Mississippi State University

Scholars Junction

5-11-2013

Beaver Movements On Managed Land In The Southeastern United States

Lance Forest McClintic

Follow this and additional works at: https://scholarsjunction.msstate.edu/td

Recommended Citation

McClintic, Lance Forest, "Beaver Movements On Managed Land In The Southeastern United States" (2013). *Theses and Dissertations*. 856.
https://scholarsjunction.msstate.edu/td/856

Beaver movements on managed land in the southeastern United States

By

Lance Forest McClintic

A Thesis
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Master of Science
in Wildlife and Fisheries Science
in the Department of Wildlife, Fisheries and Aquaculture

Mississippi State, Mississippi

May 2013

Beaver movements on managed land in the southeastern United States

By

Lance Forest McClintic

Approved:

_____
Guiming Wang
Associate Professor of Wildlife Ecology
and Management
(Director of Thesis)

_____
Jeanne C. Jones
Professor of Wildlife Ecology and
Management
(Committee Member)

_____
Jimmy D. Taylor
Supervisory Research Wildlife Biologist,
USDA/ APHIS/ NWRC
(Committee Member)

_____
Eric D. Dibble
Professor of Aquatic Sciences
(Graduate Coordinator)

_____
Bruce D. Leopold
Professor of Wildlife Ecology and
Management
(Department Head)

_____
George M. Hopper
Dean of the College of Forest Resources

Name: Lance Forest McClintic

Date of Degree: May 10, 2013

Institution: Mississippi State University

Major Field: Wildlife and Fisheries Science

Major Professor: Dr. Guiming Wang

Title of Study: Beaver movements on managed land in the southeastern United States

Pages in Study: 57

Candidate for Degree of Master of Science

I studied movement characteristics and vegetative resources effects on home range size of beavers at Redstone Arsenal (RSA) in north central Alabama, USA. Beavers were captured and radio tagged from 11 wetlands during winter and spring of 2011. I monitored movements of radio-tagged beavers using radio telemetry from May 2011–April 2012. Beavers moved faster, presumably more favorable to central place foraging, in wetland as they proceeded farther away from the central place, but did not in upland. Additionally, distributions of hourly distances from lodges were bimodal. Home range, core areas, and distance from lodge did not differ between age classes. Home range sizes increased with increasing habitat productivity and resource dispersion, whereas home ranges decreased with temporal variation in resources throughout the year. Quantity and spatial distribution of resources and patterns of foraging behavior influence movements and home ranges of central place foragers.

DEDICATION

I dedicate this thesis to my grandmother (Aena), parents (Jerry and Sara), siblings (Brett and Traci), and fiancée (Brianne). Their love, encouragement, and support during this process and values instilled in me years prior are what kept me going throughout this project.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

vii

CHAPTER I

MOVEMENT CHARACTERISTICS OF AMERICAN BEAVERS (*Castor canadensis*)

IN RELATION TO CENTRAL PLACE FORAGING

Introduction

Movement ecology has recently re-emerged as a central theme of animal ecology,

although animal movements, including migration and dispersal, have been one of the

oldest study topics (Pulido, 2007; Nathan, 2008). Animals move to search for and

acquire resources and mates as well as to avoid or escape predators. Animals can adjust

their displacement distances and directions (i.e., turning angles) in response to temporal

and spatial variation in resource availability and predation risk (Getz & Saltz, 2008;

Mueller & Fagan, 2008; Nathan et al., 2008;). Additionally, movement distances and

turning angles are related to physiological (e.g., age, reproductive condition) and

behavioral (foraging, resting, and travelling) states of moving animals (Franke et al.,

2004). However, relationships between behavioral states or patterns and movement

characteristics (e.g., speed and turning angle) of animals are poorly understood (Getz &

Saltz, 2008; Mueller & Fagan, 2008; Nathan et al., 2008).

American beavers (*Castor canadensis*, hereafter beavers) are semi-aquatic

herbivores that build bank dens or lodges for shelter and nursing of young (Collen &

Gibson, 2000). Beavers are considered central place foragers whose foraging activity is

tied to a central place such as a lodge or bank den, with a series of return trips from food

patches to the den or lodge for protection against predators and actual food consumption (Jenkins, 1980; Fryxell, 1992). Central place foraging has profound consequences to the movement and space use by central place foragers (Owen-Smith et al., 2010; Buchmann et al., 2012). However, previous studies of central place foraging by beavers have focused on relationships between distance from lodge (Fryxell, 1992) or from shoreline (Jenkins, 1980) and food-item size selection (Brzyski & Schulte, 2009). Few studies have investigated fine-scale movement characteristics of beavers in relation to central place foraging theory.

Central place foraging theory states that food searching and handling time, travel time between patches, and energetic costs of resources acquisition influence foraging decisions and behavior of central place foragers (Orians & Pearson, 1979; Fryxell, 1992). Beavers reduce foraging time but increase food item size with increasing distance from their lodges to maximize energy gains (Fryxell, 1992). Furthermore, predation risk may influence a central place forager's optimal foraging distance from central places (Andersson, 1978; Getty, 1981). Therefore, a combination of maximizing energetic gain and decreasing predation risk may lead to an inverse relationship between foraging time per unit area and distance from central places in beavers (Fryxell, 1992) or a more deliberate movement pattern (e.g., greater moving speed and smaller turning angles) at a greater distance from central places.

Central place foraging seabirds in reproductive condition often exhibit bimodal foraging trips, alternating or mixing short foraging trips (for frequently provisioning young at the cost of nesting parents) with long foraging trips (for feeding themselves) (Weimerskirch et al., 1994). Beavers are socially monogamous and live in social groups;

2

consequently, adults and philopatric yearlings may spend more time at or near lodges to nurse and protect pre-weaning newborns during the breeding season (Baker & Hill, 2003). Therefore, adult beavers may exhibit bimodal foraging trips during the breeding season, with a mode of short foraging trips near the lodge for nursing and protecting newborns from predators and a mode of long foraging trips for self feeding to acquire sufficient amounts of food. However, these predicted movement characteristics have not been tested in beavers.

Home range estimation is a common analysis of animal spatial ecology to characterize animal movement patterns (Börger et al., 2006; Downs & Horner, 2009). Movements within a bounded or restricted space for life activities (e.g., searching for and acquiring resources, resting, and reproducing) are the fundamental elements contributing to the home range of animals (Burt, 1943; White & Garrott, 1990). Although previous studies have demonstrated that home range sizes are related to gender, age, and reproductive condition of animals as well as resource availability, causes of intraspecific or within-population variation in home range sizes have been relatively poorly studied (Saïd et al., 2005; Schradin et al., 2010). Movements and home ranges of beavers have been well documented in the northern parts of their range; however, little is known about home range sizes and movement characteristics of beavers in the southeastern United States (US; Wheatley, 1997; Havens, 2006; Brzyski & Schulte, 2009) .

Methods for estimating animal home range sizes have recently come under scrutiny, because different estimation methods produce various estimates of home range size for the same animal (Börger et al., 2006; Downs & Horner, 2009). Downs and Horner (2009) found that kernel density home range estimation (KDE) tends to

overestimate home range sizes, whereas minimum convex polygon (MCP) methods underestimate home ranges. Moreover, KDE methods do not accurately estimate the elongated or linearly shaped home ranges (Blundell, et al., 2001; Downs & Horner, 2008; Downs et al., 2012). Downs and Horner (2009) proposed the characteristic hull polygon (CHP) method to improve home range estimation, which can generate home range estimates with concave edges and disjoint regions and is also suitable for linear home ranges. The CHP method may be particularly useful to estimate beaver home ranges, which often contain linear landscape features (lake shorelines, rivers, creeks). Therefore, estimation of home range sizes simultaneously with different methods may be necessary for understanding intraspecific variation in beaver home range sizes.

In this study, my main objective was to test the hypotheses that beavers would: 1) move faster with smaller relative turning angles as distance from a central place increases, particularly in wetlands where beavers could move faster in water, to avoid predation risk; and 2) exhibit a bimodal distribution of movement distance from a main lodge or central place due to bimodal foraging trips. I also estimated annual home ranges, core use areas (e.g., annual 50% KDE home ranges), and seasonal distances moved from a main lodge or bank den of beavers by age classes. Dispersal of beavers is skewed to subadults (2 year olds; Allen, 1983; Collen & Gibson, 2000). Subadults may make exploratory movements to sample settlement habitat before dispersal (Havens, 2006). I also tested the hypothesis that exploratory movements before dispersal may enlarge home ranges of subadult beavers; thus, annual home ranges and distances moved from main lodges or bank dens of subadult beavers would be greater than those of adults (3 years old) and yearlings (1 year old), respectively.

4

Methods

Study Area

I conducted my research at Redstone Arsenal (RSA), a 15,342-ha Department of Defense military installment located in Madison County, Alabama (AL), USA (34° 38' N, 86° 39' W). The arsenal is bordered by the cities of Huntsville to the North and East and Madison to the West, with the Tennessee River as the southern boundary. Average monthly temperatures ranged from 8°C in December 2012 to 28°C in July 2011, with an average monthly temperature of 18°C throughout the study. Total precipitation from May 2011 to April 2012 was 125.5 cm, and monthly precipitation varied from 3.4 cm in October to 19.8 cm in January (Huntsville-Decatur International Airport weather station, the National Oceanic and Atmospheric Administration station ID: 014064; approximately 14 km from study sites). The RSA landscape was relatively flat with elevation ranging from 165 to 365 m. The landscape was composed of agricultural fields, military test ranges, upland pine forests, mixed forests, and different types and quality of beaver habitat, such as bottomland hardwood forests, various water bodies, and many seasonal swamps and marshes that became inundated with water during the rainy season.

I captured beavers from 11 wetlands located predominantly in the southern half of RSA (Fig. 1.1). The 11 wetlands varied in size, shape, and type (Table 1.1) and were initially selected due to presence of beaver activity. Visually predominant vegetation types were obtained from a cursory inspection of each of the 11 wetlands to help better describe individual wetland types. Average distance between sites was 4,942 m, with a minimum distance of 278 m and maximum distance of 9,806 m (Table 1.1).

Capture, Tagging, and Radio Telemetry

From January 21 to May 11, 2011, I live captured beavers using Hancock live traps, which weigh 15 kg and have a dimension of 71 × 91 × 10 cm (Hancock Trap Company, Custer, South Dakota, USA). I placed Hancock traps next to dams, movement corridors, and scent mounds of beavers in each of the 11 wetlands, and used commercial castor or food-based lures (Backbreaker or Woodchipper, Dobbins' Products, Goldsboro, North Carolina [NC], USA) to attract beavers and increase trapping success. I activated traps with lures daily before 1500 h and checked traps the following morning by 0900 h.

I weighed captured beavers in traps using a hanging scale (Moultrie Feeders, Alabaster, AL, USA) to the nearest 0.1 kg, and estimated individual beaver body mass using difference in weight between a trap with and without a captured beaver. I classified captured beavers into four age classes according to body mass: <6.8 kg as 0-12 month old kits; 6.8-10.8 kg as 13-24 month old yearlings; 10.9-16.0 kg as 25-36 month old subadults; and >16 kg as ≥37 month old adults (Breck et al., 2001; McNew Jr & Woolf, 2005) .

I anesthetized beavers weighing >6.8 kg with an intramuscular injection of ketamine hydrochloride (10 mg/kg) and xylazine hydrochloride (1 mg/kg) before radio tagging live beavers (Havens, 2006; Arjo et al., 2008; Bloomquist & Nielsen, 2010). I then attached radio transmitters (Model 3530, Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA), weighing < 0.05% of beaver body mass, to tails of anesthetized beavers using methods first developed by Rothmeyer et al. (2002) and modified by Arjo et al. (2008). Transmitters had an estimated battery lifetime of 647 days. I also

6

monitored body temperatures, pulses, and respiration rates of anesthetized beavers during

radio transmitter attachment.

After secure transmitter attachment, I inserted a passive integrated transponder

(PIT tag; Avid Identification Systems, Inc., Norco, California [CA], USA)

subcutaneously between scapulae with a single use disposable syringe for permanent

identification of beavers (Bond et al., 2001; Arjo et al., 2007). I collected hair samples

and tail tissue biopsy (3mm) on all captured beavers for future DNA analysis. I released

radio-tagged beavers at the location of capture once fully recovered (i.e., alert and

responsive). Sedation and handling time ranged from 30 to 60 minutes for each beaver.

Trapping and handling of beavers was approved by the Institutional Animal Care and Use

Committee of the United States Department of Agriculture National Wildlife Research

Center (Protocol #: QA-1626).

