1-1-2017

Spatiotemporal Variation in Space Use by Eastern Wild Turkeys in Mississippi

Ryo Ogawa

Spatiotemporal variation in space use by eastern wild turkeys in Mississippi

By

Ryo Ogawa

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, Fisheries, and Aquaculture Sciences
in the Department of Wildlife, Fisheries, and Aquaculture

Mississippi State, Mississippi

December 2017

Spatiotemporal variation in space use by eastern wild turkeys in Mississippi

By

Ryo Ogawa

Approved:

Guiming Wang
(Major Professor)

Adam B. Butler
(Committee Member)

Scott A. Rush
(Committee Member)

Kevin M. Hunt
(Graduate Coordinator)

Andrew J. Kouba
Wildlife, Fisheries, and Aquaculture Department Head

George M. Hopper
Dean
College of Forest Resources

Name: Ryo Ogawa

Date of Degree: December 11, 2017

Institution: Mississippi State University

Major Field: Wildlife, Fisheries, and Aquaculture Sciences

Major Professor: Guiming Wang

Title of Study: Spatiotemporal variation in space use by eastern wild turkeys in Mississippi

Pages in Study 63

Candidate for Degree of Master of Science

Spatiotemporal variation in animal space use is critical for understanding how individual animals respond to changes in resource availability across space and time. My study was aimed to: 1) determine functional responses of habitat selection by eastern wild turkeys (*Meleagris gallopavo silvestris*) across 7 study sites in Mississippi; and 2) determine the effect of temporal vegetation variation on order-II habitat selection by wild turkeys over 12 years. I developed resource selection functions using radio telemetry location data. Individual-specific coefficients of order-III habitat selection for forest were related inversely to forest availability in meta-regressions. Yearly coefficients of order-II habitat selection for forest were related inversely to the mean normalized difference vegetation index (NDVI) in April, but the coefficients for open fields were related positively to coefficient of variation in the NDVI from March to May. Wild turkeys exhibited functional responses of habitat selection to spatiotemporal forest availability across Mississippi.

DEDICATION

I dedicate this thesis to my grandfather, who passed away just before the completion of my project. His lessons to catch insects and animals in my childhood were the first experiences when I got interested in wildlife.

ACKNOWLEDGEMENTS

I thank my advisor Dr. Guiming Wang for mentoring me to pursue my master's degree. He helped me with both my graduate school and U.S. life since I arrived at Mississippi. He knew how international students could be challenged by the difficulty of living in foreign countries and always suggested me how I could tackle with them. I really appreciate his all kind help and suggestion. I also thank my committee members Adam Butler and Dr. Scott Rush for their advice and suggestion. I thank Dr. Darren Miller for his help with my thesis support and attending my closed meeting. I am grateful to Dr. Ian Munn for his constructive comments on my thesis.

I thank many graduate students and Landscape ecology laboratory members for being with me and helping my English all the time. Isidro Barela is one of the greatest housemates since I came to the U.S., and is still teaching me American and New Mexican culture. Hinggan surprisingly shows me how we international students should be socialized here. Ciera Rhodes is a great English writer and always helps me with my writing. Conner Almond teaches me the practical knowledge of wild turkey field work and advised me on my discussion about turkey biology. I thank my former advisor Dr. Malcolm Hunter for introducing me to Dr. Wang and encouraging me to study here. I also thank to my family. My parents accepted me to study abroad and wish my success in the U.S. Without all of their support and encouragement, I could not complete my project. Mike Conner, Benjamin Jones, James Inglis, Brad Holder, Matt Mckinney, and

Kyle Marable provided me with the wild turkey relocation data. I thank Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP). This study was funded by MDWFP wild turkey population project.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Movement ecology focuses on the mechanisms underlying animal movement and space use in response to spatiotemporal variation in resources (Nathan et al. 2008, Davies et al. 2012, Van Moorter et al. 2016). Understanding the variation in animal space use is critically important for explaining variability of wildlife population demographic rates, such as survival and productivity, in spatiotemporally heterogeneous environments (Figure 1; McLoughlin et al. 2010, Matthiopoulos et al. 2015, Sánchez-Clavijo et al. 2016). Nevertheless, studies of animal space use have been inconsistent concerning what drivers are most important for explaining animal movements and space use. Such inconsistencies may be in part due to insufficient geospatial models and negligence of several potential causes of inferential biases (e.g., functional responses and multiscale habitat selection) (Levin 1992, Mysterud and Ims 1998, Van Moorter et al. 2013).

Geographical and environmental space use analysis

Patterns of animal space use have two components: geographical space and environmental space (Van Moorter et al. 2016). Geographical space use includes individual home ranges and spatial distributions (Moorcroft 2012). Factors influencing geographical space have been investigated for several decades (Figure 2). McNab (1963) proposed that the home range size of animals would be proportional to animal body size. This hypothesis is potentially versatile and has been extrapolated to relationships between home range size and resource availability or intra-specific body size. Greenwood (1980) and Dobson (1982) hypothesized that mating systems, sexes (male/female), and ages (juvenile/adult) might affect space use and dispersal propensities of birds and mammals. Additionally, the resource dispersion hypothesis posits that spatially or temporally dispersed resource patches would make animals share resources with one another without cooperation, and predicts that animal home range size increases as resources become spatially dispersed (Geffen et al. 1992, Johnson et al. 2002, Macdonald and Johnson 2015). Nevertheless, geographical space analyses often do not evaluate explicitly whether animals select or randomly use resources.

Environmental space use is referred to as resource selection (Manly et al. 2002), which can overcome the aforementioned drawback of geographical space use analyses by determining non-random use of space. Johnson (1980) proposed hierarchical levels of habitat selection: The order-II selection as home range positioning on the landscape and order-III selection as fine scale space use within the home range. Resource availability and inter- or intra-specific interactions may influence geographic locations of animal home ranges on the landscape (Figure 2). For instance, individual animals may be distributed spatially in proportion to resource availability to maximize net or gross energy intake (the ideal free distribution; Fretwell and Lucas, 1970), or individuals may defend in territories and expel other individuals to the suboptimal habitat (the ideal despotic distribution; Fretwell, 1972; Rosenzweig, 1981). Within home ranges, on the other hand, individuals tend to forage in a resource patch within an optimal amount of time (i.e., residence time) and leave the patch at a time that maximizes net energy intake potential (give-up time) (optimal foraging theory; Charnov 1976). Optimal foraging takes into consideration costs of traveling, foraging, food handling, and predation risks, and benefits of gross energy intake (Mysterud and Ims 1998, Godvik et al. 2009, Herfindal et al. 2009, Laforge et al. 2015a). Therefore, spatiotemporal variation in resource availability is a pivotal external factor shaping animal space use and movement.

