 2007).

For black bears, primiparous litters tend to be smaller than multiparous litters, with fewer cubs produced in a female's first litter compared to subsequent litters (Noyce and Garshelis 1994; McLaughlin 1999; Garrison et al. 2007). The age of primiparity, or first reproduction, is a useful metric of a bear's reproductive performance and physical condition. This age can vary greatly among geographic regions and even among populations within a region (Elowe 1987; McLaughlin et al. 1994). The size and

condition of adult female black bears may influence her reproductive performance, including her age of primiparity, litter sizes, and offspring recruitment rates (Noyce and Garshelis 1994; Samson and Huot 1995). A study of 45 female bears in Minnesota found that a mother bear's weight was the best predictor of yearling size. In the study, no juvenile females produced their first litter if they weighed less than 41kg during the previous March. Conversely, 57% of juvenile females produced their first litters if they weighed greater than or equal to 41kg during the previous March (Noyce and Garshelis 1994). Condition and size of black bears is most closely linked to diet, specifically the amount of high fat and high carbohydrate foods a bear eats (Elowe and Dodge 1989; Benson 2005). For this reason, differences in food quality and availability may be one of the major factors that determine the age of primiparity of black bears in different regions and populations.

Maine Black Bears

Similar to other black bear populations along the same latitude, Maine black bears usually den from mid-October to April and give birth in January or February. Although black bears have been observed to produce up to six cubs in a single litter, the average litter size in Maine is 2.5 cubs (McLaughlin 1999). Black bears are a naturally long-lived species and can survive for over 25 years in the wild, although this is rare in an extensively hunted population (McLaughlin 1999). Hunting of black bears is legal in Maine and done through a variety of methods including baiting, hounds, trapping, and still-hunting/stalking. Although roadkills and other incidental deaths do occur, hunting is the only significant source of mortality for the state's adult black bears, with bear survival increasing to almost 100% in the absence of hunting (McLaughlin 1999; Maine

Chapter of the Wildlife Society 2011). Regional information regarding black bear populations and their trends is useful for understanding how best to manage those populations (Noyce and Garshelis 1994; McLaughlin 1999). For Maine bears, updated information on primiparity would allow for further analysis of related reproductive parameters, resulting in an improved estimate of the black bear population in the state.

Research Objectives

Black bears exist throughout most of the state of Maine, with the greatest density in the northern half of the state. The current Maine black bear population is estimated to be greater than 30,000, making it one of the largest populations in the United States (MDIFW 2014). The Maine Department of Inland Fisheries and Wildlife (MDIFW) has conducted a research and monitoring program of the state's bears since 1975, resulting in 40 years of population and denning data, the only large, long-term black bear dataset of its kind. The objectives of this research were to determine 1) if there is regional variation in the age of primiparity of Maine black bears, 2) the relationship between the age of primiparity and the probability of recruitment from the primiparous litter, 3) the relationship between the age of primiparity and female lifetime productivity, and 4) the relationship between female body condition and the age of primiparity.

Justification

Life history and reproductive strategies are important aspects of species and population dynamics that can be influenced by extrinsic ecological factors (Leggett and Carscadden 1978; Heppel 1998; Stearns 2000; Saether et al. 2013). Understanding the factors that contribute to a species' or population's life history strategies can provide

further insight into the behavior of those organisms and the strategies needed to manage them effectively. Age-specific life history traits, such as the age of primiparity, are especially useful when examining population specific differences in life history strategies (Saether et al. 2013).

With regard to Maine black bears, a better understanding of primiparity and associated reproductive life history strategies could allow for more precise and directed management of bear populations, primarily through harvest regulations. The examination of regional differences in primiparity will provide an update to current state primiparity information (McLaughlin et al. 1994). This update also includes primiparity information about a newer, current study area that was not in use at the time of the last analysis. This primiparity update, combined with a more thorough understanding of other reproductive parameters such as recruitment and lifetime productivity of black bears, may be useful for inclusion in state population models to aid in estimating and managing Maine's black bear population.

METHODS

Study Areas

The MDIFW black bear monitoring program is an ongoing program that has been conducted in four study areas across Maine: Spectacle Pond, Stacyville, Bradford, and Downeast (Figure 2.1). The Spectacle Pond study area has been in use since 1975 and is located in northern Maine, making it the northernmost study area. The landcover in this study area is predominantly deciduous forest and the land is used for commercial logging. There are no paved roads or permanent human structures (Schooley et al. 1994).

Spectacle Pond has historically contained the least diverse and dependable food supplies of all the study areas, with bears utilizing hard mast such as beech nuts (*Fagus grandifolia*) during mast years. Some soft mast, such as raspberries (*Rubus spp.*), is available along old logging roads (Seger et al. 2013).

The Stacyville study area was active from 1975 to 2004, when the last radiocollared bear's signal was lost. It is located in north-central Maine and is divided by a branch of the Penobscot River. One half of the study area is composed of deciduous forest while the other half contains agricultural fields and several small towns (Schooley et al. 1994).

The Bradford study area has been active since 1982 and is located in central Maine. The landcover in this study area is predominantly coniferous forest, however, there are also several bogs and swamps, and it is bordered by the Penobscot River. Bradford has the most abundant and reliable food supplies with high densities of soft mast, beaver (*Castor canadensis*), and white-tailed deer (*Odocoileus virginianus*) (R.A. Cross, MDIFW, personal communication, 2012). The study area contains small towns and several agricultural areas, including farms and apple (*Malus domestica*) orchards (Schooley et al. 1994).

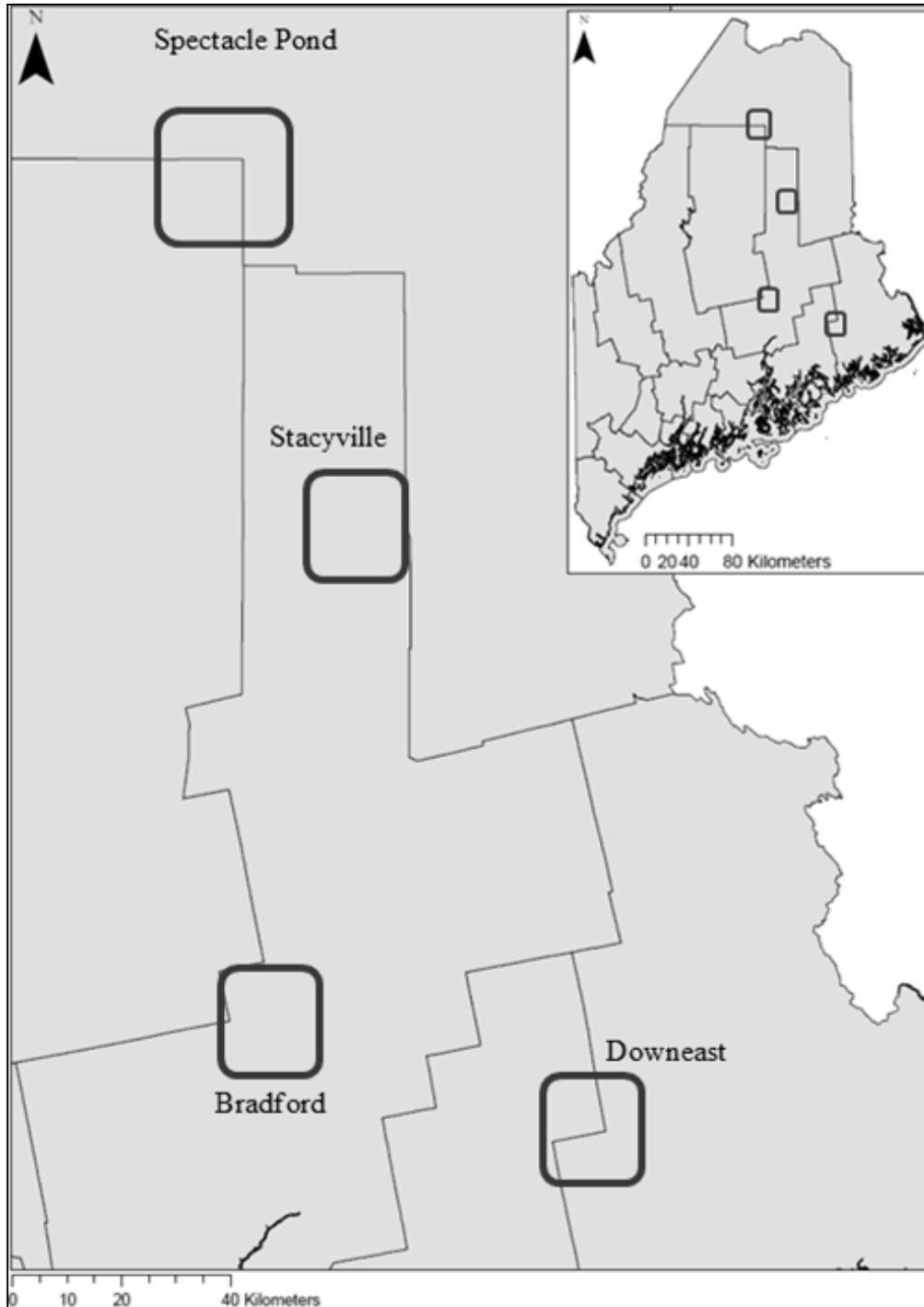


Figure 2.1. Approximate locations of the four Maine Department of Inland Fisheries and Wildlife (MDIFW) black bear study areas. Study areas are indicated by black boxes. Inset shows the approximate location of the four study areas within the entire state of Maine.