I monitored beaver movements throughout a 12-hour period (1800-0600 h) on

foot using radio telemetry methods with an ATS hand-held 3-element Yagi antenna, an

R-1000 receiver (Communications Specialist Inc., Orange, CA, USA), and a look-

through compass (Model KB-20/ 360R, Suunto, Vantaa, Finland). I modified the

compass for nighttime radio telemetry using a clear straw and 3.81-cm miniature glowing

sticks. I located radio-tagged beavers using triangulation methods by taking ≥ 3 azimuths

with an overall separation of 60-120° in ≤ 15 minutes (Cochran et al., 1963; White &

Garrott, 1990). I recorded Universal Transverse Mercator (UTM) coordinates of my

(observer) positions using a handheld Global Positioning System (GPS) unit (Model

GPSMap 76, Garmin Ltd., Olathe, Kansas, USA) with ≤ 3m accuracy. Approximately 3

degrees were subtracted from each azimuth before estimating beaver locations to account

for compass declination throughout the study period (www.ngdc.noaa.gov/ geomagmodels/struts/calcDeclination). I estimated UTM coordinates of radio-tagged beavers using program LOCATE III (Nams, 2006).

Hourly Movement Distances

I monitored hourly movements of beavers at Igloo Pond and Igloo Drain, approximately 1,030 m apart, by locating all beavers in the two wetlands hourly throughout a 12-hour period (1800 to 0600 h) via triangulation methods. I repeated hourly monitoring 12 times from May 17, 2011 to June 29, 2011 in 2 to 5-day intervals for the dry season and once on March 13, 2012 for the wet season. Dry season at my study site was from April through August, and wet season was from September through March with seasonal total precipitation of 37.95 cm and 87.60 cm, respectively. I calculated Euclidian distance (m) between two successive locations and relative turning angles (θ) using function ltraj in R package adehabitatLT (Calenge, 2006), as well as distance from the departing location of an hourly trip to main lodge (m) using function spDistsN1 in R package sp (http://rspatial.r-forge.r-project.org) and the R 2.13.1 environment (R Development Core Team, 2011). I classified a lodge as the main lodge or bank den by searching for radio-tagged beavers during the middle of daylight hours. If a beaver was located at a particular lodge or bank den location consistently, I then considered that lodge or bank den as the main lodge or den for that beaver. Using data over all beavers, I calculated average hourly distance moved, average relative turning angle, and average hourly distance from main lodge over all radio-tracked beavers by seasons, respectively. Because locations were collected hourly, distance moved between two consecutive locations were converted to hourly movement speed (m/h).

Home Range, Core Use Area, and Distance Moved from Lodge

I monitored radio-tagged beavers from May 09, 2011 to July 27, 2011 ≥ 2 times

weekly and from August 19, 2011 to April 21, 2012 biweekly. I varied wetland order

and time of night of radio tracking for each beaver across all tracking occasions to get an

unbiased temporal distribution of estimated locations over beavers' most active periods

between 1700 and 0800 h (Mott et al., 2011). However, I only considered beavers having

≥20 locations with location estimates of 95% error ellipse <0.5 ha throughout the study

period for annual home range estimation ($n = 26$ bevers).

 I estimated annual home range size (ha) for each radio-tagged beaver using the

KDE method with a least squared cross validation smoothing parameter (Worton, 1989),

the MCP method (Mohr, 1947), and the CHP method (Duckham et al., 2008; Downs &

Horner, 2009), respectively. I estimated 50% and 95% KDE, and 50% and 95% CHP

home ranges using ArcMap10 (ESRI, Redlands, CA, USA) through the Geospatial

Modelling Environment (GME version 0.7.1.0, Toronto, Ontario, Canada) and the R

2.13.1 environment. I also calculated 95% and 50% MCP home range using the function

mcp in R package adehabitat (https://r-forge.r-project.org/projects/adehabitat/). I used

50% KDE, 50% CHP, and 50% MCP home ranges as core use areas of radio-tagged

beavers. In a preliminary analysis, I found that 3 beavers at Thiokol Wetland had home

range sizes 5-8 times larger than those of remaining 23 beavers; therefore, I calculated

mean home range sizes of all 26 radio-tagged beavers and 23 beavers without Thiokol

Wetland, respectively.

I calculated mean distance and maximum distance moved from main lodge (m)

for each radio-tagged beaver by seasons using function spDistsN1 in the R package sp. I

9

then calculated seasonal mean distance and mean maximum distance to main lodge of beavers by age classes and seasons, respectively.

I also estimated water surface area of 11 wetlands by creating polygons outlining the water surface area for each wetland during the wet season from an aerial image of RSA, taken January-March 2011 (Bing Maps Aerial, ArcMap 10 Basemap) and then calculating area of the water surface polygon using ArcMap10. I used water surface area as an index of wetland size to determine relationships between wetland size and beaver home range size.

Statistical Analysis

I conducted linear regression to evaluate relationships between distance of departing location from main lodge and hourly movement speed during the dry and wet season, respectively, using linear mixed models in the SAS procedure MIXED (SAS, version 9.2, SAS Institute Inc., Cary, NC, USA). I included wetland ID as a random factor to account for interdependence of movements between beavers in the same wetland. I calculated correlation between relative turning angle and distance from lodge using circular linear correlation (Batschelet, 1981). Mean and standard deviation of relative turning angles were computed with the R package circular (https://r-forge.r-project.org/projects/circular/). I used the expectation-maximization method in the R package mixtools (Benaglia et al., 2009) to fit 3 different finite mixture models to data on distance from lodge for the dry and wet seasons, respectively, to determine if beaver movements away from the lodge fit a unimodal or bimodal movement distribution. The 3 models included a mixture of 2 normal distributions with different means and different variances, a mixture of 2 normal distributions having different means and identical

variances, and a single normal distribution. I used the Akaike information criterion (Burnham & Anderson, 2002) to select the best approximating model and competing models for each season. The best approximating model has the least AIC value, whereas a competing model has a ΔAIC less than 2 (Burnham & Anderson, 2002). The ΔAIC of a model is the difference in AIC between the model and best approximating model.

I used mixed-effects analysis of variance (ANOVA) in the SAS procedure MIXED with the Tukey-Kramer adjustment to compare mean home range sizes and mean distances moved from main lodge between age groups, respectively, with individual beaver identification number (ID) as a random factor. I used natural logarithmic transformation to normalize home range data (Di Stefano et al., 2011; Bloomquist, et al., 2012). Furthermore, I used linear regression of 95% KDE home range sizes on 95% CHP home range sizes to assess the relationship between the two estimators for beaver home ranges. I also regressed naturally logged home range sizes of beavers on wetland water surface areas using linear mixed models with wetland ID as a random factor. All tests were conducted at $\alpha = 0.05$. All means were reported ± 1 standard deviation (SD).

Results

Hourly Movements

I calculated mean hourly movement distances for 7 beavers from Igloo Pond (IPW) colony and 3 beavers from Igloo Drain (IDW) colony during the dry season of 2011 and 5 and 3 beavers for IPW and IDW, respectively, during the wet season of 2012. Mean hourly movement distances were 138.44 ± 86.37 m and 126.93 ± 119.97 m during the dry and wet seasons, respectively, for IPW; and 90.95 ± 58.29 m and 124.68 ± 91.55 m during the dry and wet seasons, respectively, for IDW. Mean hourly turning angles

were -3.06 ± 1.33 and -2.77 ± 2.30 during dry and wet seasons, respectively, for IPW; and -3.00 ± 1.47 and -2.96 ± 1.39 for dry and wet seasons, respectively, for IDW.

Hourly moving speed of beavers was not related to distance from main lodge for beavers in IPW ($R^2 = 0.02$, $F_{1, 413} = 9.54$, $P = 0.002$) or IDW ($R^2 = 0.001$, $F_{1, 406} = 0.45$, $P = 0.505$; Fig. 1.2b). Relative turning angles were not correlated with distance from lodge during 2011 dry season ($\rho = 0.11$, $P = 0.05$), but were weakly correlated with distance from lodge during the 2012 wet season ($\rho = 0.42$, $P = 0.03$; Fig. 1.2a). Likewise, relative turning angles were not related to distance from lodge on wetland land cover, with the 2011 and 2012 data combined ($\rho = 0.1$, $P = 0.36$). However, hourly moving speed was related positively to distance from lodge for the subset of beaver locations in wetland areas ($R^2 = 0.89$, $F_{1, 217} = 1694.41$, $P < 0.001$; Fig. 1.3). Model selection for distribution of hourly movement locations away from the lodge showed the best model with least AIC value to be a bimodal distribution for the 2011 dry and 2012 wet seasons. The 2011 dry season AIC values were 12020.17, 12056.91, and 12054.91 for the mixtures of 2 different normal distributions having different means and different variances, 2 normal distributions with two difference means and identical variances, and a single normal distribution, respectively; whereas, 2012 wet season AIC values were 564.88, 617.05, and 615.03 for the same models, respectively (Fig. 1.4).

Home Range, Core Use Area, and Distance Moved from Lodge

Mean annual 95% KDE home range and 50% KDE core use area were 20.89 ha and 4.55 ha, respectively, for 26 beavers (Table 1.2) but 11.86 ha and 2.20 ha, respectively, for 23 beavers when excluding 3 Thiokol Wetland beavers with unusually large home ranges. Neither mean KDE nor CHP home range sizes or core use areas

differed significantly between age classes in the analysis of 26 radio-tagged beavers ($P >$ 0.05); however, mean 95% MCP home range sizes differed between subadults and yearlings ($P = 0.01$) and between subadults and adults ($P = 0.02$). Mean 50% CHP core use area also differed between adults and yearlings ($P = 0.04$, Table 1.3). When excluding 3 beavers of Thiokol wetland from analysis, mean 95% MCP, 50% CHP, and 50% KDE home ranges of subadults were significantly larger than those of yearlings (Fig. 1.5). Additionally, mean 95% CHP home range sizes of subadults were significantly larger than those of adults in the analysis of 23 beavers. Ninety-five percent KDE home range sizes were related positively to 95% CHP home range sizes ($R^2 = 0.95$, $P < 0.001$, $n = 26$), but were not related to wetland water surface area in the analysis of either 26 ($R^2 = 0.29$, $P = 0.15$) or 23 beavers ($R^2 = 0.29$, $P = 0.18$). Although mean and maximum distances from main lodge increased successively for yearlings, adults, and subadults (Table 1.4), neither age class nor season was significant in mixed ANOVA ($P >$ 0.05).

Discussion

As a central place forager, beavers may select larger food items for energetic profits and spend less time foraging due to predation risk avoidance as they move farther away from the edge of water or a central place (Jenkins, 1980; Novak, 1987; Fryxell, 1992). Boyce (1981) suggested that beavers forage close to the shoreline to avoid predation. However, my data on hourly movements support my hypothesis that beavers move faster with increasing distance from their central place in wetlands, probably to avoid predation risk (Fig. 1.3). Radio-tagged beavers did not appear to move faster in upland areas when occupying areas that were a greater distance from lodges.

Nevertheless, the distribution of hourly distance from lodges was bimodal (Fig. 1.4), consistent with the bimodal foraging trip hypothesis for central place foragers (Weimerskirch et al., 1994).

Multiple factors may contribute to the lack of evidence supporting my hypothesis that beaver movements would be more deliberate as they moved farther from the lodge in upland areas. First, beaver mobility may be constrained on upland habitat causing their terrestrial movements to be slower compared to movements in water. Second, beavers are known to construct multiple bank dens and lodges throughout their home range (Baker & Hill, 2003). Bloomquist et al. (2012) observed 8-10 active lodges within a 50% kernel home range of beavers. Covich (1976) suggested that a multiple refuge strategy may allow burrowing herbivores access to more foraging areas with a decreased risk of predation. Beavers might have used different locations throughout the upland area of Igloo Wetland as refuges, and this condition may have had a confounding effect on expected relationships between movement speed or relative turning angle and distance from the main lodge. Finally, beavers may have few effective predators in the southeastern US (Bloomquist & Nielsen, 2010); therefore, beavers may not have to be as wary of their surroundings when moving and foraging in the southeastern US, unlike smaller, more vulnerable central place foragers. Common mammalian predators found in the southeastern US, such as bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and river otters (*Lontra canadensis*) contribute little to the predation of beavers (reviewed by Baker & Hill, 2003). Alligators (*Alligator mississippiensis*) may also feed on beavers (Hill, 1976; Novak, 1987); however, I found no alligators at wetlands where I radio tracked beavers.