Geographical space consists of a set of observed animal locations connected by movements (Moorcroft 2012). Movements may determine the range or size of environmental space available to the animal (Van Moorter et al. 2009). Thus, animal movement is a mechanism that connects geographical and environmental space use (Figure 3; Van Moorter et al. 2016). In fact, Herfindal et al. (2009) demonstrated an inverse relationship between home range size and strength of order-II habitat selection of moose (*Alces alces*). Furthermore, when food resources are more dispersed spatially, animals need to move more, resulting in larger home ranges to maximize energy intake (Marable et al. 2012, Macdonald and Johnson 2015). Although such connections can facilitate the development of theoretical and methodological advances in movement ecology, fewer studies have investigated relationships between the geographic and environmental space use by animals (Van Moorter et al. 2016).

Main challenges in contemporary studies of animal space use

There are three potential factors that can bias inferences of spatiotemporal variation in animal space use patterns: 1) spatial scale; 2) functional responses; and 3) temporal environmental heterogeneity (Mysterud and Ims 1998, Van Moorter et al. 2013, McGarigal et al. 2016). Spatial scale includes two components: extent and grain size (Hobbs 2003). Spatial extent is defined by the hierarchical levels of habitat selection (Johnson 1980), while grain is defined as the minimum spatial unit of landscape characteristics animals perceive (Wiens 1989). Empirical studies estimate the grain size of habitat selection as the size of an area surrounding animal locations, within which habitat or landscape data best describe the probability of resource selection (Laforge et al. 2015b). Spatial scaling is an important component to correct for the inferential biases of environmental space use (Wiens 1976, 1989, Levin 1992). Wiens (1989) pointed out that animals may perceive landscape characteristics at different spatial scales from what humans perceive. Misidentification or negligence of grain size may cause biases in the interpretation of data on animal-habitat relationships. Moreover, behavior-specific (e.g., feeding, resting, or escaping from predators) habitat selection could also differ in spatial scales or grain sizes; therefore, habitat selection needs to be assessed on appropriate spatial scales (Addicott et al. 1987). For example, Laforge et al. (2015b) studied spatially scale-dependent resource selection by evaluating habitat selection of white-tailed deer (*Odocoileus virginianus*) with multiple grain sizes. Laforge et al. (2015b) suggested that optimal grain size of habitat selection by white-tailed deer varied among land cover types. Nevertheless, fewer studies have evaluated animal habitat selection explicitly at multiple spatial scales (Mayor et al. 2009, McGarigal et al. 2016).

Individual variation in animal behavior may result in functional responses in habitat selection (Bell et al. 2009, Leclerc et al. 2016). Functional responses in habitat selection are defined as a process, in which individuals vary habitat selection depending on resource availability (Figure 4; Mysterud and Ims 1998). For example, when the availability of feeding habitat is low, selectivity can be positively significant. On the contrary, when the resource availability is sufficient, selectivity of feeding habitat may not be significant. Considering functional responses in habitat selection is critically important because habitat selection at the population level can be masked by such individual variation in animal behavior. Many studies have found evidence supporting the hypothesis concerning functional responses in habitat selection (Godvik et al. 2009, Herfindal et al. 2009, Laforge et al. 2015a). However, a question remains whether regional differences in habitat selection are caused by individual level selection based on functional responses (i.e., plasticity) or by population level selection resulting from regional ecological factors.

Temporal environmental heterogeneity caused by vegetation growth and anthropogenic disturbance can alter animal space use. Quantifying habitat selection patterns in variable environments is critical for understanding ecological and evolutionary processes underlying habitat selection (Levin 1992). Patterns of animal space use can also vary at multiple temporal scales, such as daily, seasonal, and annual scales (Addicott et al. 1987, Wiens 1989, Levin 1992). Several studies have investigated the mechanisms of daily and seasonal variation in animal space use (Miller et al. 2000, Hebblewhite and Merrill 2008, Tardy et al. 2014). However, to the best of my knowledge, few studies have investigated the mechanisms of inter-year variation in animal space use. The inter-year variation in animal space use can help understand how phenotypic plasticity happens according to environmental heterogeneity over years (Scheiner 2013). The resource dispersion hypothesis predicts that temporally dispersed resources make individuals increase home range sizes (Macdonald and Johnson 2015). Larger home ranges may contain more resource patches to buffer against temporal variability in resources, in case resources are depleted in some patches due to temporal environmental variation.

Previous studies of habitat selection by eastern wild turkeys

Eastern wild turkeys (*Meleagris gallopavo silvestris*; hereafter, referred as wild turkeys) are one of the most common game bird species in the United States. Wild turkey populations suffered dramatic declines in the early 20th century due to unregulated hunting and habitat loss. Wild turkeys have recovered through successful restoration programs and research efforts of state and federal agencies as well as non-governmental organization such as the National Wild Turkey Federation (NWTF) since the 1950's (Kennamer et al. 1992). Wild turkey populations have stabilized in most of this species' range with slight declines in some regions after 2000 (Butler et al. 2015, Eriksen et al. 2015). In 2014, the population size of wild turkeys in the United States was estimated between 4.5 and 4.6 million (Eriksen et al. 2015).

Wild turkeys usually do not fly long distances but are highly mobile (Pelham and Dickson 1992). Wild turkeys are known as habitat generalists, requiring forests for cover and food (Porter 1992, McKinney 2013, Davis 2016) and cropland and open fields for food resources (Hurst 1992, Groepper et al. 2015).