The Downeast study area is located in east-central Maine and has been active since 2004, as a replacement for the defunct Stacyville study area. This study area's landcover was dominated by deciduous forests, but now also contains regenerating coniferous and mixed-species forests. The Downeast study area contains abundant soft mast, including several nearby lowbush blueberry (*Vaccinium angustifolium*) fields. Hard mast is also available during mast years (Seger et al. 2013).

Data Collection

This study utilized several decades of previously collected black bear denning data. Each summer, MDIFW biologists trapped, measured, and radiocollared female black bears using the protocols and methods described by Schooley et al. (1994). Biologists then visited the dens of radiocollared bears each winter to collect data on the female, any offspring she may have had, and the den itself. All cubs received an ear tag for identification and yearling females were fitted with their own radiocollars, so they could be tracked to their own dens in the future (MDIFW 2011).

Data Acquisition and Pre-Processing

Denning data collected from February 10, 1981 to March 22, 2013 were acquired from MDIFW in the form of several Microsoft Excel spreadsheets. These raw field data contained fields for each den including study area, bear identification number, den date, x and y UTM coordinates, and den type. If any offspring were present in the den, the offspring identification number, age class, and sex were also included. Capture data collected from May 21, 1975 to July 7, 2013 were also acquired from MDIFW in the form of several Microsoft Excel spreadsheets. These raw field data contained fields

including study area, bear identification number, capture date, age class, weight, and length. These data contained information recorded during both summer trapping periods and winter den visits.

Primiparity and Recruitment Classifications

Female black bears were identified as primiparous only if they were captured in their den every year consecutively from their first solo subadult den until their primiparous den. This classification method resulted in a conservative estimate of the number of primiparous bears, but ensured that only bears with known ages of primiparity were included in the analysis. Of the study's 477 female black bears, 85 bears satisfied the aforementioned requirements and are known to have been primiparous.

For this study, recruitment was defined as the survival of a cub to the yearling age class. Beyond the yearling den, it is difficult to assess survival, as not every radiocollared bear is captured in its den every single year. Additionally, MDIFW's program only tracks female bears to their dens. Beyond the yearling den, survival of individual males is largely unknown, so recruitment measured in any other way would exclude approximately half of the study's offspring. Orphaned black bears have been reported to be capable of surviving without their mothers during the yearling denning period (Erickson 1959; Kolenosky and Strathearn 1987; Garrison et al. 2007), indicating that bears as young as yearlings may be self-sufficient and successfully recruited into the population.

In this study, a bear was considered to be recruited if it was a) present in a cub den with its mother, and either b) present in a yearling den with its mother, or c) present

in its own den without its mother during the yearling denning period. Bears that did not have both cub and yearling denning data were considered to have unknown recruitment and were excluded from analysis.

Data Organization

An Excel file was created to include only the denning information of the 85 primiparous dens. I calculated the age of primiparity for each bear based on known birth year and year of first den with cubs present. Using the capture data, I added the mass of each cub to the primiparous dens file and calculated total litter masses for each of the 85 primiparous dens. For each primiparous female, I calculated combined lifetime litter mass by adding the masses of all cubs produced by that female throughout its lifetime. The mass and length of each primiparous female were also added, both for its primiparous year and for the year prior to primiparity, or its last nulliparous year. These data were used to calculate the body condition of each female in both years by taking the residuals of the regression of body mass vs. length (Cattet et al. 2002).

Data Analysis

All analyses were performed using R version 2.15.1 (R Core Team 2012). Statistical tests were considered significant when $P \leq .05$.

Regional Variation in Age of Primiparity

Mean age of primiparity was analyzed by calculating unbiased mean ages of primiparity for each study area using the methods and procedure described in Garshelis et al. 1998. Calculations using this method utilize all nulliparous, or pre-primiparous bears,

for each age group regardless of cub production at that age. This method incorporates bears that die or are otherwise lost from the study prior to reaching primiparity, avoiding bias that would usually cause the omission of bears with an older age of primiparity and a mean age of primiparity that is skewed low (Garshelis et al. 1998). This unbiased method was chosen over the more traditional weighted mean method due to the prevalence of black bear hunting in Maine and the high likelihood of bears being harvested prior to reaching primiparity.

A two-tailed paired t-test was performed to compare the mean ages of primiparity calculated via the unbiased and traditional methods to determine if a difference exists between the two methods for Maine black bears. The t-test was performed using the `t.test` function within the stats package in R version 2.15.1 (R Core Team 2012). Regional variation in age of primiparity was analyzed using a one-way analysis of variance (ANOVA) test, followed by a multiple comparison procedure using Tukey's HSD post-hoc test. The ANOVA and Tukey's HSD test were performed using the `aov` and `TukeyHSD` functions within the stats package in R version 2.15.1 (R Core Team 2012).

Age of Primiparity and Primiparous Recruitment

The relationship between age of primiparity and primiparous recruitment was modeled using logistic regression. This type of generalized linear model was chosen because the response variable, primiparous recruitment, was binomial, representing either unsuccessful or successful recruitment of at least one offspring from each known primiparous female's first litter. The logistic regression model was created using the `glm` function within the stats package in R version 2.15.1 (R Core Team 2012).

Age of Primiparity and Lifetime Productivity

A one-way ANOVA test was performed in order to determine if lifetime productivity, represented by combined lifetime litter mass, varies as a function of a female's age of primiparity. Combined lifetime litter mass was chosen as a measure of lifetime productivity because litter mass has been shown to reflect the availability of high quality food and predict offspring survival; both essential components of reproductive success (Rogers 1987; Seger et al. 2013). The ANOVA was followed by a multiple comparison procedure using Tukey's HSD post-hoc test, to identify if there were significant differences in lifetime productivity between specific pairwise primiparous ages. The ANOVA and Tukey's HSD test were performed using the `aov` and `TukeyHSD` functions within the `stats` package in R version 2.15.1 (R Core Team 2012).

Age of Primiparity and Body Condition

A two-tailed paired t-test was performed to compare the body condition of females during their primiparous year and the year prior to their primiparous year to determine if a conditional difference that corresponds to primiparity exists. The t-test was performed using the `t.test` function within the `stats` package in R version 2.15.1 (R Core Team 2012). A one-way analysis of variance ANOVA test was performed in order to determine if primiparous body condition varies as a function of a female's age of primiparity. The ANOVA was followed by a multiple comparison procedure using Tukey's HSD post-hoc test to determine which primiparous years were significantly different from one another with respect to body condition. The ANOVA and Tukey's

HSD test were performed using the aov and TukeyHSD functions within the stats package in R version 2.15.1 (R Core Team 2012).

RESULTS

Regional Variation in Primiparity

A total of 85 observed primiparous females were used to examine regional variation in primiparity (Figure 2.2). The age of primiparity ranged from two to seven years of age with nearly 50% of observed primiparous bears being four years old (Figure 2.2). Two, three, and seven year old primiparous bears were rare (combined 7% of total), while 93% of observed primiparous bears were between four and six years of age. The majority of observed primiparous bears were from Spectacle Pond, comprising almost 52% of the total. All observed primiparous bears under the age of four were from Bradford, while 83% of observed primiparous bears over the age of five were from Spectacle Pond.

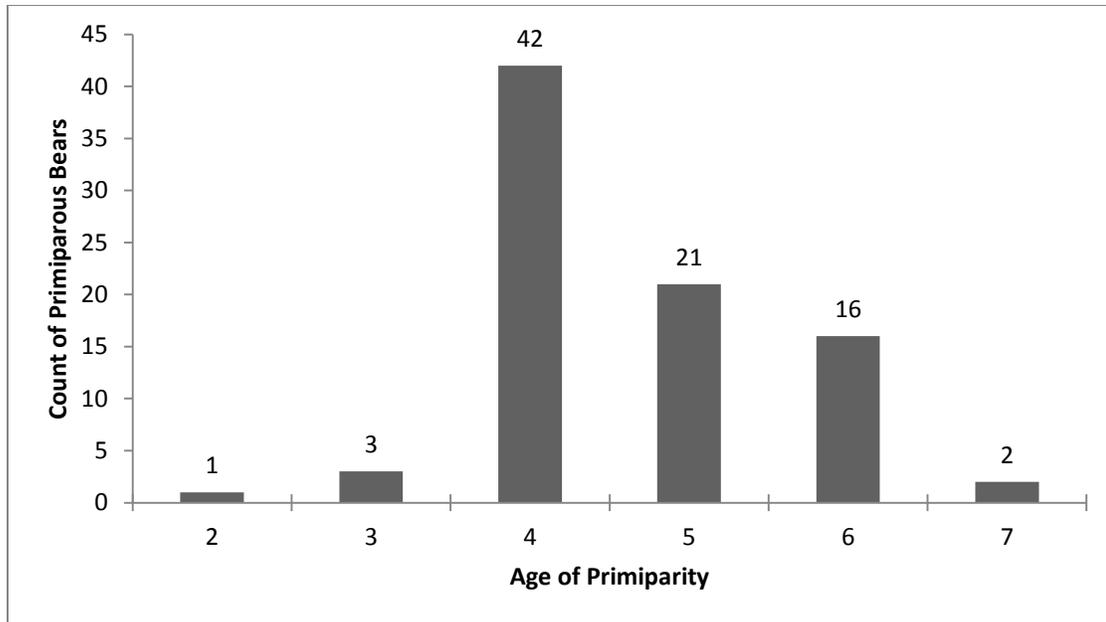


Figure 2.2. Count of 85 observed primiparous female black bears by age of primiparity in Maine. Data were collected from 1981-2013 in Maine, USA.