14

I found support of the bimodal foraging hypothesis for beavers, with bimodal distribution of hourly distance during the breeding seasons (Fig. 1.4). Radio-tagged beavers spent more time at or near lodges to nurse and protect newborns in May-June, when birth or parturition peaks, than in March, when parturition just begins. Although I did not directly measure distribution of feeding trip time, distributions of hourly distance from lodges during feeding activity provide information on how far beavers travelled during feeding trips. Consequently, bimodal distribution of hourly distance indicates the bimodal foraging trip by beavers, assuming that it takes more time to travel a greater distance. The bimodal foraging trips may result from the tradeoff between provisioning young and self feeding by adults (Weimerskirch et al., 1994), particularly when the self feeding locations differ from provisioning feeding locations (Ydenberg & Davies, 2010). Ydenberg and Davies (2010) predicted that the bimodal foraging trips are widespread among central place foragers. Future studies are warranted to measure feeding trip time and locate feeding habitat to test the bimodal foraging hypothesis in American beavers.

My data on age-specific home range sizes provided mixed support for my hypothesis that subadult beavers would have larger home ranges than those of adults and yearlings due to subadult's propensity to explore new habitat before dispersal. Comparative results of age-specific home ranges differed between estimators and between analyses of 23 and 26 beavers, respectively. Mean home range sizes by the KDE or CHP estimator did not differ between age groups, but mean 95% MCP home ranges of subadults were greater than those of yearlings and adults in the analysis of 26 beavers (Table 1.3). Nevertheless, mean 95% MCP home range size, 50% KDE core use area, and 50% CHP core use area of subadults were greater than those of yearlings in the

15

analysis of the 23 beavers (Fig. 1.5), partially supporting my hypothesis. Smaller

yearling beavers may be tied more to a lodge or bank den for protection and parental care

than are larger subadults. Nevertheless, it is uncertain why mean home range sizes did

not differ between adults and subadults of 23 beavers. Bloomquist et al. (2012) did not

find differences in home range size between age groups in beavers of southern Illinois.

Although I was not able to sex captured beavers in the field, home range sizes of beavers

did not differ between genders in southern and central Illinois (Havens, 2006; Bloomquist

et al., 2012).

Mean 95% KDE home range sizes (11.86-20.89 ha) of beavers at my study site

were smaller than those of beavers in southern Illinois (25.5 ha; Bloomquist et al., 2012)

and central Illinois (105 ha; Havens, 2006). Increases in beaver home range sizes from

my site in Alabama to the northern sites in Illinois may be caused by decreases in primary

productivity with increasing latitude. Animals have larger home ranges in less

productive habitat (the habitat productivity hypothesis; McNab, 1963). In northern

Alabama, plant growing seasons are longer at my site (271 frost-free days per year) than

in central (181 frost-free days per year) and southern (206 frost-free days per year)

Illinois (Havens, 2006; Bloomquist et al., 2012). Therefore, greater primary productivity

at my site probably results in smaller home ranges of beavers than in central and southern

Illinois.

In summary, beavers moved faster in wetland habitat (probably in water) when

distance from their main lodge increased. The apparent lack of deliberate movements in

uplands was likely due to either existence of multiple refuges within beaver home ranges

or constrained mobility on land. Beavers appeared to make bimodal foraging trips during

breeding seasons probably due to tradeoffs between travelling farther to feed themselves and staying close to lodges to nurse and protect newborns. Additionally, mean home range sizes in this study were less than those in Illinois potentially due to decreases in primary productivity with increasing latitudes (the energy hypothesis). Therefore, foraging behavioral patterns and habitat conditions may shape the movement characteristics of American beavers

Table 1.1   Site descriptions for 11 wetlands inhabited by American beavers equipped with radio-transmitters at Redstone Arsenal in north central Alabama, USA, 2011-2012.

Wetland	Location	Water Surface Area (ha)	Wetland Classification	Visually Predominant Vegetation
Blueberry	34° 33' 52" N 86° 40' 14" W	23.32	Palustrine	*Alteranthera philoxeroides, Cephalanthus occidentalis, Nyssa sylvatica*
Corkwood Road	34° 33' 19" N 86° 39' 50" W	23.79	Palustrine	*Cephalanthus occidentalis, Lemna spp, Platanus occidentalis, Salix nigra*
Corkwood	34° 33' 27" N 86° 39' 48" W	5.68	Palustrine	*Cephalanthus occidentalis, Nyssa sylvatica, Salix nigra*
DDT Abatement	34° 37' 28" N 86° 38' 52" W	29.09	Palustrine	*Acer spp, Alteranthera philoxeroides, Sparganium spp, Typha spp*
DDT Spring Branch	34° 36' 53" N 86° 38' 35" W	35.56	Riverine	*Alteranthera philoxeroides, Ludwigia spp, Salix nigra, Typha spp*
Hudson Park Field	34° 35' 21" N 86° 36' 32" W	8.46	Riverine	*Acer spp, Alteranthera philoxeroides, Cephalanthus occidentalis, Nyssa sylvatica*
Hudson Park	34° 34' 50" N 86° 36' 58" W	17.77	Palustrine	*Alteranthera philoxeroides, Cephalanthus occidentalis, Nyssa sylvatica*
Igloo Drain	34° 34' 44" N 86° 39' 20" W	56.88	Palustrine	*Cephalanthus occidentalis, Nuphar luteum, Salix nigra*
Igloo Pond	34° 35' 06" N 86° 39' 29" W	63.74	Palustrine	*Alteranthera philoxeroides, Cephalanthus occidentalis, Salix nigra*
Patton Road	34° 38' 02" N 86° 37' 51" W	7.46	Palustrine/Riverine	*Alteranthera philoxeroides, Equisetum spp, Salix nigra*
Thiokol Pond	34° 37' 20" N 86° 35' 40" W	46.36	Palustrine	*Alteranthera philoxeroides, Ludwigia spp, Nyssa sylvatica, Quercus spp*

Table 1.2   Annual home range sizes and core use areas by age class for 26 American beavers in Madison County, Alabama, USA, May 2011- April 2012.

Age Class	Number of Beavers	Method[1]	Mean (ha)	Standard Deviation	Min[2]	Max[2]
Adult	12	MCP95	11.38	12.77	2.53	37.36
		KDE95	29.91	37.27	5.42	101.51
		CHP95	12.29	13.53	2.04	40.18
		MCP50	3.00	3.41	0.44	12.03
		KDE50	7.01	9.65	0.73	25.53
		CHP50	3.23	3.33	0.75	12.57
Subadult	9	MCP95	8.00	3.00	4.07	13.57
		KDE95	16.52	5.19	8.04	22.37
		CHP95	7.25	2.66	3.93	10.88
		MCP50	1.73	0.75	0.90	3.30
		KDE50	3.08	1.10	1.35	4.55
		CHP50	2.05	0.85	1.11	3.61
Yearling	5	MCP95	3.05	1.57	1.80	5.75
		KDE95	7.10	2.27	4.73	10.11
		CHP95	3.41	1.89	1.99	6.62
		MCP50	0.79	0.61	0.44	1.87
		KDE50	1.28	0.36	0.90	1.71
		CHP50	0.84	0.71	0.32	2.09
All Ages Combined	26	MCP95	8.61	9.22	1.80	37.36
		KDE95	20.89	26.54	4.73	101.51
		CHP95	8.84	9.79	1.99	40.18
		MCP50	2.14	2.48	0.44	12.03
		KDE50	4.55	6.87	0.73	25.53
		CHP50	2.36	2.46	0.32	12.57

[1]Home ranges were estimated by minimum convex polygon (MCP), kernel density estimation (KDE), and characteristic hull polygon (CHP) methods.
[2]Symbols "Max" and "Min" stand for maximum and minimum home range sizes, respectivcely.

Table 1.3   Comparisons of annual home range sizes (HR) and core use areas (CA) between age classes of 26 American beavers in Madison County, Alabama, USA from May 2011 to April 2012, using differences of least squared means (LSM) with Tukey-Kramer adjustment.

Estimation Method[1]	Age Class Comparison	LSM difference	Standard Error	Degrees of Freedom	t-value	Adjusted P-value
95% MCP HR	Adult-Yearling	0.082	0.098	14	0.83	0.689
	Adult-Subadult	-0.303	0.094	14	-3.24	**0.015**
	Subadult-Yearling	0.385	0.116	14	3.32	**0.013**
95% KDE HR	Adult-Yearling	0.074	0.132	14	0.56	0.843
	Adult-Subadult	-0.219	0.126	14	-1.74	0.226
	Subadult-Yearling	0.292	0.156	14	1.87	0.183
95% CHP HR	Adult-Yearling	0.086	0.120	14	0.72	0.758
	Adult-Subadult	-0.151	0.115	14	-1.31	0.411
	Subadult-Yearling	0.237	0.143	14	1.66	0.253
50% MCP CA	Adult-Yearling	0.155	0.208	14	0.75	0.741
	Adult-Subadult	-0.044	0.196	14	-0.23	0.972
	Subadult-Yearling	0.200	0.244	14	0.82	0.699
50% KDE CA	Adult-Yearling	0.160	0.223	14	0.72	0.758
	Adult-Subadult	-0.214	0.211	14	-1.02	0.579
	Subadult-Yearling	0.374	0.262	14	1.43	0.355
50% CHP CA	Adult-Yearling	0.507	0.224	14	2.26	**0.040**
	Adult-Subadult	-0.026	0.209	14	-0.12	0.992
	Subadult-Yearling	0.532	0.261	14	2.04	0.139

[1]Home ranges were estimated with minimum convex polygon (MCP), kernel density estimation (KDE), and characteristic hull polygon (CHP) methods

Table 1.4   Mean, minimum (Min), and maximum (Max) distances moved from lodge of 26 radio-tagged American beavers in Madison County, Alabama, USA, May 2011- April 2012.