Habitat selection by wild turkeys differs between sexes, ages, and seasons. Miller et al. (2000) found that males selected the same habitat as females for mating in central Mississippi during the pre-nesting season, but randomly used habitat types during the summer. Females' space use is affected by nesting and parental activities (Hurst 1992). In pre-nesting seasons, female wild turkeys in central Mississippi were located closer to riparian corridors and burned pine sawtimber stands (Miller et al. 2000). In nesting seasons, female turkeys selected upland pine forest and spatially heterogeneous vegetation areas (Miller et al. 2000, Dreibelbis et al. 2015). For nesting female turkeys, vertical visual obstruction by ≤ 1m tall vegetation was required for nest site concealments (Badyaev 1995, Nguyen et al. 2004, McKinney 2013). The main food source of young turkeys is invertebrates, so adult females and the offspring often select open areas, such as pasture or forest opening, during brood-rearing seasons (Hurst 1992, Jones et al. 2005, Streich et al. 2015). However, young turkeys were also found using various types of forest stands (Jones et al. 2005). In autumn and winter seasons, previous studies observed that both males and females selected hardwood forests, where hard and soft mast were available (Healy 1992, Miller 1997, McShea et al. 2015). Chamberlain et al. (2000) found that wild turkeys selected roost sites for pine and pine-hardwood forested areas, closer to creeks, and near older aged stands. Davis (2016) investigated the statewide spatial distributions (i.e., order-I habitat selection) and landscape-abundance relationships of wild turkeys in Mississippi. Wild turkeys in Mississippi were more likely to use heterogeneous forest covers (Davis 2016).

My study focuses on spatiotemporal variation in space use by wild turkeys. Changes in resource availability across geographic regions modulated movement patterns of wild turkeys (Marable 2012, McKinney 2013, Little et al. 2016). However, little is known regarding whether regional differences in habitat selection are caused by the functional responses (i.e., individual variation) or by factors other than functional responses. Few studies have investigated long-term (> 10 years) variation in space use by wild turkeys. Several studies have recommended assessing effects of landscape heterogeneity on habitat selection by wild turkeys at multiple spatial scales (Byrne and Chamberlain 2015, Conley et al. 2015, Fleming and Porter 2015, Porter et al. 2015), and no studies, to the best of my knowledge, have assessed habitat selection of wild turkeys with multiple grain sizes.

My study is specifically aimed to improve the management of Mississippi wild turkey. Spatial scales of wild turkey habitat selection are relevant to managing appropriate landscape configuration to improve habitat quality. Findings of functional responses in habitat selection can help plan region-specific habitat management. For example, if wild turkeys exhibited functional responses to changes in hardwood forest availability across regions, wild turkey managers need to recommend region-specific hardwood forest management for wild turkeys. Lastly, understanding annual and seasonal variation in habitat selection can help wildlife biologists and managers predict how wild turkeys would react to the temporal variation in habitats.

Objectives

The goal of my research was to address a general question: How does spatiotemporal resource heterogeneity make animal space use change? To answer this overarching question, I addressed two specific objectives: 1) How does wild turkey space use differ among physiographic regions at multiple spatial scales? Does space use of wild turkeys follow functional responses or region-specific patterns? 2) How does seasonal variation in vegetation affect seasonal space use of wild turkeys?

For objective 1, I tested two alternative hypotheses concerning spatial variation in habitat selection by wild turkeys. Functional responses would determine habitat selection patterns of wild turkeys (H1; Mysterud and Ims 1998), or the habitat selection would exhibit region-specific patterns independent of functional responses (H2).

For objective 2, I tested two alternative hypotheses concerning seasonal variation in habitat selection by wild turkeys. Wild turkeys would avoid spaces with highly variable vegetation between years (H3; Wiens 1989, Levin 1992), or the inter-year vegetative variation would not affect habitat selection by wild turkeys because wild turkeys would not recognize temporal variation in vegetation (H4).

Figures

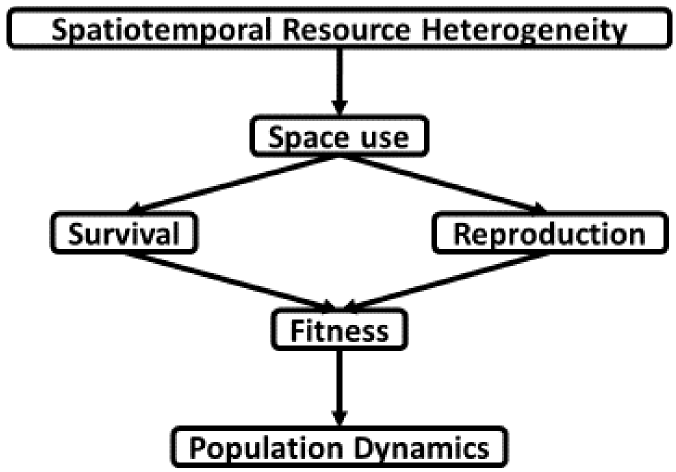

Figure 1 Diagram illustrating the roles of space use in connecting spatiotemporal resource heterogeneity with population dynamics.

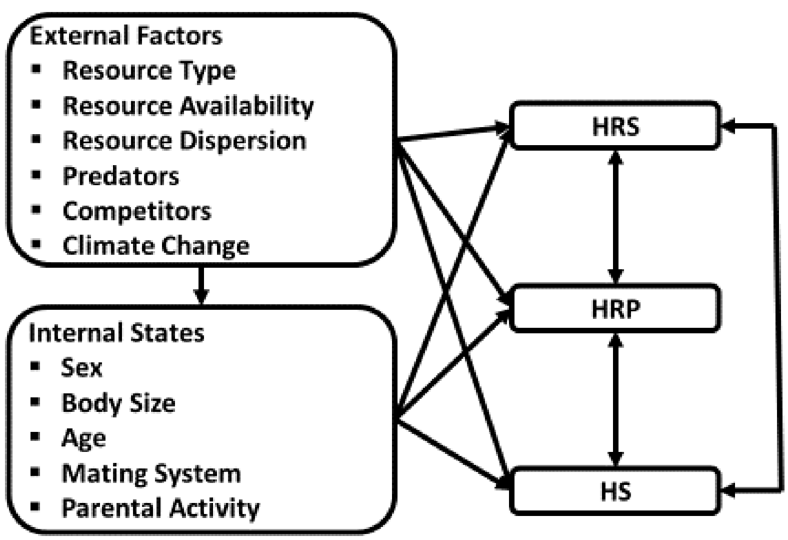

Figure 2 Diagram of the effects of external factors and internal states on home range size (HRS), home range positioning (HRP), and fine scale use (HS).