Mean age of primiparity was calculated for each study area using two distinct methods (Table 2.1). The first method, resulting in a traditional mean, was calculated using the mean age weighted by the number of bears that produced cubs at that age. The second method, resulting in an unbiased mean, was calculated using the methods outlined in Garshelis et al. (1998). Bradford had the lowest traditional weighted mean age of primiparity and Stacyville had the highest (range = 4.00 years – 5.00 years). Bradford also had the lowest unbiased mean age of primiparity, however Spectacle Pond had the highest (range = 4.17 years – 5.04 years).

There was little difference between the traditional weighted mean age of primiparity and unbiased mean age of primiparity for most study areas. Bradford exhibited the largest age difference between methods ($\Delta = .17$ years). Spectacle Pond, the most heavily harvested study area, had an age difference of 0.09 years between the two

methods. Downeast and Stacyville exhibited no difference in age of primiparity between the two methods. A two-tailed paired t-test between the weighted means and unbiased means indicated that there was no difference between the mean ages of primiparity calculated using the traditional weighted method and the unbiased method ($t = 1.702$, $df = 3$, $p = 0.1873$).

Table 2.1. Mean age of primiparity results for 85 observed primiparous female black bears by study area. Weighted Mean calculated using traditional mean calculation methods and Unbiased Mean calculated using methods described by Garshelis et al. (1998). Mean ages of primiparity (prim) presented as years. Data were collected from 1981-2013 in Maine, USA.

Study Area	Weighted Mean Age of Prim	Unbiased Mean Age of Prim
Spectacle Pond	4.95	5.04
Stacyville	5.00	5.01
Bradford	4.00	4.17
Downeast	4.38	4.38

Using a one-way ANOVA test of the original primiparity data, I found there was regional variation in age of primiparity among the study areas. ($F = 7.841$, $p = < 0.001$). Multiple comparison testing indicated there was regional variation in age of primiparity for two study area pairs: Spectacle Pond – Bradford ($p = < 0.001$) and Stacyville – Bradford ($p = 0.009$) (Figure 2.3). There was no regional variation in age of primiparity among any of the other study area pairs.

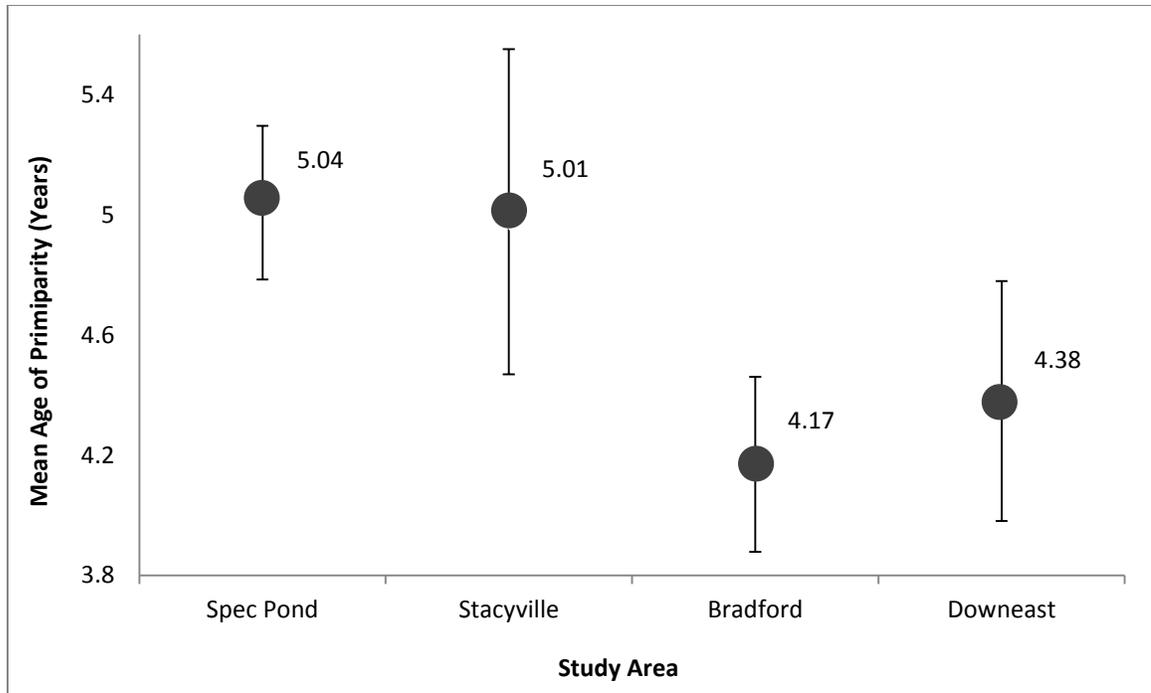


Figure 2.3. Mean age of primiparity of female black bears in four Maine study areas. Mean ages derived from 85 observed primiparous female black bears using the unbiased method described by Garshelis et al. (1998). Error bars indicate 95% confidence intervals for each study area. Data were collected from 1981-2013 in Maine, USA.

Age of Primiparity and Recruitment

A total of 64 primiparous dens with known offspring recruitment data were used to examine the relationship between age of primiparity and recruitment. Of the 164 cubs present in these primiparous dens, 62 (54%) were recruited while 52 (46%) were not recruited. The number of recruited primiparous-den offspring varied based on the age of primiparity of the mother (Figure 2.4). Although there was only one two year old primiparous bear, she did not successfully recruit offspring. Four year old primiparous bears produced the most cubs, with 19 (37%) being recruited and 33 (63%) not recruited. Five year old primiparous bears were very successful recruiters, with 23 (85%) offspring

recruited and only 4 (15%) offspring not recruited. All cubs produced by observed seven year old primiparous bears were successfully recruited.

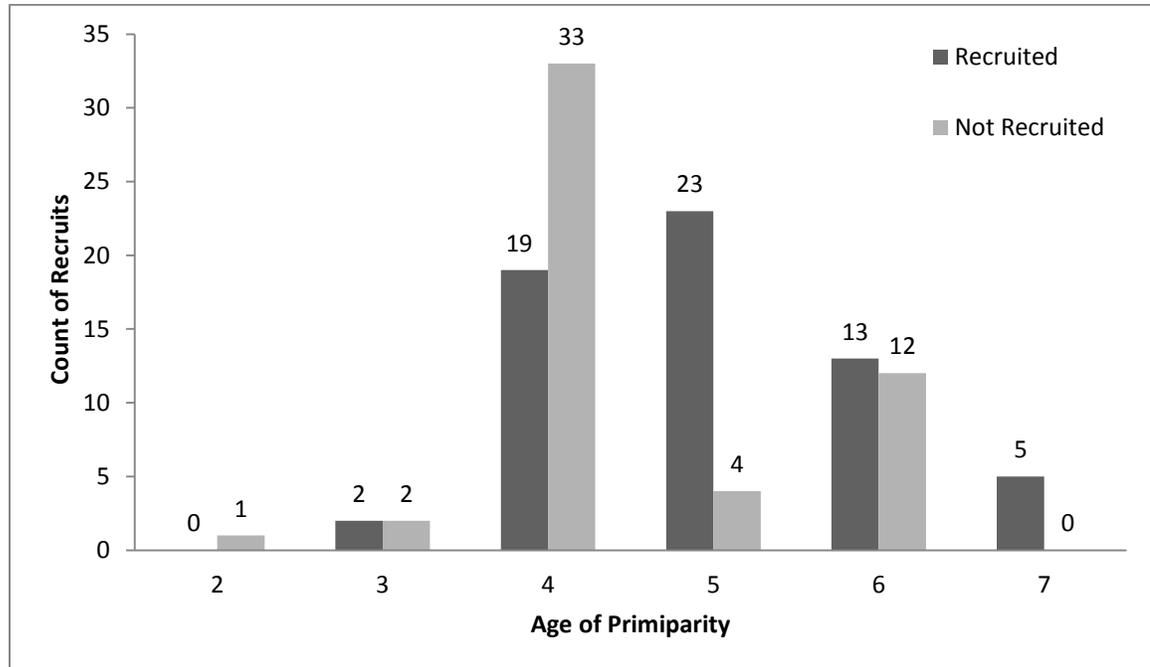


Figure 2.4. Count of 164 recruited and not recruited offspring from the primiparous den by age of primiparity of mother. Only offspring with known recruitment included. Data were collected from 1981-2013 in Maine, USA.

The number of primiparous dens that produced at least one successful recruit also varied based on the age of primiparity of the mother (Figure 2.5). Of the 64 total observed primiparous dens, 35 (55%) had at least one successful recruit and 29 (45%) had no successful recruits. Four year old primiparous dens were the most prevalent, with 10 (32%) producing at least one successfully recruited offspring and 21 (68%) not producing any recruited offspring. Five year old primiparous dens were the second most prevalent, with 13 (93%) producing at least one successfully recruited offspring and 1 (7%) not producing any recruited offspring. The largest percentile difference in

successfully recruited den rate occurred between four year olds and five year olds, increasing by 61% with a primiparity difference of one year.