Age Class	# Beavers	Season[1]	Distance from Lodge	Mean (m)	Standard Deviation	Min	Max
Adult	11	Dry	Mean	181.85	154.01	66.37	509.48
		Wet	Mean	207.61	182.49	78.55	645.95
		Dry	Maximum	451.48	224.28	184.94	854.16
		Wet	Maximum	369.70	223.25	79.51	871.46
Subadult	10	Dry	Mean	228.17	134.21	102.63	422.78
		Wet	Mean	281.78	238.41	96.83	800.28
		Dry	Maximum	534.36	187.45	259.86	828.41
		Wet	Maximum	491.96	251.95	182.33	858.56
Yearling	5	Dry	Mean	89.00	18.36	66.38	110.23
		Wet	Mean	77.72	30.48	40.57	114.75
		Dry	Maximum	252.39	129.11	138.05	469.97
		Wet	Maximum	225.47	176.32	79.05	480.05
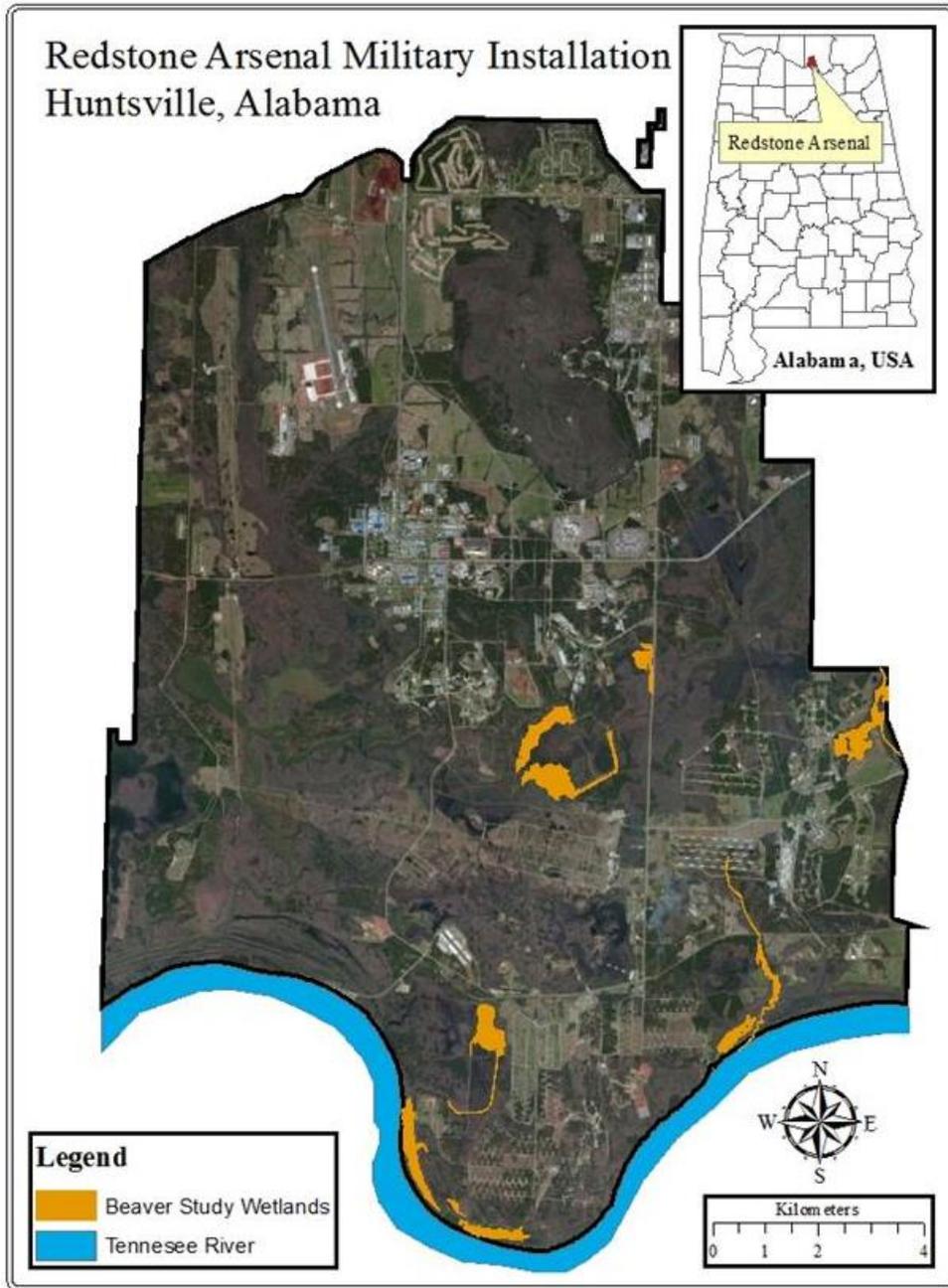
Figure 1.1   Bing Maps Aerial$^{©}$ map (ArcMap10 Basemap) of the study site and 11 study wetlands at Redstone Arsenal, Madison County, Alabama, USA.
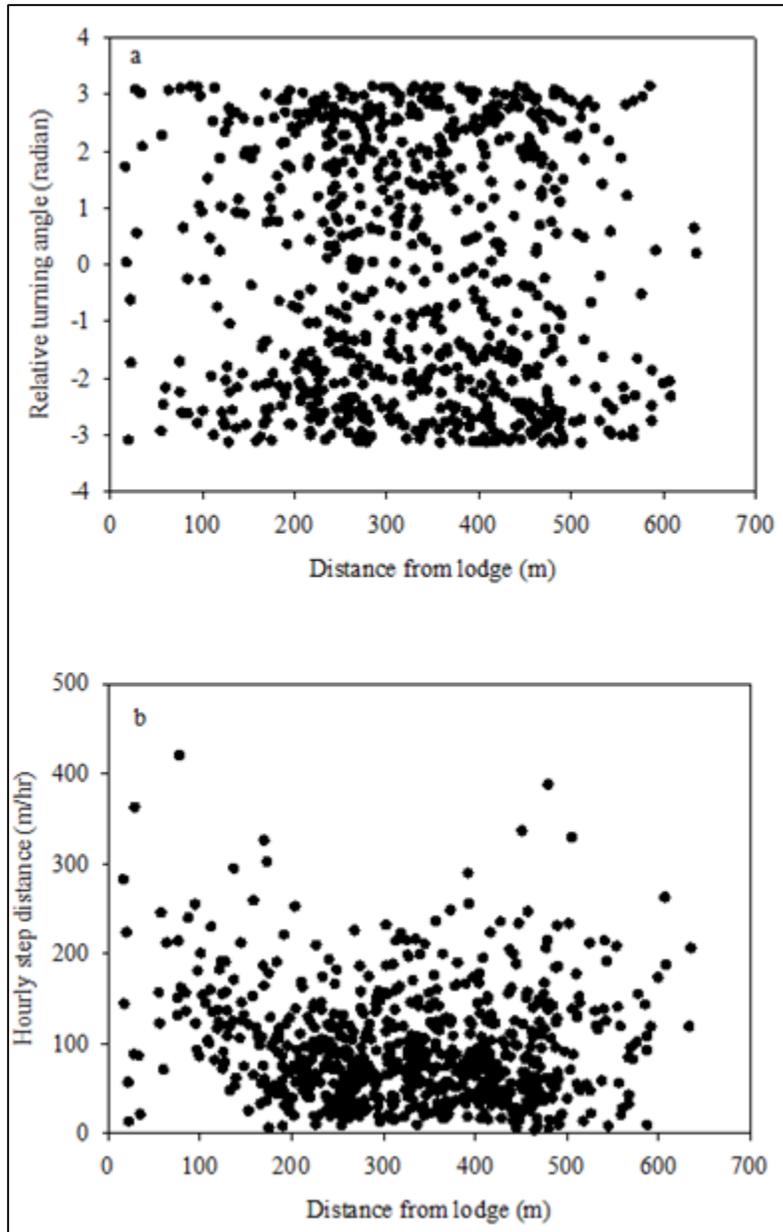
Figure 1.2   Relationship between distance from main lodge and relative turning angle
(a) and hourly step distance (b) of American beavers in upland land covers
at Igloo Wetland, Madison County, Alabama, USA, May 2011- June 2011
and March 2012.
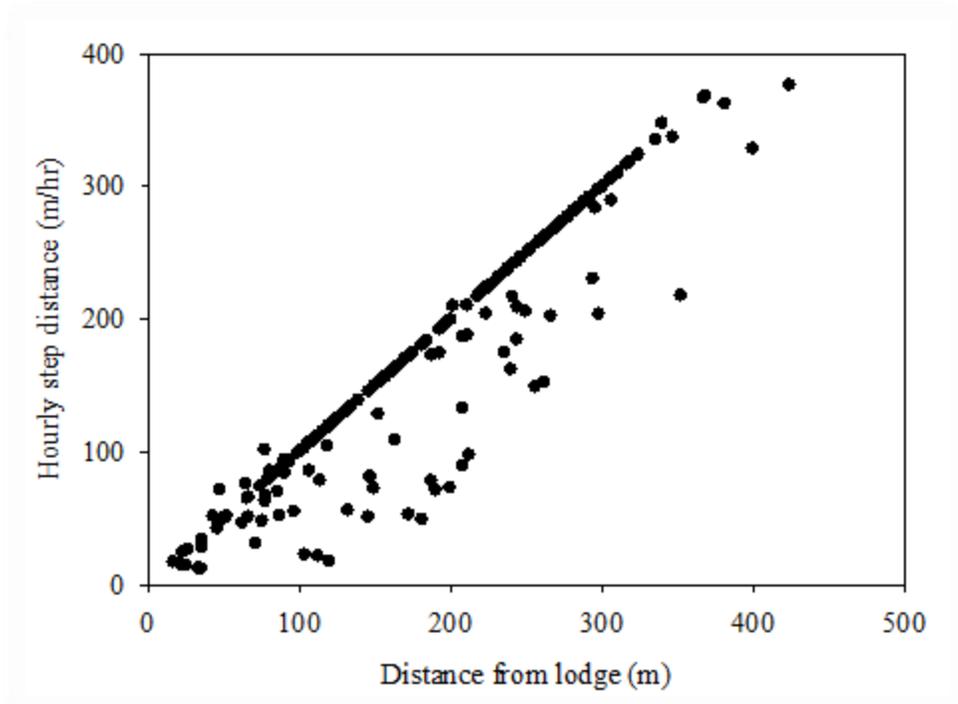
Figure 1.3   Relationship between distance from main lodge and hourly step distance of American beavers located in wetland land cover at Igloo Wetland, Madison County, Alabama, USA, May 2011- June 2011 and March 2012
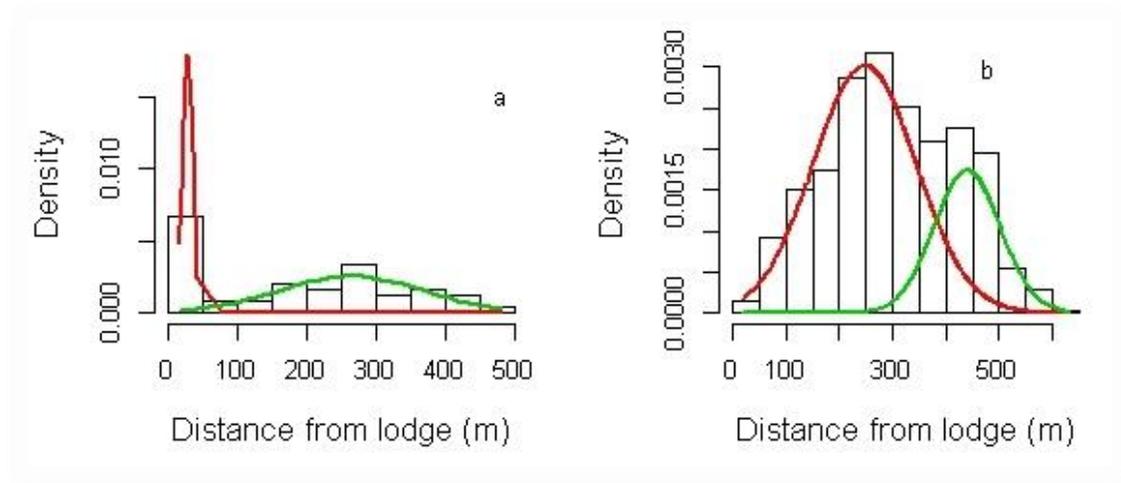
Figure 1.4   Estimated kernel densities for distributions of hourly distances from lodges of American beavers at Igloo Pond Wetland, Madison County, Alabama, USA during (a) March 2012 and (b) May-June 2011.
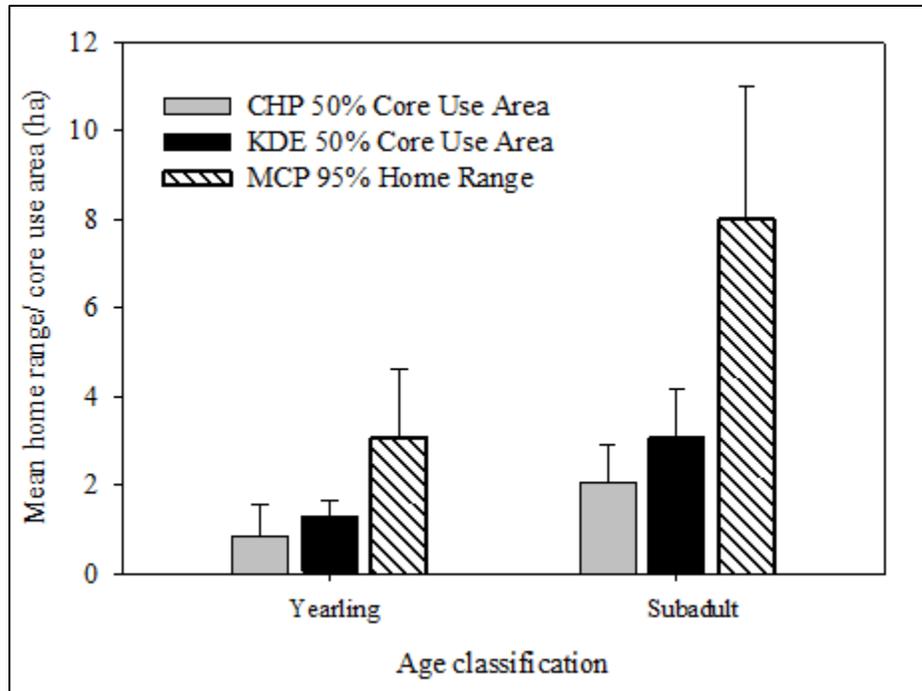
Figure 1.5   Mean annual home range sizes and core use areas (CA) of yearlings and
             subadults over 23 American beavers, Madison County, Alabama, USA,
             May 2011- April 2012.

Home ranges were estimated by characteristic hull polygon (CHP), kernel density estimation (KDE), and minimum convex polygon (MCP) methods. Vertical lines are ± 1 standard deviation.

CHAPTER II

EFFECTS OF SPATIOTEMPORAL RESOURCE HETEROGENEITY ON HOME

RANGE SIZE OF AMERICAN BEAVER (*Castor canadensis*)

Introduction

A reoccurring theme in animal ecology is the influence of resource abundance and

distribution on animal movements and space use, such as home range size (McNab, 1963;

Kie et al., 2002; Saïd et al., 2009; Owen-Smith et al., 2010). Home range is defined as

the smallest area used by an animal to conduct 95% of its life activities, including

foraging, resting, and reproduction (Burt, 1943; White & Garrott, 1990; Downs &

Horner, 2009). Estimation of home range produces a fundamental, conceptual

understanding of not only where, but also quantity of habitat used by an animal (Burt,

1943; White & Garrott, 1990; Börger et al., 2008; Downs & Horner, 2009). Therefore,

analysis of home ranges provides a foundation for studying effects of spatiotemporal

distributions of resources on animal movement ecology and demography (Johnson, 1980;

Börger et al., 2006; Stopher et al., 2012).