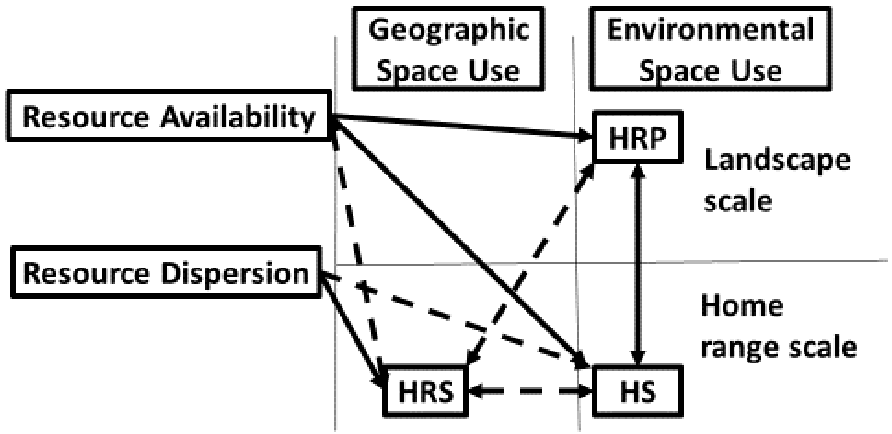

Figure 3 Schematics of the theoretical framework for relationships between resource availability or dispersion and animal space use (home range size [HRS], home range positioning [HRP], and fine scale use [HS]). Arrows represent the directional effect of one component to the other. Solid and dashed arrows represent positive and negative effects, respectively.

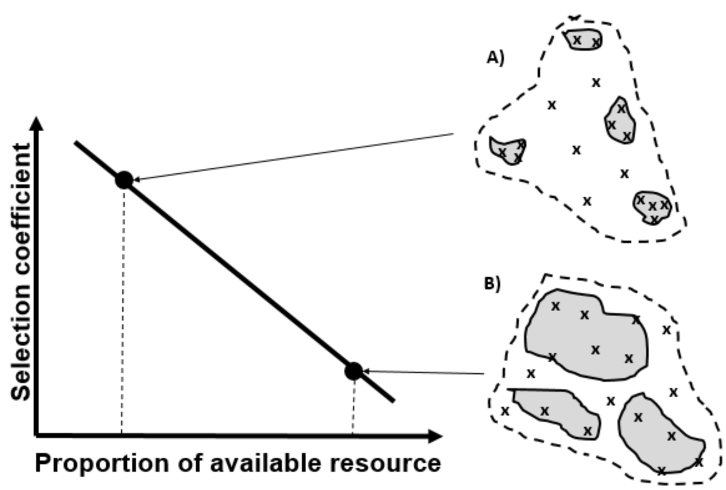

Figure 4 Functional responses in resource selection. Dashed lines represent the boundary of home range, gray areas food resource patches, and cross points animal telemetry locations.

CHAPTER II

METHODS

Study areas

I used radio-telemetry data collected from Tallahala Wildlife Management Area (TWMA), a site in Kemper County (Kemper), a site near Quitman County (Quitman), Malmaison Wildlife Management Area (MWMA), Caston Creek Wildlife Management Area (CCWMA), and Leaf River Wildlife Management Area (LRWMA) for objective 1 (Table 1; Figure 5) and only TWMA for objective 2. Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP) divided Mississippi into 5 wild turkey management regions (WTMR; Figure 5): TWMA and Kemper are located in the east-central region; Quitman in the Delta region; MWMA in the northeast, Delta, and east-central regions; CCWMA in the southwest region; and LRWMA in the southeast region (MDWFP 2012).

Tallahala Wildlife Management Area

TWMA was 14,410 ha in size, located within the Bienville National Forest in parts of Scott, Newton, Jasper, and Smith counties in the east-central WTMR of Mississippi (32°12'N, 89°16'W; Miller 1997). The site was within the Lower Coastal Plain Province and the Blackland Prairie Resource Area (Pettry 1977). The area was 95% forested with 37% in mature pine (*Pinus* spp.) forests, 30% in mature bottomland hardwood forests, 17% in mixed pine-hardwood forests (30-70% pine), and 11% in 1-14-year-old loblolly pine (*P. taeda*) plantations. The study area included old fields (4%) and agriculture fields (1%). The site had a 0–16% slope in topography and experienced several periods of extreme environmental conditions between 1984 and 1995. Prescribed fire was used as a management practice in uplands stands at an average return interval of 6.25 years. Yearly precipitation recorded at the nearest weather station, Meridian Key Field, was about 1,509 mm (standard deviation [SD] = 198 mm, range = 1,254–1,868 mm). The mean temperature was 18.2°C (SD = 0.6°C, range = 17.4–19.3°C). January was the coldest month (1.4°C) in a year, and July was the hottest (33.4°C). The mean number of days below 0°C within a year was 46.7 days (SD = 12.8d, range = 30–65d).

Kemper site

The study site was located in the East Gulf Coastal Plain in the Interior Flatwoods Resource Area (Pettry 1977), approximately 6 km southwest of Scooba in Kemper County in the east-central WTMR of Mississippi (32°47'N, 88°31'W; Miller and Conner 2007). The study site was owned and managed by Weyerhaeuser Company for timber production. Topography was flat, with many intermittent and perennial streams. Overstory tree species were dominated by loblolly pine, hickory (*Carya* spp.), and hardwoods. Common midstory species were hardwoods, hickory, maple (*Acer* spp.), sweetgum (*Liquidambar straciflua*), and dogwood (*Cornus* spp.). The study site consisted of intensively managed pine forests (46%), mature pine-hardwoods (28%), mature hardwoods (15%), and agriculture fields (11%). Within the managed pine forests, mature hardwoods were mainly within streamside management zones (SMZs). Managed pine stands consisted of 76% thinned pine forests, 17% unthinned pine forests, and 7% pine generation areas. As typical silviculture, clearcut harvest was conducted at 27–32 year-old trees, followed by site preparation and planting at approximately 1,100 trees/ha, vegetation management, commercial thinning, pruning, and fertilization. Prescribed burning was also conducted starting in pine stands 9–10 year-old trees at intervals of 3–5 years (Smith et al. 1990, Miller and Conner 2007). The nearest weather station, Kipling, recorded yearly precipitation of approximately 1,388 mm (SD = 278 mm, range = 1,095–1,814 mm). The average temperature was 17.5°C (SD = 0.6°C, range = 16.7–18.3°C). January and July were, respectively, the coldest (1.0°C) and hottest (32.5°C) months in a year. The number of days below 0°C within a year averaged 54.4 days (SD = 9.6d, range = 37–67d).