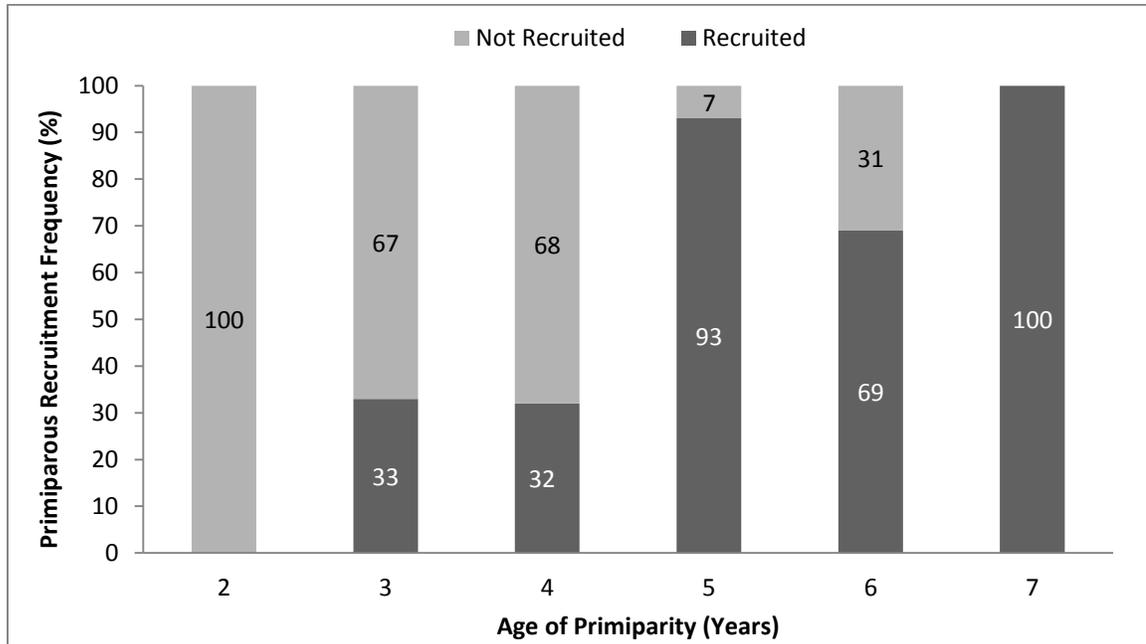


Figure 2.5. Primiparous recruitment frequency of 64 observed primiparous dens by age of primiparity of mother. Recruitment dens produced at least one successfully recruited offspring. Only offspring with known recruitment included. Data were collected from 1981-2013 in Maine, USA.

Logistic regression indicated that there was a difference in the successful recruitment of at least one offspring from the primiparous den among the primiparous ages ($p = 0.002$). The predicted probability of a successfully recruited primiparous offspring increased with increasing age of primiparity (range = 0.075 – 0.938) (Figure 2.6). The greatest change in predicted primiparous recruitment probability occurred between four year old females ($P(4) = 0.399$) and five year old females ($P(5) = 0.654$) ($P(\Delta) = 0.255$). Seven year old primiparous bears had the maximum predicted probability of successfully recruiting at least one primiparous offspring ($P(7) = 0.938$) (Figure 2.6).

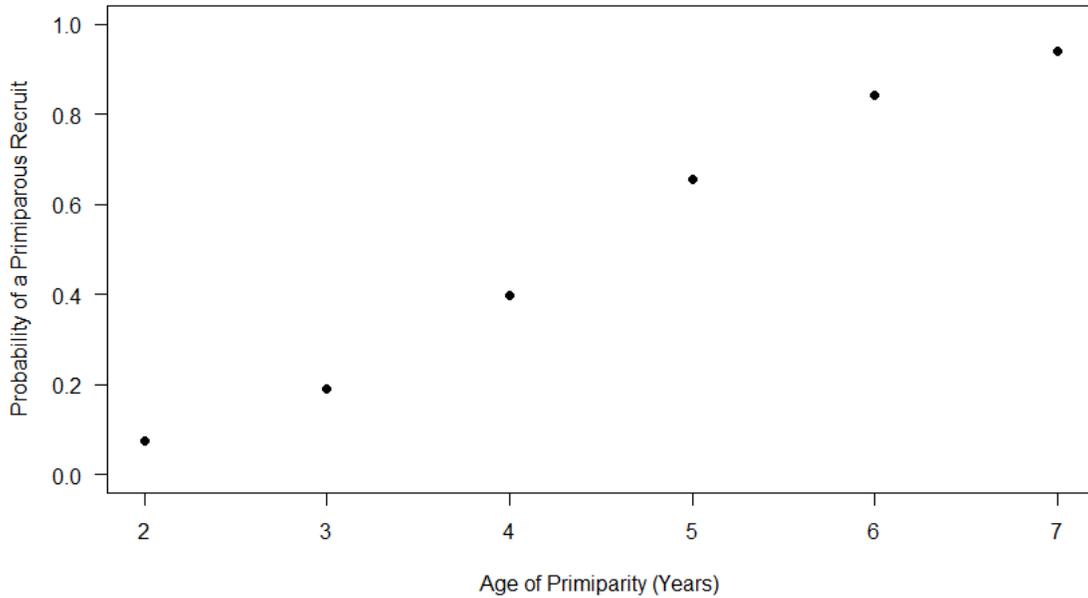


Figure 2.6. Probability of a successfully recruited offspring from the primiparous litter by age of primiparity derived from 64 female black bears with known recruitment. Probability derived from the distribution function of the coefficients of the logistic regression of age of primiparity on recruitment. Successful recruitment was defined as the survival of a cub to the yearling age class. Data were collected from 1981-2013 in Maine, USA.

Age of Primiparity and Lifetime Productivity

A total of 85 primiparous females were used to examine the relationship between age of primiparity and lifetime productivity, as measured by combined lifetime cub mass (Rogers 1987; Seger et al. 2013). There were 364 cubs produced in observed primiparous dens, with a combined total mass of 775.62 kg. Individual cub mass varied (range = 0.28 kg – 4.32 kg, mean = 2.08 kg), as did the number of cubs per primiparous female lifetime (range = 1 – 16, mean = 4.52). Lifetime litter mass varied among individual primiparous females (range = 0.62 kg – 33.79 kg, mean = 9.12 kg).

Using a one-way ANOVA test, I found there was no difference in lifetime productivity among the primiparous ages ($F = 0.83$, $p = 0.532$) (Figure 2.7). The age of

primiparity pair that exhibited the greatest lifetime litter mass difference was 2 year old – 3 year old ($p = 0.403$).

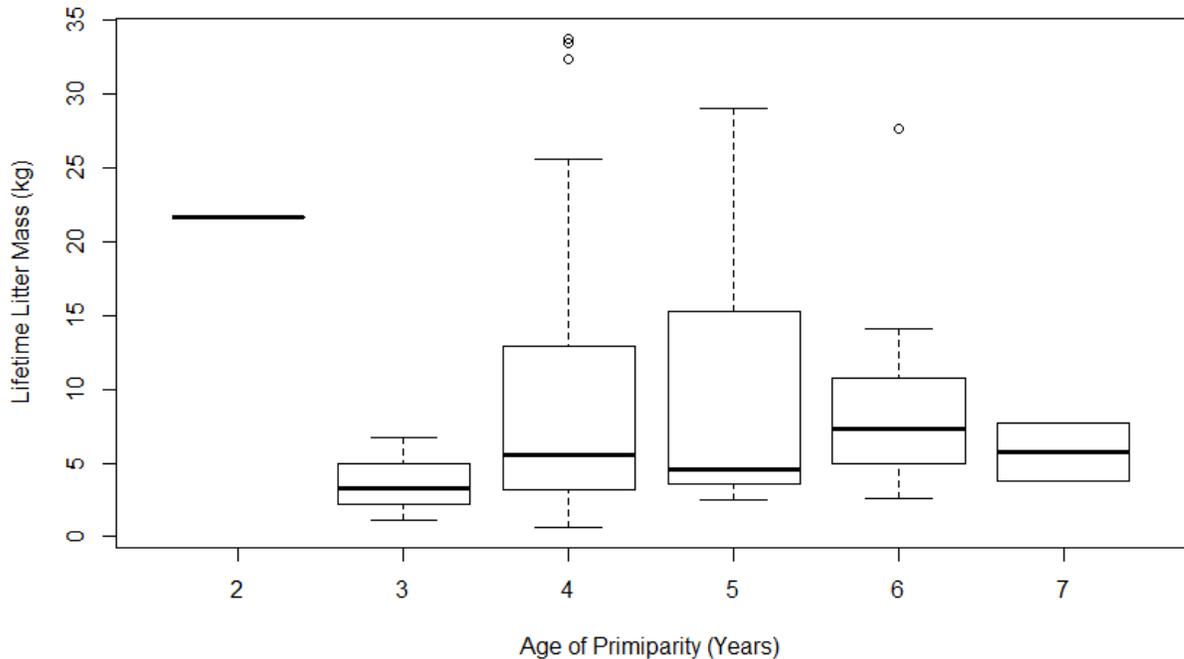


Figure 2.7. Boxplots of the lifetime combined litter mass of 85 observed primiparous female black bears by age of primiparity. Data were collected from 1981-2013 in Maine, USA.