Multiple factors contribute to variation in home range size of animals. Early

studies of these factors focused on three relatively simple energy-related metrics: body

size, metabolic requirements, and food productivity within an animal's habitat (McNab,

1963). According to McNab (1963), increased habitat productivity (or food abundance

per unit area) would lead to a decrease in animal home range size. The habitat

productivity hypothesis has been supported in multiple species (Tufto et al., 1996; Fisher, 2000; Saïd et al., 2009); however, recent studies have suggested that spatial distribution and configuration of resources may also play an important role in shaping movement patterns and space use of animals (Dussault et al., 2005; Mueller & Fagan, 2008; Di Stefano et al., 2011).

Spatial distribution of resources has been shown to affect animal movements and home range sizes in birds and mammals (MacDonald, 1983; Johnson et al., 2002; Marable et al., 2012). The resource dispersion hypothesis predicts that as resources become more spatially dispersed throughout a landscape, movements and home range size of animals will increase (MacDonald, 1983). For instance, fragmented habitats have been shown to increase movement distances and home range sizes of eastern wild turkeys (*Meleagris gallapovo silvestris*) in the Mississippi Alluvial Valley, USA (Marable et al., 2012). Also, Loveridge et al. (2009) found that African lions (*Panthera leo*) may increase home range size partially due to increased dispersion of watering holes. When a habitat becomes fragmented, animals may move to multiple areas to acquire necessary resources for survival and reproduction; in contrast, more resources can often be found together on less fragmented habitat, reducing an animal's need to travel long distances to acquire a sufficient amount of resources.

The resource heterogeneity hypothesis expands on the habitat productivity and the resource dispersion hypothesis. The resource heterogeneity hypothesis takes into account resource composition and spatial configuration in proximity and suggests that increased heterogeneity (or diversified resources) in proximity will lead to a decrease in home range size (Di Stefano et al., 2011). For example, Tufto et al. (1996) observed that roe

27

deer (*Capreolus capreolus*) spent more time near habitat edge possibly due to multiple resources being present in one edge area. Furthermore, Di Stefano et al. (2011) found that an index of resource heterogeneity predicted home range size of swamp wallaby (*Wallabia bicolor*) better than single covariates of resource availability. Home ranges sizes of swamp wallabies decreased with increasing resource heterogeneity within a habitat (Di Stefano et al., 2011).

Though much research has evaluated effects of resource availability and resource spatial distribution on home range size in various species, few studies have empirically investigated relationships between temporal heterogeneity of resource availability, such as seasonal variation in food abundance, and home range sizes (Mueller & Fagan, 2008; van Beest et al., 2011). Additionally, central place foragers often deplete resources in parts of their home ranges due to intensive foraging at restricted distances from central places. It is uncertain how a central place forager's home range size is affected by spatiotemporal variability in resources (Buchmann et al., 2012).

American beavers are semi-aquatic central place foragers with well bounded home ranges (Baker & Hill, 2003). Beavers may respond to spatiotemporal resource heterogeneity differently from terrestrial patrolling foragers that can move throughout landscapes more freely without being tied to a particular lodge or den site (Owen-Smith et al., 2010; Buchmann et al., 2012). In this study, I further expanded the resource heterogeneity hypothesis to include a temporal dimension of resource availability. My objectives were to test 3 hypotheses concerning intraspecific variation in beaver home range sizes, investigate: 1) the habitat productivity hypothesis that home range sizes of beavers would be smaller in more productive habitats but larger in less productive

habitat; 2) the resource dispersion hypothesis that more spatially dispersed resources

would cause an increase in home range sizes of beavers; and 3) the resource

heterogeneity hypothesis that home range sizes of beavers would be smaller with more

temporal variability in resource availability throughout the year. I also predicted that

American beavers would increase home range sizes to include more woody plants

probably to offset depleting woody forage like Eurasian beavers (*Castor fiber*; Campbell

et al., 2005).

Methods

Study Area

I conducted my study at 11 wetlands inside Redstone Arsenal (RSA), a 15,342 ha

United States Department of Defense military installation located in Madison County,

Alabama (AL), USA (34° 38' N, 86° 39' W). Redstone Arsenal is bordered by the cities

of Huntsville to the North and East and Madison to the West, with the Tennessee River as

the southern boundary. The RSA landscape is relatively flat but very diverse, offering

many different types and quality of wildlife habitat, with elevation ranging from 165 to

365 m. Landscape is composed of agricultural fields, military test ranges, bottomland

hardwood forests, upland conifer forests, mixed forests, and various water bodies,

including many seasonal swamps and marshes that become inundated with water during

the rainy season. Average monthly temperatures ranged from 8°C in December 2012 to

28°C in July 2011, with an annual mean throughout my study of 18°C. Total

precipitation from May 2011 to April 2012 was 125.5 cm and monthly precipitation

varied from 3.4 cm in October to 19.8 cm in January (Huntsville-Decatur International

Airport weather station, the National Oceanic and Atmospheric Administration (NOAA) station ID: 014064; approximately 14 km from study sites).

I captured beavers from 11 wetlands located in the southern half of RSA. Distances between selected wetlands ranged from 278 to 9,806 m and averaged 4,942 m (SD = 2,420 m). All wetlands were initially selected due to presence of beaver activity and varied in size, shape, and wetland type.

Capture, Radio Tagging, and Radio Telemetry

During January to May 2011, I live captured beavers using Hancock live traps, which weigh 15 kg and have a dimension of 71 × 91 × 10 cm (Hancock Trap Company, Custer, South Dakota, USA). I placed Hancock traps next to beaver dams, scent mounds, and movement corridors in each of the 11 wetlands. Because beavers rely greatly on olfactory cues, commercial castor-based or food-based lures were placed in traps to attract beavers and increase trapping success. Traps with lures were activated daily before 1500 h and checked the following morning by 0900 h.

Captured beavers were weighed in traps using a hanging scale (Moultrie Feeders, Alabaster, Alabama, USA) to the nearest 0.1 kg. Individual beaver body mass was estimated with difference in weight between a trap with and without a captured beaver. I classified captured beavers into four age classes according to body mass: <6.8 kg as 0-12 month old kits; 6.8-10.8 kg as 13-24 month old yearlings; 10.9-16.0 kg as 25-36 month old subadults; and >16 kg as ≥37 month old adults, respectively (Breck et al., 2001; McNew Jr & Woolf, 2005). I was not able to sex captured beavers in the field.

Beavers weighing >6.8 kg were anesthetized with an intramuscular injection of ketamine hydrochloride (10 mg/kg) and xylazine hydrochloride (1 mg/kg) to aid in

handling of live beavers (Arjo et al., 2008; Bloomquist & Nielsen, 2010). While sedated, beavers were wrapped in a blanket to prevent hypothermia due to cold weather and lack of muscle activity. I attached ATS Model 3530 radio transmitters (Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA) to beavers using tail-mounting methods developed by Rothmeyer et al. (2002) and modified by Arjo et al. (2008). Transmitters weighed < 0.05% of beaver's body mass and had a mortality pulse rate of 110 pulses per minute after 8 hours of inactivity and a battery life of 647 days.

After secure transmitter attachment I inserted a passive integrated transponder (PIT) (125 kHz, Avid Identification Systems, Inc., Norco, California [CA], USA) subcutaneously between scapulae using a single use disposable syringe for permanent identification of beavers (Bond et al., 2001; Arjo et al., 2007). Hair samples and tail tissue biopsy (3mm) were collected for future DNA analysis on all captured beavers. Radio-tagged beavers were released at the location of capture once fully recovered (i.e., alert and mobile). Sedation and handling time ranged from 30 to 60 minutes for each beaver. Trapping and handling of beavers was approved by the Institutional Animal Care and Use Committee of the USDA National Wildlife Research Center (Protocol #: QA-1626).

I monitored radio-tagged beavers ≥ 2 times weekly from May 2011 to July 2011 and biweekly from August 2011 to April 2012 using radio telemetry (White & Garrott, 1990; McNew Jr & Woolf, 2005). I located radio-tagged beavers throughout a 12-hour period (1800-0600 h) with an ATS 3-element hand-held Yagi antenna, an R-1000 receiver (Communications Specialist Inc., Orange, CA, USA), and a look-through compass (Model KB-20/ 360R, Suunto, Vantaa, Finland) modified for nighttime radio

telemetry using a clear straw and 3.81-cm miniature glowing sticks. I varied wetland

order and time of night for tracking each radio-tagged beaver across all tracking

occasions to avoid biased temporal distributions of relocations during beaver's most

active periods between 1700 and 0800 h (Mott et al., 2011). I used triangulation methods

to estimate Universal Transverse Mercator (UTM) coordinates of beaver locations

(Cochran et al., 1963; White & Garrott, 1990), with the program LOCATE III (Nams,

2006). I recorded ≥ 3 azimuths per animal with an overall separation of 60-120° in ≤ 15

minutes and adjusted azimuths for approximately 3° compass declination at my study site

(www.ngdc.noaa.gov/geomagmodels/ Declination.jsp). I recorded UTM coordinates of

my (observer) positions using a handheld Global Positioning System (GPS) unit (Model

GPSMap 76, Garmin Ltd., Olathe, Kansas, USA) with an accuracy of ≤ 3 m.

Home Range Estimation

   I used fixed kernel smoothing methods with a least squared cross validation

smoothing parameter in the Geospatial Modelling Environment (GME) (http://www.

spatialecology.com/gme) of ArcMap10 (ESRI, Redlands, CA, USA) to estimate annual

95% kernel home range sizes (ha; Worton, 1989). I used a subset of ≥23 location

estimates with 95% error ellipse <0.5 ha for estimation of beaver home range sizes.

Additionally, I estimated wet and dry season core use areas (50% kernel smoothing home

ranges) with all location estimates (54 to 202 locations per animal) for individual beavers,

respectively. I then measured the distance (m) between seasonal home range centroids

for each beaver in ArcMap10 to determine if beavers shifted their seasonal core use

areas. Dry season at my study site was from April through August and wet season was

from September through March, with seasonal total precipitation of 37.95 cm and 87.60

cm, respectively. The 11 wetlands were less linear or elongated except for Corkwood

Road and Hudson Park Field; thus, kernel smoothing methods for home range estimation

were appropriate for beavers at my study site (Downs & Horner, 2008; Bloomquist et al.,

2012).

Normalized Difference Vegetation Index (NDVI) within Home Range

I used normalized difference vegetation index (NDVI) to measure vegetation

greenness as an index of plant standing biomass. Because red light is absorbed by

chlorophyll and near infrared light (NIR) is scattered by mesophyll, differences in

reflectance by land covers between the two light waves can be differentiated by satellite

sensors and used to provide information on plant productivity/greenness (Pettorelli, 2005;

Li et al., 2008). The theoretical index value ranges from -1 to 1; however, typical range

of NDVI is from 0.1 to 0.7 for a vegetated landscape and negative or zero for non-

vegetative areas (e.g., roads and water; Li et al., 2008).

I obtained cloud-free Landsat Thematic Mapper (TM) 5 imagery for my study site

acquired on 14 February 2011, 3 April 2011, 5 May 2011, 6 June 2011, 25 August 2011,

and 10 September 2011, respectively from the United States Geological Survey (USGS)

Earth Resources Observation and Science Center (EROS) remote sensing data archives

(http://glovis.usgs.gov/). I used the Landsat TM 5 red light band with a wavelength of

0.63–0.69 mm and the NIR band with a wavelength of 0.76–0.90 mm to compute NDVI

for each cell (30m × 30m) with the formula: $NDVI = (NIR – red)/(red + NIR)$ (Rouse et

al., 1974; Lauer et al., 1997) . I used the raster calculator tool from the spatial analyst

toolbox in ArcMap10 to compute NDVI of the study area for all six months. I used the

program IDRISI Taiga 15.0 (Clark Labs, Worcester, Massachusetts, USA) to calculate

mean total NDVI, mean cell-wise NDVI, and coefficient of variation (CV) in mean cell-wise NDVI within 95% fixed kernel home range over the six months for each study animal. I used CV in mean cell-wise NDVI within home ranges (hereafter, temporal CV in NDVI) to measure seasonal or temporal variability in food availability within beaver home ranges.

Land Cover Diversity

I used National Land Cover Classification Database 2006 (www.mrlc.gov/nlcd2006.php) to derive a land cover and land use map at the 30-m resolution for the study area (Fry et al., 2011). I combined the original four levels of developed class (class values 21-24) into one class, i.e., developed area. The resulting land cover types included water, developed area, deciduous forest, evergreen forest, mixed forest, shrubland, grassland, cropland, and wetland. I determined landscape diversity within beaver home ranges using the Shannon Diversity Index (*SI*) with the formula:

$$SI = \sum_{i=1}^{n=9} -p_i \ln p_i$$

(Eq. 2.1)

where p_i is the proportion of the ith land cover type (Tramer, 1969). The greater the Shannon's diversity index values, the more vegetation patches within beaver home ranges.