Quitman site

The study site was located in Quitman County within Delta WTMR of Mississippi. One site was in the northern part of the county (Quitman North [QN]; 34°19'N, 90°17'W) and the other in the southern part (Quitman South [QS]; 34°10'N, 90°21'W; Marable 2012, McKinney 2013). The site in QN was 51% hardwood regeneration (3,202 ha; oak *Quercus* spp., ash *Fraxinus* spp., bald cypress *Taxodium distichum*, eastern cottonwood *Populus deltoids*, hickory), 26% agriculture fields (1,669 ha), and 22% mature bottomland hardwoods (1,357-ha; tupelo *Nyssa* spp., bald cypress, oak, ash, and hickory). The site in QS was approximately 59% hardwood regeneration (4,840 ha; oak, ash, cypress, the eastern cottonwood, hickory), 29% agriculture fields (2,379 ha), and 12% bottomland hardwoods (961 ha; tupelo, oak, ash, hickory, bald cypress, and the eastern cottonwood). Hardwood regeneration included an early successional understory of grasses (*Poaceae*), forbs, vines (*Vitis* spp., *Campsis radicans*), and small shrubs. Agriculture fields included corn, soybeans, cotton, and wheat in QN and QS. Annual precipitation records at the near weather station, Lambert, were approximately 1,269 mm (SD = 562 mm, range = 871–1,667 mm). The mean temperature was 16.8°C (SD = 1.2°C, range = 15.9–17.7°C). January was the coldest (-1.7°C), and July was the hottest (35.2°C) month in a year. The average number of days below 0°C within a year was 66 days (SD = 11.3d, range = 58–74d).

Malmaison Wildlife Management Area

The study site was located in Grenada, Carroll, and Leflore counties, along the borders of northeast, Delta, and east-central WTMRs of Mississippi (33°43'N, 90°00'W; Holder 2006). The 3,600-ha of this area was owned by MDWFP. The management area was within the alluvial floodplain of the Yalobusha River. The eastern portion was primarily loess hills. The study site included mature bottomland hardwoods, upland hardwoods, and pine-hardwood forests, wetlands, old fields, and managed wildlife openings. The dominate bottomland tree species were sycamore (*Platanu occidentalis*), elm (*Ulmus* spp.), sugarberry (*Celtis laevigata*), water oak (*Q. nigra*), willow oak (*Q. phellos*), overcup oak (*Q. lyrata*), swamp chestnut oak (*Q. michauxii*), cherrybark oak (*Q. pagoda*) and pecan (*Carya illinoensis*). Gound cover included sedges (*Carex* spp.), switch cane (*Arundinaria gigantea*), greenbriar (*Smilax* spp.), trumpet creeper (*Campsis radicans*), Virginia creeper (*Parthenocissus quinquefolia*), pepper vine (*Ampelopsis arborea*), may apple (*Passiflora incarnate*), poison ivy (*Toxicodendron radicans*), muscadine grape (*V. rotundifolia*) broomsedge (*Andropogon virginicus*), clover (*Trifolium* spp.), foxtail (*Setaria* spp.) and several grasses (*Andropogon* spp. and *Paspalum* spp.). White oak (*Q. alba*), loblolly pine, beech (*Fagus grandifolia*), and elm were the dominant upland species.. Understory vegetation had similar plant species to bottomlands and also included blackberry (*Rubus* spp.), kudzu (*Pueraria montana*) and honeysuckle (*Lonicera japonica*). The study site had approximately 1- to 3-ha managed opening interspersed for wild turkeys and other wildlife, such as white-tailed deer and northern bobwhites (*Colinus virginianus*; Holder 2006). The nearest weather station, Grenada, recorded annual precipitation of about 2,184 mm (SD = 845 mm, range = 1,586–2,782 mm). The average temperature was 16.2°C (SD = 0.4°C, range = 15.9–16.4°C). January and August were the coldest (-2.4°C) and hottest (30.9°C) months, respectively, in a year. The number of days below 0°C within a year was averagely 72.5 days (SD = 3.5d, range = 70–75d).

Caston Creek Wildlife Management Area

This study area was located in the 11,253-ha Franklin and Amite Counties, within the 76,950-ha Homochitto National Forest and the southwest WTMR of Mississippi (31°24'N, 90°54'W; Jones 2001). This site include the lower thin loess, southern Mississippi valley silty uplands soil. The western border of CCWMA was along the Homochitto River drainage and included a transition zone between pure longleaf pine forests in the east and mixed pine-hardwoods in the west (Frost et al. 1986). Mixed pine-hardwoods constituted 36% of the total area, including loblolly pine, slash pine (*P. elliotti*), shortleaf pine (*P. echinata*), and longleaf pine (*P.palustris*), oak, hickory, blackgum (*Nyssa sylvatica*), and yellow poplar (*Liriodendron tulipifera*) along lower slopes and ephemeral drainages. Pure pine stands covered 19% of the total area, including loblolly pine, slash pine, shortleaf pine, and longleaf pine. Bottomland hardwoods constituted 3% of the total area with oak, beech, and magnolia (*Magnolia grandiflora*) along perennial river drainages. Private lands within CCWMA contained fields, hardwood regeneration, mature hardwoods, and mixed pine-hardwoods. Yearly precipitation recorded at the near weather station, Meadville, was about 1,152 mm (SD = 71 mm, range = 1,102–1,202 mm). The mean temperature was 19.2°C (SD = 0.8°C, range = 18.6–19.8°C). December was the coldest month (0.1°C), and August was the hottest (35.2°C) months in a year. The average number of days below 0°C within a year was 37.5 days (SD = 13.4d, range = 28–47d).