Age of Primiparity and Body Condition

A total of 63 female black bears with known primiparous body conditions and pre-primiparous body conditions were used to examine body condition changes between a bear's last nulliparous year and its primiparous year. A one-tailed paired t-test between the nulliparous and primiparous body conditions indicated that a female's primiparous body condition was not greater than its last nulliparous body condition. ($t = -0.011$, $df = 62$, $p = 0.5043$).

A total of 74 female black bears with known primiparous body conditions were used to examine the relationship between age of primiparity and primiparous body

condition. Using a one-way ANOVA test, I found there was no difference in body condition among the primiparous ages ($F = 1.041$, $p = 0.401$) (Figure 2.8).

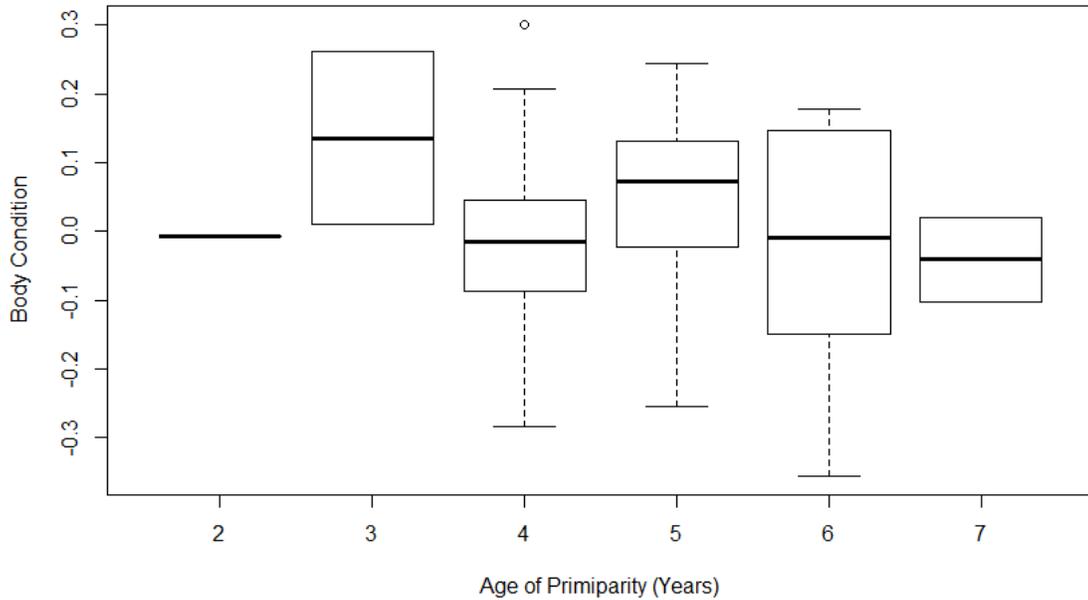


Figure 2.8. Boxplots of the calculated primiparous body condition of 74 observed primiparous female black bears by age of primiparity. Data were collected from 1981-2013 in Maine, USA.

DISCUSSION

Regional Variation in Primiparity

The majority of observed primiparous bears in Maine were between four and six years old, with four year olds being the most common (Figure 2.2). This supported previous primiparity research conducted on black bears in the Northeast, including Maine, which found most bears to be four years old at the time of primiparity (Elowe and Dodge 1989; Schooley et al. 1994). Variation in the observed age of primiparity, however, differed from previous Maine studies. In 1994, the earliest observed age of primiparity of Maine bears from all study areas was four years old (McLaughlin et al.

1994). The earliest observed age of primiparity documented in this study was two years old, with three additional 3 year old primiparous bears (Figure 2.2). All females with ages of primiparity younger than 4 years old were found in the Bradford study area, which was active during the previous primiparity analysis in 1994. This suggests that changes in food quality and abundance, especially regionally in Bradford, may have occurred during the last 20 years in order to facilitate young ages of primiparity in some black bears.

Regional variation in the age of primiparity of black bears exists in Maine (Figure 2.3). Weighted mean ages of primiparity ranged from 4.0 years to 5.0 years, but differed significantly for two study area pairings: Bradford-Spectacle Pond and Bradford-Stacyville (Figure 2.3). This type of population-specific, regional variation in age of primiparity may be attributed to regional variation in food quality and abundance. Black bear reproduction is primarily controlled by fluctuating food supplies and differences in these food supplies often result in differences in reproductive strategies (Rogers 1983). For instance, black bears in regions with reliable, high-quality food produced their primiparous litters early, often at only 3 or 4 years of age (Alt 1980; Kordek and Lindzey 1980). Conversely, black bears in regions with unreliable or low-quality food produced their primiparous litters as late as 8 years of age (Jonkel and Cowan 1971). Age of primiparity has been shown to be a nutritionally influenced, weight-dependent parameter for black bears (Noyce and Garshelis 1994). The delay in primiparity for black bears with low food quality and abundance is the result of poor nutritional condition which may cause hormonal changes that result in termination and reabsorption of pregnancy (Nutting and Meyer 1963; Jainudeen and Hafez 1980; Kaltenbach and Dunn 1980; Elowe and

Doge 1989). These physiological responses may prevent early ages of primiparity in regions with poor food quality or abundance.

Previous black bear researchers in Maine postulated that Spectacle Pond bears had the oldest mean age of primiparity as a result of periodic food shortages that delayed growth and development (McLaughlin et al. 1994). Spectacle Pond has historically had the least predictable food supplies of the study areas, with bears being largely dependent on biannual beech nut masts (Schooley et al. 1994). Bradford has historically had the most predictable, high-quality food supplies of the study areas, providing bears with both hard and soft masts (R.A. Cross, MDIFW, personal communication, 2012). Hard and soft masts differ greatly in the nutritional value they supply to black bears. Hard masts (e.g., red oak acorns (*Quercus rubra*), beech nuts) are high in fats and proteins, while soft masts (e.g., raspberries, low bush blueberries), are high in sugar and carbohydrates (Roehl 1984). Black bears with diets high in fat and carbohydrates are typically the most reproductively successful (Elowe and Dodge 1989). This indicates that black bear diets should ideally contain a combination of both hard and soft masts. Spectacle Pond offered primarily unpredictable hard mast which may have led to poorer nutritional condition of black bears from that study area, resulting in a higher mean age of primiparity. Conversely, Bradford offered both hard and soft masts in high abundance which may have led to better nutritional condition of black bears from that study area, resulting in a lower mean age of primiparity.

Although unbiased mean ages of primiparity were calculated for each study area using the methods described by Garshelis et al. (1998) to avoid bias caused by the removal of bears due to hunting or radiocollar loss, these means did not differ from

traditionally-calculated weighted mean ages of primiparity. The unbiased mean method is especially useful when analyzing a hunted population because bias may be high if bears are killed prior to reaching primiparity, resulting in a low-skewed mean age of primiparity (Garshelis et al. 1998). Despite the existence of a black bear harvest in Maine, the lack of an age difference between traditional weighted and unbiased methods of calculating age of primiparity of Maine bears may be due to insufficient hunting pressure. Maine black bear harvest objectives have not been met since 2005 and there has been a decline in bear hunting permit sales over the last decade (MDIFW 2014). The lack of an age difference may indicate that current harvest levels in Maine do not significantly impact the reproductive strategies of black bears.

Age of Primiparity and Recruitment

Although age of primiparity was a regionally important and telling parameter for Maine black bears in its own right, it also impacted other reproductive parameters. Age of primiparity influenced the number of recruited offspring from primiparous black bear dens (Figure 2.4). The impacts of litter order on litter size and viability are well-documented for black bears. Primiparous litters are smaller and have fewer offspring recruited than subsequent litters (McLaughlin et al. 1994; Noyce and Garshelis 1994; Garrison et al. 2007). Although other factors may play a role, the inexperience of young female bears is the likely cause of low primiparous recruitment (Higgins 1997; White et al. 2001; Garrison et al. 2007). Comparing offspring recruitment of primiparous bears of different ages is not well-studied and is unique because all primiparous bears equally lack maternal experience.

The number of recruited offspring from primiparous dens in Maine varied based on the mother's age of primiparity (Figure 2.4). Although four year old primiparous bears produced the most cubs in the primiparous den, they only had a recruitment rate of 37%. Five year olds had an 85% recruitment rate, making them the most productive recruiters, responsible for 37% of primiparous recruitment (Figure 2.4). Despite a 100% recruitment rate for seven year old primiparous females, only a small percentage (3%) of the total primiparous cubs were produced by bears of this age. Similar to the count of successfully recruited offspring, age of primiparity also influenced the number of primiparous dens producing at least one successful recruit (Figure 2.5). The only two year old bear did not successfully recruit cubs from its primiparous den. Five year old primiparous bears had the most successful primiparous dens, comprising 37% of recruiting dens (Figure 2.5).

Logistic regression indicated that there was a difference in the successful recruitment of at least one offspring from the primiparous den among the primiparous ages. The probability of successful recruitment increased with increasing age of primiparity (Figure 2.6). Nutrition and the abundance of high quality food may play a big role in black bear reproduction, not only influencing the age of primiparity, but also recruitment rates. A black bear's age of primiparity is influenced by nutritional condition. The condition and size of black bears is closely linked to diet, resulting from food availability and quality (Noyce and Garshelis 1994). Similarly, black bear recruitment rates are also related to the quality of food (Wathen 1983; Brody 1984). Body weight is a good indicator of maternal condition (Noyce and Garshelis 1994). This suggests that older, larger primiparous bears may reach the necessary size and condition to

successfully produce and recruit offspring, even if younger primiparous bears are the largest of their age and capable of reproducing.