Statistical Analysis

I computed pair-wise Pearson's correlation *r* of total NDVI, mean NDVI, temporal CV of NDVI, Shannon's Diversity Index, and beaver body mass to test for multicolinearity between pairs of predictor variables before regression on beaver home

34

range sizes. Mean NDVI was correlated with temporal CV in NDVI (r = -0.70, P < 0.01) and thus was excluded from regression. My preliminary analysis also showed that body mass had no significant effect on home range size, so it was excluded in my subsequent analysis. Other studies have also suggested that beaver home range sizes were not related to age and body mass (Bloomquist et al., 2012). I also used natural log transformation to normalize home range sizes and to linearize relationships between raw home range and predictor variables (Di Stefano et al., 2011; Bloomquist et al., 2012).

I built eight linear models to determine relationships between log-transformed home range size and three predictor variables: total NDVI, temporal CV of NDVI, and Shannon Diversity Index, which represent the habitat productivity, resource heterogeneity, and resource dispersion hypotheses, respectively. I did not consider an interaction term because of relatively small sample size (n = 26). I conducted regression using linear mixed models with wetland identification (ID) as a random factor to account for interdependence between beavers of the same wetland, using the procedure MIXED of SAS (version 9.2, SAS Institute Inc., Cary, North Carolina, USA). I conducted model selection using an information-theoretic approach with Akaike information criterion corrected for small sample size (AICc; Burnham and Anderson 2002). The best approximating model among my candidate models had least AICc value or greatest Akaike weight (Burnham & Anderson, 2002). I also calculated ΔAICc of a model as the difference in AICc between the model and best approximating model. A model with ΔAICc < 2.0 was a competing model with the best approximating model. If a predictor was included in the best approximating model or a competing model, I concluded that the predictor significantly affected beaver home range sizes. To test if home range sizes of

beavers were related to proportion of woody plant cover, I regressed log-transformed

home range sizes on proportions of total woody plant covers (deciduous forest, evergreen

forest, mixed forest, and shrubland) within home ranges, using mixed models with

wetland ID as a random factor. In mixed model analysis, AICc values were computed

with maximum likelihood methods for model comparisons, whereas model coefficients

and their P-values were estimated by restricted maximum likelihood methods.

Due to unusually large home range size of 3 beavers at Thiokol Pond Wetland (5-

8 times larger than mean annual home range size of the remaining 23 beavers), I

conducted separate regressions for 23 and 26 beavers, respectively. Means of home

range sizes were reported with ± 1 standard deviation (SD). All statistical analyses were

conducted at $\alpha = 0.05$.

Results

I radio tracked 26 beavers for 12 months and obtained 1,717 locations (66 ± 46

locations per beaver). Mean 95% kernel home range size was 20.89 ± 26.54 ha for 26

beavers but 11.86 ± 5.66 ha for 23 beavers, excluding 3 beavers at Thiokol Pond. Mean

seasonal shift in core area was approximately 63.18 ± 55.1 m for the 23 beavers and

414.38 ± 68.79 m for the 3 beavers at Thiokol Pond.

With all 26 radio-tagged beavers, the best model with least AICc included total

NDVI and temporal CV in NDVI. However, there were 3 other competing models within

2.0 ΔAICc for 26 beavers (Table 2.1). Home range sizes were related positively to total

NDVI ($F_{1,\,14} = 64.5$, $P < 0.001$), but were related inversely to temporal CV in NDVI ($F_{1,\,14} = 4.08$, $P = 0.063$). The best model for 23 radio-tagged beavers included total NDVI

and Shannon's diversity index. There were no competing models for the 23 beavers

(Table 2.2). Home range sizes increased with increasing total NDVI within home ranges ($F_{1, 13} = 562.45$, $P < 0.001$; Fig. 2.1a) and Shannon's diversity index of land covers ($F_{1, 13} = 11.66$, $P = 0.005$; Fig. 2.1b). Mean percent coverage of woody plants was 36.43% ± 10.06% within home ranges. Sizes of home ranges were related positively to proportion of woody plant cover within home range ($F_{1, 14} = 7.8$, $P = 0.02$, $n = 23$; Fig. 2.2). Mean NDVI and total NDVI within beaver home ranges were related positively ($r = 0.49$, $P = 0.016$).

Discussion

My results supported the habitat productivity hypothesis (Tables 2.1 and 2.2). Beavers enlarged their home ranges to access greater total primary production available within home ranges (Fig. 2.1a). Annual home range sizes of 23 beavers averaged 11.86 ha, about half of that of beavers in southern Illinois which exhibited home range sizes of 25.5 ha (Bloomquist et al., 2012). The habitat productivity hypothesis predicts that beavers in the northern part of the species range have larger home ranges than those in the southern portions of the range, because primary productivity decreases with increasing latitudes. However, the 3 beavers in Thiokol Pond had home ranges 3 to 4 times greater than mean annual home range of beavers in southern Illinois and 5 to 8 times greater than mean annual home range of the 23 beavers in this study. Mean distance between seasonal core area centroids of 3 beavers at Thiokol Pond was 6.56 times greater than that of the remaining 23 beavers. Therefore, the 3 beavers likely dispersed seasonally. Data on 23 and 26 beavers also supported the resource dispersion hypothesis, with Shannon's diversity index of land covers as a significant covariate (Tables 2.1, 2.2; Fig. 2.2). The best and competing models for 26 beavers supported the

resource heterogeneity hypothesis; however, model selection results for the 23 beavers did not support the resource heterogeneity hypothesis (Table 2.2).

Habitat Productivity Hypothesis

Beavers moved more probably to acquire more resources as predicted by the habitat productivity hypothesis (Fig. 2.1a). Although the habitat productivity hypothesis also predicts an inverse relationship between home range size and mean NDVI, mean NDVI and total NDVI within beaver home ranges were not related inversely. Schradin et al. (2010) observed that although larger home ranges of female striped mice (*Rhabdomys pumilio*) had a greater abundance of annual and perennial food plants, quality of food plants per hectare was less. Furthermore, home range sizes increased with increasing proportion of woody plant cover within home ranges (Fig. 2.2). American beavers likely increased home range size to include more available forage (e.g., woody plants) to meet energetic requirements, like Eurasian beavers (Campbell et al., 2005).

Resource Dispersion Hypothesis

Shannon diversity index of land cover used in my study represents diversity of land cover at a landscape scale, not plant diversity per unit area. More diverse vegetation types within home ranges suggested increased habitat fragmentation, which may make beavers move more between patches to gain sufficient resources, increasing home range sizes (Fig. 2.1b). The positive relationship between home range size and resource dispersion predicted by the resource dispersion hypothesis has been supported in mammalian carnivores (review by Di Stefano et al., 2011). My results suggest that

resource dispersion may also play an important role in determining home range sizes of mammalian herbivores.

Resource Heterogeneity Hypothesis

Model selection results provided mixed support to the resource heterogeneity hypothesis. Temporal CV in NDVI was included in the best model and a competing model for 26 beavers (Table 2.1). Home range sizes became smaller as temporal CV in NDVI increased, with 3 seasonally dispersing beavers included. However, home range sizes of 23 beavers with well bounded home ranges were not related to temporal CV in NDVI (Table 2.2). The discrepancy was possibly due to relatively small sample sizes of my study ($n = 23$ and 26).

Temporal pulses in quality of food resources can increase body mass in herbivores (Searle et al., 2010). Altering resource use in space and time within a home range to correspond to pulses or temporal variation in vegetation may be an effective way to increase nutritional benefits (Willems et al., 2009; Searle et al., 2010). A seasonal core use area shift of about 60 m may be explained by alterations in resource use. Roberts and Arner (1984) observed a shift in vegetative consumption from the bark of trees in fall and winter to herbaceous vegetation in spring by beavers in Mississippi. Temporal variation in plant production and seasonal shifts in food habits potentially allows beavers to utilize different food resources and smaller home ranges.

In summary, beavers occupy a home range for multiple years and intensively exploit food patches near lodges as a central place forager (Baker & Hill, 2003). Additionally, recovery or renewal of woody plants damaged by beaver foraging can be a slow process (Baker, 2003). Therefore, altering utilization of food resources in space and

time within home ranges may be essential to increasing nutritional benefits and avoiding

over exploitation of resources in central place foragers such as beavers (Campbell et al.,

2005).

Table 2.1 Model selection of eight candidate models for 26 radio-tracked beavers in northern Alabama, USA, 2011-2012

Models	AIC_c	ΔAIC_c	Akaike weight
Total NDVI + Temporal CV	0.7	0.0	0.410
Total NDVI	1.8	1.1	0.237
Total NDVI + Temporal CV + Shannon's Index	2.2	1.5	0.194
Total NDVI + Shannon's Index	2.6	1.9	0.159
Temporal CV	32.0	31.3	0.000
Temporal CV + Shannon's Index	33.8	33.1	0.000
Null	39.5	38.8	0.000
Shannon's Index	40.2	39.5	0.000

Total NDVI, Shannon's Index, and Temporal CV represent total normalized difference vegetation index within home range, Shannon's diversity index of land covers, and coefficient of variation in mean NDVI over a 7-month period, respectively.

41

Table 2.2   Model selection of eight candidate models for 23 radio-tracked beavers excluding seasonally dispersing beavers in northern Alabama, USA, 2011-2012

Models	AIC$_c$	Δ AIC$_c$	Akaike weight
Total NDVI + Shannon's Index	-50.3	0.0	0.642
Total NDVI + Temporal CV + Shannon's Index	-48.0	2.3	0.203
Total NDVI	-47.1	3.2	0.130
Total NDVI + Temporal CV	-43.8	6.5	0.025
Temporal CV	18.9	69.2	0.000
Temporal CV + Shannon's Index	19.1	69.4	0.000
Shannon's Index	22.9	73.2	0.000
Null	23.9	74.2	0.000