Leaf River Wildlife Management Area

This study area was located within the 144,000-ha DeSoto National Forest (DSNF) in Perry County in the southeast WTMR of Mississippi (30°58'N, 88°55'W; Inglis 2001). This site included the Lower Coastal Plain with a 0–16% slope. The study site was about 16,915 ha in size. Seventy-nine percent of the area was covered by pine forest and 7.6% by pine-hardwood forest. Fifty-six percent of the pine forests consisted of longleaf pine, including mature, natural regeneration, and young plantations. Prescribed burning was conducted annually on approximately 20,500 ha. Annual precipitation recorded at the near weather station, Beaumont Experimental Station, was about 1,206 mm (SD = 209 mm, range = 1,058–1,354 mm). The mean temperature was 19.5°C (SD = 0.2°C, range = 19.4–19.6°C). December and August were, respectively, the coldest (0.9°C) and hottest (36.5°C) months in a year. The number of days below 0°C within a year averaged 46.5 days (SD = 4.9d, range = 43–50d).

Telemetry location data

Tallahala Wildlife Management Area

Female wild turkeys were captured by cannon nets or with alpha-chloralose from 7 January to 4 March and from 1 July to 25 August from 1984 to 1995 (Williams et al.

1967, Bailey 1976, Miller et al. 1999). However, male turkeys were captured only from 1986 to 1989. A 108-g very high frequency (VHF) radio transmitter with a motion sensor was attached to each captured turkey with a backpack harness (Wildlife Materials, Carbondale, IL, USA) (Knowlton et al. 1964). Observers conducted telemetry relocations using hand-held 3-element Yagi antennas and Telonics (Mesa, AZ, USA) or Wildlife Materials receivers. Locations were estimated by triangulation using two fixed-telemetry stations with azimuths less than 12 minutes apart and differing by between 60° and 120° (Cochran and Lord 1963). Average telemetry error was 7.2 degrees (SD = 6.3; n = 43; Palmer 1990). Females were located at least once per day from 14 March to 1 June of each year and 3 or more times per week during the remainder of study periods. Brood-rearing females were located 6 times per day and 3 times per week. Males were located twice a day every other day from January to August (Miller 1997).

Kemper site

Female turkeys were captured by cannon nets between the third week of January and the second week of March from 1986 to 1992 and between late June and mid-August from 1986 to 1992 (Miller and Conner 2007). A 108-g VHF radio transmitter was attached to each turkey with a backpack harness. Telemetry relocations were conducted by triangulation similar to those of the TWMA study. All turkeys were located 3 times per day and 3 days per week during March to June, and twice a day and two days a week during the rest of the field seasons (Weinstein 1994, Miller and Conner 2007).

Quitman site

Wild turkeys were captured using cannon nets throughout Mississippi from January to March in 2009 and 2010 and were relocated to Quitman (Marable 2012). Mean distance between Quitman and trapping sites was approximately 207 km (SD = 133 km). Captured turkeys were transported to the study site by a truck with NWTF wild turkey transport boxes (35 × 56 × 65 cm; International Paper, Memphis, TN, USA). A71.2-g VHF radio transmitter (Model A1540, Advanced Telemetry Systems [ATS], Isanti, MN, USA) was attached to each captured turkey with a backpack harness. Observers used 3-element Yagi antennas (AF Antronics, Inc., Urbana, IL, USA) and ATS R4000 receivers for triangulation (Marable 2012). Average telemetry error was 8.3 degrees (SD = 7.1 M; n = 40; Marable 2012). Radio-tagged turkeys were located at least two days per week from February 2009 to August 2011 (Marable 2012, McKinney 2013).

Malmaison Wildlife Management Area

Wild turkeys were captured with rocket and cannon nets by MDWFP personnel from 21 January to 13 March in 2004 (Eriksen et al. 1993, Holder 2006). Each captured turkey was equipped with a 90-g backpack style ATS transmitter using nylon coated rubber tubing (Norman et al. 1997). Observers triangulated radio-tagged turkeys. Three-element Yagi antennas (Isanti, MN, USA), multi-frequency receivers (Wildlife Materials, Carbondale, IL, USA), and ATS receivers were used for triangulation (Holder 2006). Average telemetry error was 8 degrees (SD = 2.5; n = 45; Holder 2006). Captured turkeys were located more than two days a week from 15 March to 13 August (Holder 2006).

Caston Creek Wildlife Management Area

Wild turkeys were captured with cannon nets across CCWMA between middle January and early March, 1999 and 2000 (Jones 2001). Captured turkeys were transported in NWTF transport boxes and released. Every captured turkey was equipped with a 90-g ATS transmitter of mortality sensor (Isanti, MN, USA) using a backpack harness. Triangulation method was conducted for turkey relocations. Average telemetry error was 8.33 degrees (SD = 6.03; n = 225; Jones 2001). Captured turkeys were relocated through reproductive seasons from March 1999 to July 2000. When adult female turkeys were with broods, adult turkeys were relocated three times a day (Jones 2001).

Leaf River Wildlife Management Area

Wild turkeys were captured with rocket and cannon nets in the core area of LRWMA between 1 February and 10 March, 1999 and 2000 (Inglis 2001). Each captured turkey was equipped with a 100-g backpack style ATS transmitter of a 2-hour mortality switch (Isanti, MN, USA). Triangulation method was used for relocations with Telonics TR-2 receivers and 4-element Yagi antennas. Average telemetry system error was 4.93 degrees (SD = 3.33; n = 3,313; Inglis 2001). Telemetry monitoring was conducted from 1 March 1999 to 28 February 2000 (Inglis 2001).

Landscape data preparation and statistical analyses of Study 1

Land cover data

I processed land cover data for the 7 study sites from the 30-m resolution National Land Cover Database (NLCD, https://www.mrlc.gov/) using the R package “raster”

(Homer et al. 2015, Hijmans 2016, R Development Core Team 2016). I used NLCD 1992 for Kemper (study year: 1991–1992) and TWMA (1991–1992), NLCD 2001 for CCWMA (1999–2000) and LRWMA (1999–2000), and NLCD 2011 for Quitman (2009–2010). NLCD 2001 and 2006 were used to interpolate the 2004 land cover data of MWMA. I only included total forest (i.e., deciduous forest, evergreen forest, mixed forest, and woody wetland) and hardwood forest (deciduous forest and woody wetland) as land cover types in study 1 to test for functional responses of habitat selection by wild turkeys to varying availability of forest covers.