Although all primiparous bears have the same lack of maternal experience, they may differ when it comes to life experience. Older primiparous bears have successfully survived to an older age and have more years of life experience that may help to explain some of the increase in older primiparous recruitment success. These older bears simply have had more time to learn where food-rich areas are located and how to survive during times of poor food conditions. Older bears have also had more denning experience and may learn to use safer, more protective den types than younger bears (Alt 1984; Wathen et al. 1986; Martorello and Pelton 2003). This food and denning knowledge may translate into more informed and effective maternal care, leading to a greater chance of offspring survival and recruitment.

Age of Primiparity and Lifetime Productivity

Analysis of variance indicated that a black bear's age of primiparity does not influence its lifetime productivity (Figure 2.7). Unlike recruitment, which required survival of offspring, lifetime productivity did not require cubs to survive their first year. Combined lifetime litter mass was used to represent lifetime productivity because litter mass has been shown to reflect the availability of high quality food (Rogers 1987; Seger et al. 2013). Similar to other reproductive parameters, such as age of primiparity and recruitment, productivity may be regulated by nutrition and high quality food (Rogers 1987; Schoen 1990).

Lifetime litter mass did not differ among bears with different ages of primiparity (Figure 2.7). Lifetime litter mass can be viewed as the interplay between the number of cubs produced and the mass of those cubs, both of which vary individually (MacArthur and Wilson 1967). Lifetime cub production is dependent on both the number of cubs per litter and the number of litters during a lifetime. The combination of these factors can result in different lifetime litter masses, depending on the age of primiparity of a female.

To further explain this concept, we can observe two hypothetical female black bears. Both females live to 13 years of age before they are harvested. Female A has its primiparous litter at age 3 and Female B has its primiparous litter at age 7. Black bears typically have cubs every other year, so an interbirth interval of 2 years can be assumed in this situation (Noyce and Garshelis 1994; Ryan 1997). Female A has six litters (at ages 3, 5, 7, 9, 11, and 13), while Female B has four litters (at ages 7, 9, 11, and 13). Because Female A had more litters than Female B, we can assume that she also produced more cubs. If number of cubs were the only contributing factor to lifetime litter mass, then bears with younger ages of primiparity would have more lifetime productivity, holding lifetime lengths the same. However, lifetime litter mass results from both the number of cubs and the mass of those cubs. Maternal mass results from high quality food resources and is a good indicator of cub mass (Noyce and Garshelis 1994; Seger et al. 2013). Female B is larger and heavier due to age, so she can produce larger cubs than Female A. As indicated by the similar lifetime litter masses among the primiparous ages, reproductive life history traits such as number of offspring, frequency of reproduction, and mass of offspring in black bears can balance out. A bear with a younger age of primiparity likely produces many lightweight offspring, while a bear with an older age of

primiparity likely produces fewer heavy offspring over the same lifetime, resulting in statistically similar total lifetime litter masses. It is this variability in cub production and cub mass that can result in similar lifetime litter masses among bears with different ages of primiparity.

The hypothetical situation described above is very simplistic and makes three major assumptions: bears reproduce only every two years, litter sizes are always the same, and all bears live to the same age. In real black bear populations, females may breed and produce cubs in two consecutive years if they lose their entire first litter prior to the start of the breeding season during the second year (Garrison et al. 2007). This would result in more frequent litters and more cubs, but likely more offspring with lower masses. Due to the relatively small sample size ($n = 85$) of primiparous bears, no age cut-off was used during this analysis. This means that lifetime lengths varied among the primiparous individuals (range: 3 years – 24 years, mean = 7.3 years), as did the lengths of their cub-producing lives (range: 0 years – 20 years, mean = 2.7 years). Of the 85 primiparous bears, 22 were lost during their primiparous year, resulting in only a single lifetime litter. However, 39 primiparous bears successfully produced at least 2 litters, including one that produced cubs for 20 years. Due to the contribution of litter frequency to lifetime productivity, the lifetime productivity of bears with shorter lifespans may be more influenced by age of primiparity than the lifetime productivity of longer-lived bears. The varying lifetime lengths of bears may bias the productivity results, however it is unlikely, given the 2.7 year mean of multiparous production, resulting in a mean of 2 litters per observed primiparous bear.

Age of Primiparity and Body Condition

The body condition of Maine black bears during their primiparous year was not greater than during their last nulliparous year ($p = 0.5043$). Body condition was calculated by taking the residuals of the regression of body mass vs. length (Cattet et al. 2002). A body condition or mass threshold, as seen in some populations (Noyce and Garshelis 1994), did not influence primiparity in Maine black bears. The body condition of black bears is closely linked to the abundance and quality of food resources (Noyce and Garshelis 1994). As a result, it is likely that body condition, both during nulliparous and primiparous years, is influenced by a bear's diet.

The lack of a change between nulliparous and primiparous years may support this study's findings on the relationship between age of primiparity and recruitment. This lack of a body condition difference may be part of the reason low ages of primiparity (2 and 3 years old) have been observed in Maine, however the probability of offspring recruitment from the primiparous den did not significantly increase until a bear was 4 or 5 years old (Figure 2.5). Unlike populations with mass or condition thresholds to primiparity, Maine black bears are capable of successfully reproducing, even with body conditions equal to that of a nulliparous bear. This reproductive capability results in lower ages of primiparity, however the quality of the offspring may be lower as well, resulting in fewer successfully recruited dens at low ages of primiparity.

Analysis of variance indicated that age of primiparity did not influence body condition (Figure 2.8). Not only is there no difference between a bear's last nulliparous and primiparous body conditions, but there is also no difference among the body

conditions of bears with different ages of primiparity. This may indicate that primiparous recruitment success is not solely driven by nutrition, but rather that other factors, such as a bear's life experiences, may influence recruitment. The lack of a relationship between age of primiparity and body condition may also be supportive of the lack of a relationship between age of primiparity and lifetime productivity. If there were a difference in body condition for bears of different ages of primiparity, it would be expected that this difference could be seen in the lifetime productivity of bears with that age of primiparity. Since there was no difference in body condition of bears of different ages of primiparity, this is consistent with the fact that there was also no difference in lifetime productivity of bears of different ages of primiparity.

CONCLUSIONS

Regional variation in the age of primiparity of black bears has been detected in Maine. Although most primiparous bears were four years old, consistent with previous research, population-specific variation in the age of primiparity was apparent and significant between both Bradford and Spectacle Pond and Bradford and Stacyville. The quality of food resources influenced black bear condition and, in turn, influenced reproductive traits such as age of primiparity. The regional variation in age of primiparity was likely due to regional variation in food quality and abundance, primarily the presence of both hard and soft masts in a study area.

Age of primiparity influences primiparous recruitment. The probability of successfully recruiting at least one offspring increased with increasing age of primiparity. Five year old primiparous bears were the most productive recruiters, responsible for 37%

of primiparous recruitment. Nutritional condition and the quality of food resources likely influenced the primiparous recruitment rates of the equally maternally inexperienced bears. Life experience, both in terms of food and denning knowledge, may have also influenced recruitment rates.

Age of primiparity does not influence lifetime productivity, as measured by combined lifetime litter mass. Lifetime litter mass measured a trade-off between quantity and quality of offspring. A younger age of primiparity may have resulted in more reproductive attempts and more cubs, but likely produced cubs with smaller masses. An older age of primiparity may have resulted in fewer reproductive attempts and fewer cubs, but likely produced cubs with larger masses. These competing strategies likely balanced each other out, resulting in no difference in lifetime productivity among different primiparous ages.

Body condition does not influence age of primiparity for Maine black bears. The body condition of a bear during its last nulliparous year and its primiparous year was similar. There was also no difference among the body conditions of bears with different ages of primiparity. These results are in line with my findings of no differences in lifetime productivity among primiparous ages as well as with the potential for non-nutritional influences on primiparous recruitment.

Population-specific reproductive strategies are evident in black bears. Although black bears are a K-selected species, individuals and even whole populations may fall at varying points along the r-K spectrum (Pianka 1970). In Maine, the placement of populations along this r-K spectrum is highly dependent on the abundance and quality of

food resources (McLaughlin et al. 1994; Schooley et al. 1994; Noyce and Garshelis 1994). Bears from the Bradford study area are more r-selected, with earlier ages of primiparity, more reproductive attempts, and more offspring. Bears from the Spectacle Pond study area are more K-selected, with later ages of primiparity, fewer reproductive attempts, and fewer offspring. The population-specific placement along the r-K spectrum, and the balance of reproductive life history traits it represents, is further exemplified by the fact that there was no relationship between age of primiparity and lifetime productivity. Reproductive biology and age-specific life history traits, including age of primiparity, number of offspring, frequency of reproduction, and offspring survival, play integral roles in population dynamics. Understanding these life history traits and the factors that create their variability are essential to understanding a species, its behavior, and its management needs.