42

Total NDVI, Shannon's Index, and Temporal CV represent total normalized difference vegetation index within home range, Shannon's diversity index of land covers, and coefficient of variation in mean NDVI over a 7-month period, respectively.
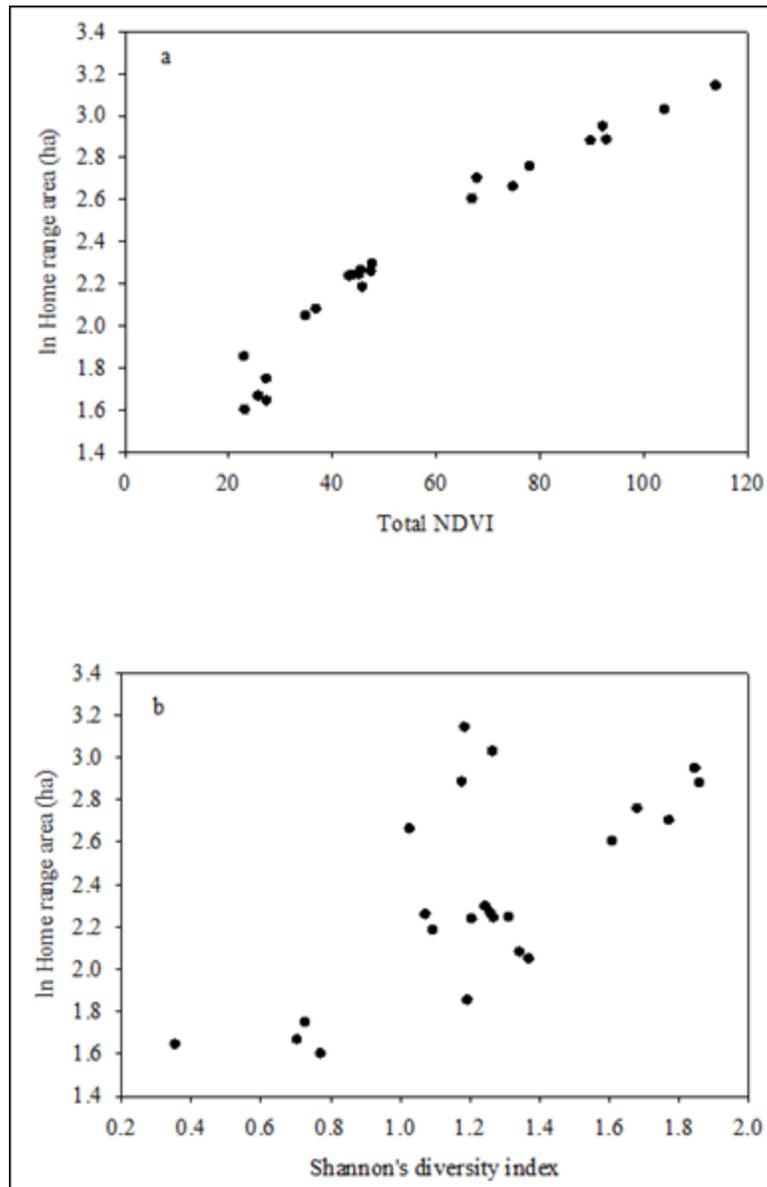
Figure 2.1   Relationships between home range sizes and (a) total within-home-range normalized difference in vegetation (NDVI) and (b) between home range sizes and Shannon's diversity index of land covers within home ranges of 23 American beavers, northern Alabama, USA, 2011-2012
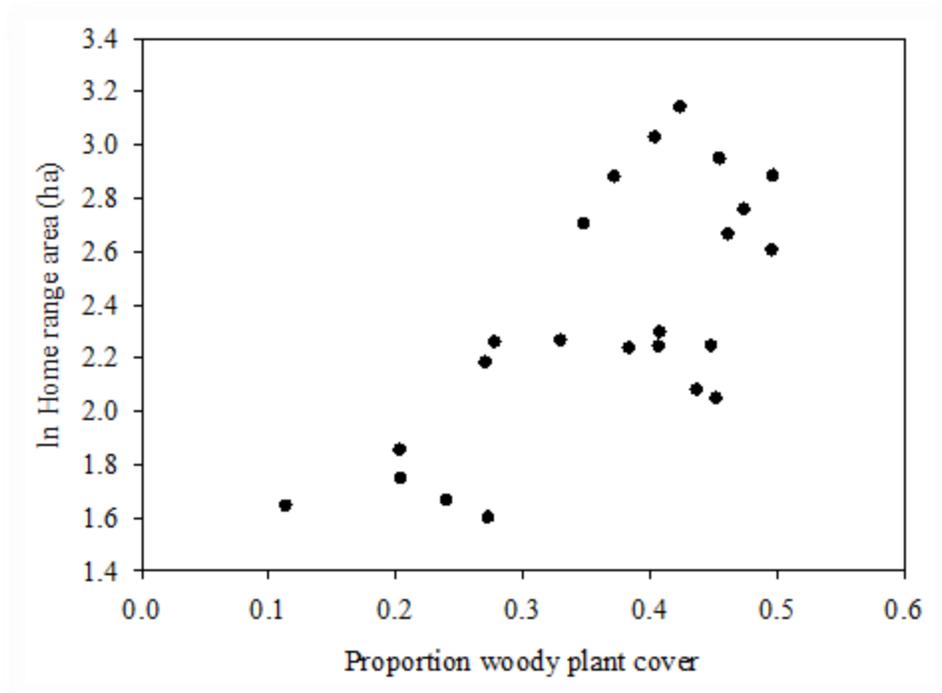
Figure 2.2   Relationship between home range sizes and proportions of wood plant cover within home ranges of 23 American beavers in northern Alabama, USA, 2011-2012.

CHAPTER III

SYNTHESIS

Movements are defined by distance and time spent for various life activities such as travelling, searching, foraging for resources (e.g., food, water, shelter; Owen-Smith et al., 2010), and evading predators (Covich, 1976). Movements made by an animal throughout space and time are also fundamental aspects of home range composition (Burt, 1943). Consequently, animal movements and home ranges are important elements in understanding the ecology of animal populations (Mueller & Fagan, 2008; Owen-Smith et al., 2010).

Two specific types of animal movements often studied in ecology are migration and dispersal. Migration is typically a seasonally reoccurring, long-distance movement between separate ranges in response to seasonal variation in resource availability (Mueller & Fagan, 2008), whereas dispersal is a one way movement away from a birth site (natal dispersal) or breeding site (breeding dispersal; Greenwood, 1980). Additionally, there are 3 general patterns of foraging movements: patrolling foraging, central place foraging, and nomadic foraging; and each of these three foragers responds to spatio-temporal dynamics of resources differently (Mueller & Fagan, 2008; Buchmann et al., 2012). Thus, it is important to incorporate foraging patterns into studies of effects of resource availability on animal movements and home ranges.

Central place foraging is characterized by foraging trips that are attached or linked to a central place (e.g., lodge, nest, den) for food consumption. Central place foraging consists of a series of round trips between food patches and a central place (Covich, 1976; Andersson, 1978; Getty, 1981). Optimal foraging theory predicts that central place foragers should adjust their searching and foraging behavior to minimize time and energetic costs of foraging and to maximize energy gain from foraging (Covich, 1976; Andersson, 1978; Fryxell, 1992). Central place foragers may use two approaches to achieving optimal foraging: 1) foraging close to a central place; and (2) becoming more selective of the size or load of food items as distance from the central place increases (Fryxell, 1992). Additionally, predation avoidance is an important factor influencing space use and movement of central place foragers (Covich, 1976; Getty, 1981). Though the specific number of central place foraging species has not been quantified, to my knowledge, there are numerous taxa that use specific "central place" locations such as, nest sites in various birds (Kacelnik, 1984; Weimerskirch et al., 1997; Ropert-Coudert et al., 2004) and den/lodge sites in various mammals (Covich, 1976; Getty, 1981; Fryxell, 1992). Therefore, by studying ecological principles underlying effects of resource heterogeneity on home ranges and movement characteristics for a single central place foraging species, one may be able to obtain a better understanding of central place foraging on a much broader scale.

The American beaver (*Castor canadensis*; hereafter beaver) is a semi-aquatic central place forager that uses bank dens or lodges for protection and rearing of young (Collen & Gibson, 2000). Beaver home range or habitat often includes uplands and wetlands (Jenkins, 1980; Raffel et al., 2009; Milligan & Humphries, 2010). Water bodies

46

within home ranges provide beavers with food and probably protection from terrestrial predators (Raffel et al., 2009). This amphibious habitat requirement makes beaver unique for studies of habitat selection and spacing behavior in the interface of aquatic and terrestrial habitat. As central place foragers, beavers leave their dens or lodges to acquire food, but then return to the central place to rest, consume food, or protect themselves from predators (Jenkins, 1980; Fryxell, 1992). Round trips for foraging from a central place to various food patches throughout a habitat are the building blocks for beaver home ranges. Therefore, beavers can serve as a model species for studies of effects of variation in resource availability in space and time on the spacing behavior of central place foragers, mediated through optimal foraging. However, little is known about beaver movements and ecology in the southeastern US.

The first objective of this study was to quantify movement characteristics and home range size of beavers in the southeastern United States and determine if there is a difference in movement characteristics between age classes. I tested the hypothesis that beavers would display hourly movement characteristics more favorable to central place foraging, such as faster movements and smaller turning angles, as they proceeded farther from the central place to avoid predation risks. The second objective was to determine effects of spatiotemporal resource heterogeneity on home range size of beavers, by testing the habitat productivity, the resource dispersion, and the resource heterogeneity hypotheses.

Movement Characteristics under Central Place Foraging

I found some evidence supporting my hypothesis that beavers would move faster as distance from the central place increased; however, I did not find support for smaller

turning angles. Beaver movements in wetlands were related positively to distance moved from main lodge, but beaver movements in upland and terrestrial land covers were not related to distance from main lodge. Support for my hypothesis of beaver movements in wetlands may be attributed to beavers being able to move faster and more fluently in wetland habitat because they can move faster swimming in water than walking on land. Consequently, the lack of support for my hypothesis of beaver movements in upland and terrestrial habitats may be attributed to multiple factors, including limited effective predators within the study area, multiple den sites closer to foraging areas, constrained mobility on upland habitat, and hourly temporal scale for data collection being too large for fine scale movement analysis. To better test this hypothesis, future studies should incorporate a finer temporal resolution to account for multiple movements back to the lodge or den site along with surveying the beavers' wetlands to determine various bank dens or lodges that may be used by beavers closer to a foraging area.

I also observed a bimodal movement distribution by beavers during the breeding season. According to Weimerskirch et al. (1994), bimodal foraging trips by central place foragers may result from a tradeoff between feeding and caring for young and self feeding by adults. Feeding, nursing, and protection of young come at a cost to the adult; however, by alternating time spent close to the central place with longer foraging trips away from the central place, adults are able to feed and reenergize before heading back to the central place. Therefore, the bimodal movement distribution that I observed may likely be due to mature beavers staying close to the lodge or bank den to protect and care for newborns, then leaving to feed themselves while other mature beavers take over watching after the young. Future studies of the duration and frequency of foraging trips,

spatial distributions of food resources, and reproductive condition of beavers are needed for better understanding of foraging movement by American beavers.

Effect of Resources on Home Range Size of Central Place Foraging Beavers

I conducted two separate analyses for 23 beavers and 26 beavers to account for 3 seasonal dispersers with unusually large home ranges. I found support for the habitat productivity hypothesis as beaver home range sizes were related positively to total normalized difference vegetation index (NDVI) and proportion of woody plant cover within home ranges. Subsequently, the 23-beaver analysis also supported the resource dispersion hypothesis with home range sizes being related positively to the diversity of land cover within home ranges. This is because increased habitat fragmentation increases a beaver's need to move more between patches to gain access to sufficient resources, in turn enlarging home range size (MacDonald, 1983). Finally, I found support for the resource heterogeneity hypothesis when considering all 26 beavers, with home range sizes being related inversely to seasonal variation in plant productivity within home ranges.

In summary, relatively fine-scale movement patterns (e.g., hourly movements) of American beavers were characterized by bimodal foraging distances and increases in moving speed with increasing distance from lodges in wetlands, as predicted by central place foraging models. Additionally, American beavers enlarged home ranges to increase their access to more woody plant cover within home ranges. As a central place forager, American beavers intensively exploit woody plants at a close distance from the lodge and deplete food resources over years (Fryxell, 1992). Thus, increases in woody plant cover probably would allow beavers to offset the lesser availability of food plants

caused by intensive herbivory. Therefore, central place foraging plays important roles in shaping the movement and home ranges of American beavers.

Management Implications

My study provides wildlife managers and biologists with information on what affects home range sizes and movements of beavers on lands that are currently being or have previously been managed for beavers in the southeastern United States. Through my research I was able to show that beavers increase their home range size in more patchy environments and also to incorporate more productive vegetative habitat and woody plants, the preferred food source for beavers. Additionally, I observed that beavers may offset depletion of resources around their central place by foraging in different areas of their home range during different seasons. Due to their habitat engineering capabilities as well as their dispersal tendencies, management of beavers can be challenging (Singleton & Taylor, 2010). However, from my findings I would suggest reducing habitat fragmentation within and around beaver wetlands to reduce beavers' needs to move greater distances to acquire necessary resources in patchy environments, while also controlling the beaver population through direct removal of individuals.

LITERATURE CITED

Allen, A. W. (1983) Habitat suitability index models: Beaver. 20pp. US Fish and Wildlife Service, Washington, DC.

Andersson, M. (1978) Optimal foraging area: Size and allocation of search effort. *Theoretical Population Biology,* **13,** 397–409.

Arjo, W. M., R. E. Huenefeld & D. L. Nolte (2007) Mountain beaver home ranges, habitat use, and population dynamics in Washington. *Canadian Journal of Zoology,* **85,** 328–337.

Arjo, W. M., R. E. Joos, C. O. Kochanny, J. L. Harper, D. L. Nolte & D. L. Bergman (2008) Assessment of transmitter models to monitor beaver *Castor canadensis* and *C. fiber* populations. *Wildlife Biology,* **14,** 309–317.

Baker, B. W. (2003) Beaver (*Castor canadensis*) in heavily browsed environments. *Lutra,* **46,** 173–181.

Baker, B. W. & E. P. Hill (2003) Beaver (*Castor canadensis*). In: *Wild mammals of North America: Biology, management, and conservation.* : 288–310. G. A. Feldhamer, B. C. Thompson & J. A. Chapman (Eds.). The Johns Hopkins University Press, Baltimore, MD, USA.

Batschelet, E. (1981) *Circular statistics in biology*. New York, NY: Academic Press.

Benaglia, T., D. Chauveau, D. R. Hunter & D. S. Young (2009) Mixtools: An r package for analyzing finite mixture models. *Journal of Statistical Software,* **32,** 1–29.

Bloomquist, C. K. & C. K. Nielsen (2010) Demography of unexploited beavers in southern Illinois. *Journal of Wildlife Management,* **74,** 228–235.

Bloomquist, C. K., C. K. Nielsen & J. J. Shew (2012) Spatial organization of unexploited beavers (*Castor canadensis*) in southern Illinois. *American Midland Naturalist,* **167,** 188–197.

Blundell, G. M., J. A. K. Maier & E. M. Debevec (2001) Linear home ranges: Effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs,* **71,** 469–489.