I used CircAn in the program Biomapper to generate proportion maps (ranging from 0 to 1) of a land cover type within a circular buffer around each 30m × 30m cell or pixel (Hirzel et al. 2002). First, I booleanized the raster images of total or hardwood forest, respectively, assigning 1 to a cell of total or hardwood forest and 0 to a cell of all other cover types. Then, I calculated the proportions of land cover types for each grid cell. For MWMA, I calculated proportion of land cover types in the NLCD 2001 and 2006, respectively. Then, I averaged the two proportions of each land cover type to represent proportions during 2004. I used three different buffer sizes to calculate forest proportions: average daily movement distance (390 m), radius of seasonal home range size (1,140 m), and annual home range size (2,100 m) (Phalen 1986, Lambert et al. 1990, Godwin 1991, Miller and Conner 2005, Marable 2012). Hereafter, I referred to the three buffer sizes as daily, seasonal, and annual movement scales.

Statistical analyses

I conducted order-III habitat selection analyses for the period from March to August (Johnson 1980). Radio-tagged wild turkeys of all 7 study sites were tracked from

March to August. I only used adult female turkeys in study 1 because no male turkeys were tracked in Kemper, MWMA, CCWMA, and LRWMA during the study period. I used telemetry locations to quantify amount of used space and randomly selected pseudo-absence locations within home ranges to measure amount of available space. If a bird was located multiple times during a day, I randomly selected one telemetry location for the day to reduce temporal autocorrelation among relocations. I used birds having at least 30 resulting telemetry locations for the reliable estimate of order-III habitat selection (Seaman et al. 1999). I first estimated 95% minimum convex polygons (MCPs) between March and August for each individual bird using the R package "adehabitatHR" (Calenge 2006). I then generated n random pseudo-absence locations (n = the number of telemetry locations) within each individual's MCP to quantify available resources. To test functional responses of habitat selection in the following generalized linear mixed models (GLMMs) and meta-analysis models, I also computed the proportions of the total forest or hardwood forest within the individual MCPs as available forest proportion.

In a preliminary analysis, I classified telemetry locations into the biological seasons of wild turkeys following the seasonal divisions by Chamberlain et al. (2000). Because habitat selection was not related to seasons (pre-nesting: β = -0.01, SE = 0.19, z = -0.06, p = 0.96), I combined data over the seasons to increase sample size (i.e., the number of individuals).

Single-variable generalized linear models for determining the optimal spatial scale of habitat selection

To determine the optimal spatial scales of order-III habitat selection (for total or hardwood forest) by wild turkeys, I built single-variable generalized linear models

(GLMs) of the logit link function with combined data over individual birds following Laforge et al. (2015b) to reduce computational costs. For total and hardwood forests, I built three GLMs for each forest proportion at three different buffer sizes: daily, seasonal, and annual movement ranges. I conducted model selection with Akaike Information Criteria corrected for small sample size (AICc) using the R package "MuMIn" (Burnham and Anderson 2002, Bartoń 2016). The most approximating or best model had the lowest AICc. Models with ΔAICc < 2 relative to the best model were considered competing models. The optimal spatial scale resulted in the lowest AICc value among the GLMs at three different buffer sizes for a forest type. I used the best supported spatial scale for the subsequent GLMMs and meta-analysis.

Generalized linear mixed models for functional responses of habitat selection

I assessed functional responses of habitat selection by wild turkeys using GLMMs of the logit link function. GLMMs included proportion of total or hardwood forest as a fixed effect, random intercepts for bird identity nested within study site and year, and a random slope of the proportion of forest. Due to the low number of study sites (n = 7), I also built GLMMs with study site only as a fixed effect to determine necessity of study site as a random effect by comparing AICc with GLMMs including study site as a random effect. I conducted model selection using a backward selection method (Burnham and Anderson 2002, Zar 2010). I developed all GLMMs using the R package "lme4" (Bates et al. 2015).

I extracted individual bird's selection coefficients (i.e., fixed slope combined with individual's random slope) of total and hardwood forests, respectively, from the best GLMM. To test the functional responses, I regressed individual-specific selection coefficients against within-home-range forest proportions of individual birds using linear models. I tested the null hypothesis concerning regression slopes of linear models at the significance level of 0.05. I concluded that functional responses of habitat selection were supported in wild turkeys if selection coefficients of individual birds were related inversely to the within-home-range proportions of total or hardwood forests.

Meta-analysis for functional responses of order-III habitat selection by wild turkeys

Differences in data collection methods, sample sizes, observers, geographic locations, and times likely resulted in different uncertainties in parameter estimation and heterogeneities in data quality among studies. To account for estimation uncertainties and data heterogeneities among the 7 studies, I used meta-analysis models as an alternative method to examine the functional responses of habitat selection by wild turkeys (Schwarzer et al. 2015). I first developed resource selection functions using the GLMs of the logit link function for each bird. I used a bootstrapping method to reduce a potential estimation bias caused by spatial autocorrelation among telemetry locations and to standardize the unequal sample sizes (i.e., number of telemetry locations) among birds. I bootstrapped 20 locations from the original telemetry locations and generated 20 random pseudo-absence locations within MCPs for each bird. I repeated the process 1,000 times (i.e., 1,000 repetitions). I fitted a GLM to each of 1,000 repetitions. I calculated the mean and variance of 1,000 estimated selection coefficients for each bird.

I conducted meta-regressions of relationships among individual bird’s habitat selection coefficients and within-home-range forest proportion with study site as covariates. I used restricted maximum likelihood estimators with Knapp and Hartung adjustment for the unbiased standard errors of coefficient estimates (Knapp and Hartung

2003). To prevent multicollinearity, I did not include forest proportion and study site simultaneously in the same models. Those two forest proportions were significantly correlated with study site (total forest: $F = 321.40$, degree of freedom $[v]_1 = 6$, $v_2 = 147$, p ≤ 0.01; hardwood forest: $F = 97.88$, $v_1 = 6$, $v_2 = 147$, p ≤ 0.01). I selected the best meta-regression model using AICc. The best model had the lowest AICc, and models with ΔAICc < 2 were considered competing. In the preliminary analyses, I included square and cube terms of forest proportions as covariates, but neither of the models was supported by AICc. Therefore, I did not include non-linear terms in my subsequent study.