Management Implications

The large, long-term MDIFW dataset allowed for exploration of the topic of primiparity and facilitated the analysis of several reproductive life history traits related to this primiparity. This research has several management applications, both for the state of Maine and elsewhere. By evaluating the influence of age of primiparity on other reproductive life history traits, this research has provided insight into how variation in primiparity may affect population dynamics at regional or population-specific scales. An understanding of these effects will provide important insight to wildlife managers to help them better understand the species' reproductive strategies, allowing for better protection or more precise hunting regulations, depending on management goals.

With regard to Maine black bears, this research has provided an update to state primiparity information, with data spanning over thirty years and including the newest study area. State population models may be strengthened by including this updated primiparity information along with the analysis of other reproductive parameters, such as recruitment and lifetime productivity. These population models may aid in providing a better estimate of Maine's black bear population and future trends for the species, to inform and guide management of bears in the state, primarily through harvest regulations.

Future research could be conducted to more precisely evaluate the food resources available to black bears in the different study areas and to examine whether reproductive parameters other than age of primiparity vary by study area, as a result of these food resources. Insight into reproductive biology and the factors that influence reproductive life history traits are important not only for black bear management, but also more broadly for wildlife management of any species that exhibits dynamic populations as a result of reproductive factors.

REFERENCES

- Alt, G.L. 1980. Rate of growth and size of Pennsylvania black bears. *Pennsylvania Game News* 51: 7-17
- Alt, G.L. 1984. Black bear cub mortality due to flooding of natal dens. *Journal of Wildlife Management* 48: 1432-1434.
- Baldwin, R.A. and L.C. Bender. 2008. Den-site characteristics of black bears in Rocky Mountain National Park, Colorado. *Journal of Wildlife Management* 72: 1717-1724.
- Beecham, J.J., D.G. Reynolds and M.G. Hornocker. 1983. Black bear denning activities and den characteristics in west-central Idaho. *International Conference on Bear Research and Management* 5: 79-86.
- Benson, J.F. 2005. Ecology and conservation of Louisiana black bears in the Tensas River Basin and reintroduced populations. Thesis, Louisiana State University, Baton Rouge, Louisiana, USA. 114 pp.
- Benson, J.F. and M.J. Chamberlain. 2007. Space use and habitat selection by female Louisiana black bears in the Tensas River Basin of Louisiana. *Journal of Wildlife Management* 71: 117-126.
- Bowyer, R.T., V. Van Ballenberghe, J.G. Kie, J.A.K. Maier. 1999. Birth-site selection by Alaskan moose: Maternal strategies for coping with a risky environment. *Journal of Mammalogy* 80: 1070-1083.
- Brody, A. J. 1984. Habitat use by black bears in relation to forest management in Pisgah National Forest, North Carolina. Thesis, University of Tennessee, Knoxville, Tennessee, USA. 123 pp.
- Burger, J. 1993. Colony and nest site selection in lava lizards *Tropidurus* spp. in the Galapagos Islands. *Copeia* 1993: 748-754.
- Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edition. New York, Springer.
- Caro, T.M. and M.D. Hauser. 1992. Is there teaching in nonhuman animals?. *Quarterly Review of Biology* 67: 151-174.
- Cattet, M.R.L., N.A. Caulkett, M.E. Obbard, G.B. Stenhouse. 2002. A body-condition index for ursids. *Canadian Journal of Zoology* 80: 1156-1161.
- Champagne, F.A. 2008. Epigenetic mechanisms and the transgenerational effects of maternal care. *Neuroendocrinology* 29: 386-397.
- Crook, A.C. and M.J. Chamberlain. 2010. A multiscale assessment of den selection by black bears in Louisiana. *Journal of Wildlife Management* 74: 1639-1647.

- Curley, J.P., F.A. Champagne, P. Bateson, E.B. Keverne. 2008. Transgenerational effects of impaired maternal care on behaviour of offspring and grandoffspring. *Animal Behaviour* 75: 1551-1561.
- Davis, H. 1996. Characteristics and selection of winter dens by black bears in coastal British Columbia, Thesis, Simon Fraser University, Burnaby, British Columbia, Canada. 148pp.
- Davis, S.K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *The Condor* 107: 605-616.
- Doan-Crider, D.L. and E.C. Hellgren. 1996. Population characteristics and winter ecology of black bears in Coahuila, Mexico. *Journal of Wildlife Management* 60: 398-407.
- Elowe, K.D. 1987. Factors affecting black bear reproductive success and cub survival in Massachusetts. Thesis, University of Massachusetts, Amherst, Massachusetts, USA. 112 pp.
- Elowe, K.D. and W.E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. *Journal of Wildlife Management* 53: 962-968.
- Erickson, A.W. 1959. The age of self-sufficiency in the black bear. *Journal of Wildlife Management* 23: 401-405.
- Figueredo, A.J., G. Vásquez, B.H. Brumbach, J.A. Sefcek, B.R. Kirsner, W.J. Jacobs. 2005. The K-factor: Individual differences in life history strategy. *Personality and Individual Differences* 39: 1349-1360.
- Garrison, E.P., J.W. McCown and M.K. Oli. 2007. Reproductive ecology and cub survival of Florida black bears. *Journal of Wildlife Management* 71: 720-727.
- Garrison, E.P., J.W. McCown, M.A. Barrett, M.K. Oli. 2012. Denning ecology of Florida black bears in north-central Florida. *Southeastern Naturalist* 11: 517-528.
- Garshelis, D.L., K.V. Noyce and P.L. Coy. 1998. Calculating average age of first reproduction free of the biases prevalent in bear studies. *International Conference on Bear Research and Management* 10: 437-447.
- Hayes, S.G. and M.R. Pelton. 1994. Habitat characteristics of female black bear dens in northwestern Arkansas. *International Conference on Bear Research and Management* 9: 411-418.
- Henner, C.M. M.J. Chamberlain, B.D. Leopold, L. W. Burger, Jr. 2004. A multi resolution assessment of raccoon den selection. *Journal of Wildlife Management* 68: 179-187.
- Hepp, G.R. and R.A. Kennamer. 1992. Characteristics and consequences of nest-site fidelity in wood ducks. *The Auk* 109: 812-818.

- Heppell, S.S. 1998. Application of life-history theory and population model analysis to turtle conservation. *Copeia* 2: 367-375.
- Hersey, K.R., A.S. Edwards and J.D. Clark. 2005. Assessing American black bear habitat in the Mobile-Tensaw delta of southwestern Alabama. *Ursus* 16: 245-254.
- Heyes, C.M. 1994. Social learning in animals: Categories and mechanisms. *Biological Review* 69: 207-231.
- Higgins, J.C. 1997. Survival, home ranges and spatial relationships of Virginia's exploited black bear populations. Thesis, Virginia Polytechnic Institute, Blacksburg, Virginia, USA. 88pp.
- Hopkins III, J.B. 2013. Use of genetics to investigate socially learned foraging behavior in free ranging black bears. *Journal of Mammalogy* 94: 1214-1222.
- Immell, D., D.H. Jackson and M.C. Boulay. 2013. Denning ecology of American black bears in the Cascade Mountains of western Oregon. *Ursus* 24: 1-12.
- Jainudeen, M.R. and E.S.E. Hafez. 1980. Reproductive failure in females. Reproduction in farm animals. Lea and Febiger.
- Joern, W.T. and J.F. Jackson. 1983. Homogeneity of vegetational cover around the nest and avoidance of nest predation in mockingbirds. *The Auk* 100: 497-499.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preferences. *Ecology* 61: 65-71.
- Johnson, K.G. 1978. Den ecology of black bears (*Ursus americanus*) in the Great Smoky Mountains National Park. Thesis, University of Tennessee, Knoxville, Tennessee, USA. 107 pp.
- Johnson, K.G. and M.R. Pelton. 1980. Environmental relationships and the denning period of black bears in Tennessee. *Journal of Mammalogy* 61: 653-660.
- Johnson, K.G. and M.R. Pelton. 1981. Selection and availability of dens for black bears in Tennessee. *Journal of Wildlife Management* 45: 111-119.
- Jonkel, C.J. and I.M. Cowan. 1971. The black bear in the spruce-fir forest. *Wildlife Monographs* 27: 3-57.
- Kaltenbach, C.C. and T.G. Dunn. 1980. Endocrinology of reproduction. Reproduction in farm animals. Lea and Febiger.
- Klenzendorf, S.A., M.R. Vaughan and D.D. Martin. 2002. Den-type use and fidelity of American black bears in Western Virginia. *Ursus* 13: 39-44.
- Kolenosky, G.B. 1990. Reproductive biology of black bears in east-central Ontario. *International Conference on Bear Research and Management* 8: 385-392.