Bond, B. T., B. D. Leopold, L. W. Burger Jr & K. D. Godwin (2001) Movements and home range dynamics of cottontail rabbits in Mississippi. *Journal of Wildlife Management,* **65,** 1004–1013.

Börger, L., B. D. Dalziel & J. M. Fryxell (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters,* **11,** 637–650.

Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari & T. Coulson (2006) Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology,* **75,** 1393–1405.

Boyce, M. S. (1981) Habitat ecology of an unexploited population of beavers in interior Alaska. In: *Proceedings of the worldwide furbearer conference*: 155–186. J. A. Chapman & D. Pursley (Eds.). Frostburg, MD.

Breck, S. W., K. R. Wilson & D. C. Andersen (2001) The demographic response of bank-dwelling beavers to flow regulation: A comparison on the Green and Yampa rivers. *Canadian Journal of Zoology,* **79,** 1957–1964.

Brzyski, J. R. & B. A. Schulte (2009) Beaver (*Castor canadensis*) impacts on herbaceous and woody vegetation in southeastern Georgia. *American Midland Naturalist,* **162,** 74–86.

Buchmann, C. M., F. M. Schurr, R. Nathan & F. Jeltsch (2012) Movement upscaled – the importance of individual foraging movement for community response to habitat loss. *Ecography,* **35,** 436–445.

Burnham, K. P. & D. R. Anderson (2002) *Model selection and multi-model inference: A practical information-theoretic approach* 2nd edn. New York: Springer.

Burt, W. H. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy,* **24,** 346–352.

Calenge, C. (2006) The package "adehabitat" for the r software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling,* **197,** 516–519.

Campbell, R. D., F. Rosell, B. A. Nolet & V. A. A. Dijkstra (2005) Territory and group sizes in Eurasian beavers (*Castor fiber*): Echoes of settlement and reproduction? *Behavioral Ecology and Sociobiology,* **58,** 597–607.

Cochran, W. W., R. D. J. Lord & R. D. Lord, Jr. (1963) A radio-tracking system for wild animals. *Journal of Wildlife Management,* **27,** 9–24.

Collen, P. & R. J. Gibson (2000) The general ecology of beavers (*Castor spp.*), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish - a review. *Reviews in Fish Biology & Fisheries,* **10,** 439–461.

Covich, A. P. (1976) Analyzing shapes of foraging areas: Some ecological and economic theories. *Annual Review of Ecology and Systematics,* **7,** 235–257.

Di Stefano, J., G. Coulson, A. Greenfield & M. Swan (2011) Resource heterogeneity influences home range area in the swamp wallaby *Wallabia bicolor*. *Ecography,* **34,** 469–479.

Downs, J. A., J. H. Heller, R. Loraamm, D. O. Stein, C. McDaniel & D. Onorato (2012) Accuracy of home range estimators for homogeneous and inhomogeneous point patterns. *Ecological Modelling,* **225,** 66–73.

Downs, J. A. & M. W. Horner (2008) Effects of point pattern shape on home-range estimates. *Journal of Wildlife Management,* **72,** 1813–1818.

Downs, J. A. & M. W. Horner (2009) A characteristic-hull based method for home range estimation. *Transactions in GIS,* **13,** 527–537.

Duckham, M., L. Kulik, M. Worboys & A. Galton (2008) Efficient generation of simple polygons for characterizing the shape of a set of points in the plane. *Pattern Recognition,* **41,** 3224–3236.

Dussault, C., R. Courtois, J. P. Ouellet & I. Girard (2005) Space use of moose in relation to food availability. *Canadian Journal of Zoology,* **83,** 1431–1437.

Fisher, D. O. (2000) Effects of vegetation structure, food and shelter on the home range and habitat use of an endangered wallaby. *Journal of Applied Ecology,* **37,** 660–671.

Franke, A., T. Caelli & R. J. Hudson (2004) Analysis of movements and behavior of caribou (*Rangifer tarandus*) using hidden markov models. *Ecological Modelling,* **173,** 259–270.

Fry, J. A., G. Xian, J. Suming, J. A. Dewitz, C. G. Homer, Y. Limin, C. A. Barnes, N. D. Herold & J. D. Wickham (2011) Completion of the 2006 national land cover database for the conterminous United States. *Photogrammetric Engineering & Remote Sensing,* **77,** 858–864.

Fryxell, J. M. (1992) Space use by beavers in relation to resource abundance. *Oikos,* **64,** 474–478.

Getty, T. (1981) Analysis of central-place space-use patterns: The elastic disc revisited. *Ecology,* **62,** 907–914.

Getz, W. M. & D. Saltz (2008) A framework for generating and analyzing movement paths on ecological landscapes. *Proceedings of the National Academy of Sciences of the United States of America,* **105,** 19066–19071.

Greenwood, P. J. (1980) Mating systems, philopatry, and dispersal in birds and mammals. *Animal Behaviour,* **28,** 1140–1162.

Havens, R. P. (2006) Beaver home ranges and movement patterns on the Embarras River watershed in east central Illinois. 133. Eastern Illinois University, Charleston, IL.

Hill, E. P. (1976) Control methods for nuisance beaver in the southeastern United States. In: *Vertebrate Pest Conference*: 85–98.

Jenkins, S. H. (1980) A size-distance relation in food selection by beavers. *Ecology,* **61,** 740–746.

Johnson, D. D. P., R. Kays, P. G. Blackwell & D. W. Macdonald (2002) Does the resource dispersion hypothesis explain group living? *Trends in Ecology & Evolution,* **17,** 563–570.

Johnson, D. H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology,* **61,** 65–71.

Kacelnik, A. (1984) Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence time. *Journal of Animal Ecology,* **53,** 283–299.

Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski & E. R. Loft (2002) Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. *Ecology,* **83,** 530–544.

Lauer, D. T., S. A. Morain & V. V. Salomonson (1997) The landsat program: Its origins, evolution, and impacts. *Photogrammetric Engineering and Remote Sensing,* **63,** 831–838.

Li, S. C., Z. Q. Zhao & F. Y. Liu (2008) Identifying spatial pattern of ndvi series dynamics using recurrence quantification analysis. *European Physical Journal: Special Topics,* **164,** 127–139.

Loveridge, A. J., M. Valeix, Z. Davidson, F. Murindagomo, H. Fritz & D. W. Macdonald (2009) Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography,* **32,** 953–962.

MacDonald, D. W. (1983) The ecology of carnivore social behaviour. *Nature,* **301,** 379–384.

Marable, M. K., J. L. Belant, D. Godwin & G. Wang (2012) Effects of resource dispersion and site familiarity on movements of translocated wild turkeys on fragmented landscapes. *Behavioural Processes,* **91,** 119–124.

McNab, B. K. (1963) Bioenergetics and determination of home range size. *American Naturalist,* **97,** 133–140.

McNew Jr, L. B. & A. Woolf (2005) Dispersal and survival of juvenile beavers (*Castor canadensis*) in southern Illinois. *American Midland Naturalist,* **154,** 217–228.

Milligan, H. E. & M. M. Humphries (2010) The importance of aquatic vegetation in beaver diets and the seasonal and habitat specificity of aquatic terrestrial ecosystem linkages in a subarctic environment. *Oikos,* **119,** 1877–1886.

Mohr, C. O. (1947) Table of equivalent population of North American small mammals. *American Midland Naturalist,* **37,** 223–249.

Mott, C. L., C. K. Bloomquist & C. K. Nielsen (2011) Seasonal, diel, and ontogenetic patterns of within-den behavior in beavers (*Castor canadensis*). *Mammalian Biology,* **76,** 436–444.

Mueller, T. & W. F. Fagan (2008) Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos,* **117,** 654–664.

Nams, V. O. (2006) Locate iii user's guide. Pacer Computer Software, Tatamagouche, Nova Scotia, Canada.

Nathan, R. (2008) An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences of the United States of America,* **105,** 19050–19051.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz & P. E. Smouse (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America,* **105,** 19052–19059.

Novak, M. (1987) Beaver. In: *Wild furbearer management and conservation in North America*: 283–312. M. Novak, J. A. Baker, M. E. Obbard & B. Malloch (Eds.). Ashton-Potter Limited, Concord, Ontario, Canada.

Orians, G. H. & N. E. Pearson (1979) *On the theory of central place foraging*. Columbus, Ohio, USA: Ohio State University Press.

Owen-Smith, N., J. M. Fryxell & E. H. Merrill (2010) Foraging theory upscaled: The behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society of London B Biological Sciences,* **365,** 2267–2278.

Pettorelli, N. (2005) Using the satellite-derived ndvi to assess ecological responses to environmental change. *Trends in Ecology & Evolution,* **20,** 503–510.

Pulido, F. (2007) The genetics and evolution of avian migration. *BioScience,* **57,** 165–174.

R Development Core Team (2011) R: A language and environment for statistical computing. *R Foundation for Statistical Computing*.

Raffel, T. R., N. Smith, C. Cortright & A. J. Gatz (2009) Central place foraging by beavers (*Castor canadensis*) in a complex lake habitat. *American Midland Naturalist,* **162,** 62–73.

Roberts, T. H. & D. H. Arner (1984) Food habits of beaver in east-central Mississippi. *Journal of Wildlife Management,* **48,** 1414–1419.

Ropert-Coudert, Y., R. P. Wilson, F. Daunt & A. Kato (2004) Patterns of energy acquisition by a central place forager: Benefits of alternating short and long foraging trips. *Behavioral Ecology,* **15,** 824–830.

Rothmeyer, S. W., M. C. McKinstry & S. H. Anderson (2002) Tail attachment of modified ear-tag radio transmitters on beavers. *Wildlife Society Bulletin,* **30,** 425–429.

Rouse, J. W. J., R. H. Hass, D. W. Deering, J. A. Schell & J. C. Harlan (1974) Monitoring the vernal advancement and retrogradation (green wave effect) of natural vegetation. The National Aeronautics and Space Administration Greenbelt, Maryland, USA.

Saïd, S., J. M. Gaillard, O. Widmer, F. Débias, G. Bourgoin, D. Delorme & C. Roux (2009) What shapes intra-specific variation in home range size? A case study of female roe deer. *Oikos,* **118,** 1299–1306.

Saïd, S., J. M. Gaillard, P. Duncan, N. Guillon, S. Servanty, M. Pellerin, K. Lefeuvre, C. Martin & G. Laere (2005) Ecological correlates of home-range size in spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. *Journal of Zoology,* **267,** 301–308.

Schradin, C., G. Schmohl, H. G. Rödel, I. Schoepf, S. M. Treffler, J. Brenner, M. Bleeker, M. Schubert, B. König & N. Pillay (2010) Female home range size is regulated by resource distribution and intraspecific competition: A long-term field study. *Animal Behaviour,* **79,** 195–203.

Searle, K., N. Hobbs & S. Jaronski (2010) Asynchrony, fragmentation, and scale determine benefits of landscape heterogeneity to mobile herbivores. *Oecologia,* **163,** 815–824.

Singleton, R. D. & J. D. Taylor (2010) Composition of beaver colonies in damage sites of the southeastern United States. In: *Southeastern Association of Fish and Wildlife Agencies*: 95–100.

Stopher, K. V., C. A. Walling, A. Morris, F. E. Guinness, T. H. Clutton-Brock, J. M. Pemberton & D. H. Nussey (2012) Shared spatial effects on quantitative genetic parameters: Accounting for spatial autocorrelation and home range overlap reduces estimates of heritabitlity in wild red deer. *Evolution,* **66,** 2411–2426.

Tramer, E. J. (1969) Bird species diversity: Components of shannon's formula. *Ecology,* **50,** 927–929.

Tufto, J., R. Andersen & J. Linnell (1996) Habitat use and ecological correlates of home range size in a small cervid: The roe deer. *Journal of Animal Ecology,* **65,** 715–724.

van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner & A. Mysterud (2011) What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology,* **80,** 771–785.

Weimerskirch, H., O. Chastel, L. Ackermann & T. Chaurand (1994) Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour,* **47,** 472–476.

Weimerskirch, H., Y. Cherel, F. Cuenot-Chaillet & V. Ridoux (1997) Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology,* **78,** 2051–2063.

Wheatley, M. (1997) Beaver, *Castor canadensis*, home range size and patterns of use in the taiga of southeastern Manitoba: III. Habitat variation. *Canadian Field Naturalist,* **111,** 217–222.

White, G. C. & R. A. Garrott (1990) *Analysis of wildlife radio-tracking data* San Diego: Academic Press.

Willems, E. P., R. A. Barton & R. A. Hill (2009) Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate. *Behavioral Ecology,* **20,** 985–992.

Worton, B. J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology,* **70,** 164–168.

Ydenberg, R. C. & W. E. Davies (2010) Resource geometry and provisioning routines. *Behavioral Ecology,* **21,** 1170–1178.