- Kolenosky, G.B. and S.M. Strathearn. 1987. Winter denning of black bears in east-central Ontario. *International Conference on Bear Research and Management* 7: 305-316.
- Kordek, W.S. and J.S. Lindzey. 1980. Preliminary analysis of female reproductive tracts from Pennsylvania black bears. *International Conference on Bear Research and Management* 4: 159-161.
- Laland, K.N. 2004. Social learning strategies. *Learning & Behavior* 32: 4-14.
- Leggett, W.C. and J.E. Carscadden. 1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): Evidence for population specific life history strategies in fish. *Journal of the Fisheries Research Board of Canada* 35: 1469-1478.
- MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press.
- Maestriperi, D. and J.M. Mateo, eds. 2009. Maternal effects in mammals. University of Chicago Press.
- Maine Chapter of the Wildlife Society. 2011. Maine black bear fact sheet. Black Bear Management Committee. Topsham, Maine.
- Maine Department of Inland Fisheries and Wildlife. 2011. Maine's black bear monitoring program. Bangor, Maine.
- Maine Department of Inland Fisheries and Wildlife. 2014. Research and Management Report 2014. Bangor, Maine.
- Maine Forest Service. 1999. The state of the forest and recommendations for forest sustainability standards. Maine Forest Service, Augusta, ME. 41 pp.
- Martorello, D.A. and M.R. Pelton. 2003. Microhabitat characteristics of American black bear nest dens. *Ursus* 14: 21-26.
- Meaney, M.J. 2001. Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. *Annual Review of Neuroscience* 24: 1161-1192.
- McLaughlin, C.R. 1999. Black bear assessment and strategic plan 1999. Bangor, Maine.
- McLaughlin, C.R., G.J. Matula, Jr., R.J. O'Connor. 1994. Synchronous reproduction by Maine black bears. *International Conference on Bear Research and Management* 9: 471-479.
- Miller, C.W., R.J. Fletcher Jr., B.D. Anderson, L.D. Nguyen. 2012. Natal social environment influences habitat selection later in life. *Animal Behaviour* 83: 473-477.

- Miller, S.D. 1994. Black bear reproduction and cub survivorship in south-central Alaska. *International Conference on Bear Research and Management* 9: 263-273.
- Noyce, K.V. and D.L. Garshelis. 1994. Body size and blood characteristics as indicators of condition and reproductive performance in black bears. *International Conference on Bear Research and Management* 9: 481-496.
- Nutting, E.F. and R.K. Meyer. 1963. Implantation delay, nidation, and embryonal survival in rats treated with ovarian hormones. Delayed implantation. University of Chicago Press.
- Person, D.K. and A.L. Russell. 2009. Reproduction and den site selection by wolves in a disturbed landscape. *Northwest Science* 83: 211-224.
- Petranka, J.W. 1990. Observations on nest site selection, nest desertion, and embryonic survival in marbled salamanders. *Journal of Herpetology* 24: 229-234.
- Phelps, Q.E., A.M. Lohmeyer, N.C. Wahl, J.M. Zeigler, G.W. Whitedge. 2009. Habitat characteristics of black crappie nest sites in an Illinois impoundment. *North American Journal of Fisheries Management* 29: 189-195.
- Pianka, E.R. 1970. On r- and K-selection. *The American Naturalist* 104: 592-597.
- Ramsay, M.A. and I. Stirling. 1990. Fidelity of female polar bears to winter-den sites. *Journal of Mammalogy* 71: 233-236.
- Reinhold, K. 2002. Maternal effects and the evolution of behavioral and morphological characters: A literature review indicates the importance of extended maternal care. *Journal of Heredity* 93: 400-405.
- Reynolds-Hogland, M.J. and M.S. Mitchell. 2007. Effects of roads on habitat quality for bears in the southern Appalachians: A long term study. *Journal of Mammalogy* 88: 1050-1061.
- Reznick, D., M.J. Bryant and F. Bashey. 2002. r- and K-selection revisited: The role of population regulation in life-history evolution. *Ecology* 83: 1509-1520.
- Rödel, H.G., G. Prager, V. Stefanski, D. von Holst, R. Hudson. 2008. Separating maternal and litter-size effects on early postnatal growth in two species of altricial small mammals. *Physiology & Behavior* 93: 826-834.
- Roehl, E. 1984. Food facts. Apollo Books.
- Rogers, L.L. 1983. Effects of food supply, predation, cannibalism, parasites, and other health problems on black bear populations. *Symposium on Natural Regulation of Wildlife Populations, University of Idaho, Forest, Wildlife and Range Experiment Station Proceedings* 14: 194-211.

- Rogers, L.L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. *Wildlife Monographs* 97: 3-72.
- Ross, S., R. Kamnitzer, B. Munkhtsog, S. Harris. 2010. Den-site selection is critical for Pallas's cats (*Otocolobus manul*). *Canadian Journal of Zoology* 88: 905-913.
- Rushton, J.P. 1985. Differential K theory: The sociobiology of individual and group differences. *Personality and Individual Differences* 6: 441-452.
- Ryan, C.W. 1997. Reproduction, survival, and denning ecology of black bears in southwestern Virginia. Thesis, Virginia Polytechnic Institute, Blacksburg, Virginia, USA. 87 pp.
- Sader, S.A., M. Bertrand and E.H. Wilson. 2003. Satellite change detection of forest harvest patterns on an industrial forest landscape. *Forest Science* 49: 341-353.
- Saether, B., T. Coulson, V. Grotan, S. Engen, R. Altwegg, K.B. Armitage, C. Barbraud, P.H. Becker, D.T. Blunstein, F.S. Dobson, M. Festa-Bianchet, J. Gaillard, A. Jenkins, C. Jones, M.A.C. Nicoll, K. Norris, M.K. Oli, A. Ozgul, H. Weimerskirch. 2013. How life history influences population dynamics in fluctuating environments. *The American Naturalist* 182: 743-759.
- Samson, C. and J. Huot. 1995. Reproductive biology of female black bears in relation to body mass in early winter. *Journal of Mammalogy* 76: 68-77.
- Schoen, J.W. 1990. Bear habitat management: A review and future perspective. *International Conference on Bear Research and Management* 8: 143-154.
- Schooley, R.L., C.R. McLaughlin, G.J. Matula Jr., W.B. Krohn. 1994. Denning chronology of female black bears: Effects of food, weather, and reproduction. *Journal of Mammalogy* 75: 466-477.
- Schwartz, C.C. and A.W. Franzmann. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. *Journal of Wildlife Management* 56: 426-431.
- Schwartz, C.C., S.D. Miller and A.W. Franzmann. 1987. Denning ecology of three black bear populations in Alaska. *International Conference on Bear Research and Management* 7: 281-291.
- Schwarzkopf, L. and R.J. Brooks. 1987. Nest-site selection and offspring sex ration in painted turtles, *Chrysemys picta*. *Copeia* 1987: 53-61.
- Scott, R.J., R. Kosick, M. Clement, D.L.G. Noakes, F.W.H. Beamish. 2005. Nest site selection and spawning by captive bred Atlantic salmon, *Salmo salar*, in a natural stream. *Environmental Biology of Fishes* 74: 309-321.

- Seger, R.L., F.A. Servello, R.A. Cross, D.H. Keisler. 2013. Body mass and mast abundance influence foraging ecology of the American black bear (*Ursus americanus*) in Maine. *Canadian Journal of Zoology* 91: 512-522.
- Skeel, M.A. 1983. Nesting success, density, philopatry, and nest-site selection of the whimbrel (*Numenius phaeopus*) in different habitats. *Canadian Journal of Zoology* 61: 218-225.
- Smith, M.E., J.L. Hechtel and E.H. Follmann. 1994. Black bear denning ecology in interior Alaska. *International Conference on Bear Research and Management* 9: 513-522.
- Stearns, S.C. 2000. Life history evolution: Successes, limitations, and prospects. *Naturwissenschaften* 87: 476-486.
- Thornton, A. and N.J. Raihani. 2010. Identifying teaching in wild animals. *Learning & Behavior* 38: 297-309.
- Waser, P.M. and W.T. Jones. 1983. Natal philopatry among solitary mammals. *Quarterly Review of Biology* 58: 355-390.
- Wathen, W.G. 1983. Reproduction and denning of black bears in the Great Smoky Mountains. Thesis, University of Tennessee, Knoxville, Tennessee, USA. 135 pp.
- Wathen, W.G., K.G. Johnson and M.R. Pelton. 1986. Characteristics of black bear dens in the southern Appalachian region. *International Conference on Bear Research and Management* 6: 119-127.
- Wesolowski, T. 2002. Anti-predator adaptations in nesting marsh tits *Parus palustris*: The role of nest-site security. *Ibis* 144: 593-601.
- White, Jr., T.H., J.L. Bowman, H.A. Jacobson, B.D. Leopold, and W.P. Smith. 2001. Forest management and female black bear denning. *Journal of Wildlife Management* 65: 34-40.
- Wilson, D.S. 1998. Nest-site selection: Microhabitat variation and its effects on the survival of turtle embryos. *Ecology* 79: 1884-1892.
- Wilson, E.O. 1975. *Sociobiology: The new synthesis*. Harvard University.
- Wolf, J.B. and M.J. Wade. 2009. What are maternal effects (and what are they not)? *Philosophical Transactions of the Royal Society B*. 364: 1107-1115.
- Wooding, J.B. and T.S. Hardisky. 1992. Denning by black bears in northcentral Florida. *Journal of Mammalogy* 73: 895-898.

BIOGRAPHY OF THE AUTHOR

Alyssa Vitale was born in Troy, New York on February 28th, 1990 and raised in Latham, New York. She graduated from Shaker High School in Latham, New York in 2008. Alyssa attended the University of Maine and graduated in 2012 with a Bachelor of Science degree in both Zoology and Ecology & Environmental Sciences with a concentration in Ecology. Alyssa returned to the University of Maine the following fall to begin her Master of Science degree, initially in Zoology before transitioning to Wildlife Ecology. Alyssa is a candidate for the Master of Science degree in Wildlife Ecology from the University of Maine in August 2015.