I also measured heterogeneity of selection coefficients with study sites. Cochran's Q statistic was used for evaluating significance of the heterogeneity (Hedges and Olkin 1985, Schwarzer et al. 2015). All meta-analysis models were developed using the R package "metafor" (Viechtbauer 2010).

Landscape data preparation and statistical analyses of Study 2

Landsat imagery

I used the 30-m resolution normalized difference vegetation index (NDVI), an index of vegetative vigor, to quantify food availability and ecological conditions of study sites (Rouse et al. 1974, Pettorelli 2013). I downloaded the 16-day products of bands 1, 3, 4, and 6 imagery of Landsat 4 and 5 Thematic Mapper (TM) from the United States Geological Service website (https://landsat.usgs.gov/) for TWMA from 1 March to 30 September, 1984–1995. I generated a 100% MCP using all telemetry locations of all tracked birds from March to September, and then created a polygon adding a 2100-m buffer to the MCP to delineate the boundary of available space for order-II habitat selection. I cropped images of Landsat TM bands 1, 3, 4, and 6 with the polygon for every 16 days from March through September each year. Wild turkeys nest from 14 April to 31 May and rear a brood of young birds from 1 June through 30 September (Chamberlain et al. 2000), so I predicted that the NDVI values could determine the timing when female turkeys start nesting.

I used bands 1 (visible blue light: wavelength 0.45–0.52 μm) and 6 (thermal-infrared light: 10.5–12.5 μm) to create cloud cover images with the R package "landsat" (Goslee 2011). I masked the bands 3 (visible red light: 0.63–0.69 μm) and 4 (near infrared light: 0.76–0.90 μm) with cloud images to assign missing values of NA to grid cells covered by cloud. I averaged two images of bands 3 and 4 within the same month of a year. Monthly NDVI was calculated from the monthly averaged bands 3 and 4 using the formula: NDVI = (band 4 – band 3) / (band 4 + band 3) (Rouse et al. 1974, Pettorelli 2013). I excluded the NDVI images, of which more than 30% of grid cells had missing values from analyses. I calculated the mean NDVIs over all grid cells of available habitat, and coefficients of variation (CVs) of the NDVI by month and year.

To test inter-year variation in habitat selection by wild turkeys, I used the absolute monthly NDVI difference between two successive years to represent inter-year variation in vegetation conditions. First, I calculated the NDVI difference (ΔNDVI) between two successive years for each month from March to September using the formula: $\Delta NDVI_{month\ i,\ year\ j+1} = NDVI_{month\ i,\ year\ j+1} - NDVI_{month\ i,\ year\ j}$. Second, I averaged ΔNDVI's over March to September by year. Last, I calculated the mean of absolute values of ΔNDVI (|ΔNDVI|) over all grid cells by year.

National land cover database

Land cover and land use types of study 2 included agriculture, developed area, forest (deciduous forest, evergreen forest, mixed forest, and woody wetland), open field (bare ground uncovered by green vegetation), and 'other' land cover (all the land cover types not being aforementioned). I used NLCD 1992 (Homer et al. 2015) to derive land cover data during study period because land covers exhibited little changes from 1984 to 1995 as shown by the GIS layers derived from the annual USGS forest information (Miller 1997). I booleanized the NLCD images for each of the 5 land cover types, and calculated proportions of each land cover type for each raster grid cell at the daily (390 m), seasonal (1,140 m), and annual (2,100 m) movement scales, respectively, using CircAn (Hirzel et al. 2002).

Statistical analyses

I conducted order-II habitat selection analyses to determine factors influencing annual variation in the spatial distribution of wild turkeys on the TWMA landscape. I used the telemetry locations of both females and males in the analyses of study 2. I averaged the UTM coordinates of all telemetry locations within a home range to estimate the home range centroids for each bird radio tracked during April, March–May, and March–September, respectively. The minimum sample size of home range centroid estimation was 10 telemetry locations following Signer et al. (2015). Although the number of locations constituted a small sample size for estimating home range size, the objective of this study was not to estimate home ranges. I used the home range centroids to represent positioning of home ranges on landscapes. I computed a 100% MCP using all the centroids to delineate the used habitat of all tracked birds for each period (i.e., April, March–May, and March–September). I generated n random locations within the MCP (n = number of the centroids) as pseudo-absence locations to quantify the amount of available habitat.

Single-variable generalized linear models for determining the optimal spatial scale of order-II habitat selection

I built single-variable GLMs with the logit link function to determine the best spatial scale (daily, seasonal, or annual movement scales) of order-II habitat selection for each of the 5 land cover types using the same approach as the study 1. I conducted model selection based on AICc values. The optimal spatial scale resulted in the lowest AICc values among the three GLMs of a land cover at three different buffer sizes.

I tested correlations among the proportions of land cover types to prevent multicollinearity in the subsequent regression. If the proportions of two land cover types were highly correlated (Pearson's correlation: $|r| > 0.7$), I selected the land cover type of the most biologically meaningful interpretations.

Generalized linear mixed models for determining the significant covariates of habitat selection

I used GLMMs with a logit link function to determine the significant covariates (i.e., proportion of land cover) of order-II habitat selection by wild turkeys. Fixed effects of GLMMs included year, sex, and proportions of land cover types at the spatial scale determined by the aforementioned single-variable GLMs. I included a random intercept with bird identity as a random effect. The best models had the lowest AICc scores. If a covariate was included in the best model and had the p value of < 0.05, the covariate was used in the subsequent meta-analysis. I developed GLMMs using the R package "lme4" (Bates et al. 2015).

Meta-analysis models for relationships between land cover selection and normalized difference vegetation index

I used meta-analyses to evaluate how yearly variation in NDVI affected order-II habitat selection during April, March–May, and March–September, respectively. April had the most variable NDVI values over years (Figure 6), so I predicted inter-year variation in April NDVIs could change turkey order-II habitat selection patterns.

First, I conducted order-II habitat selection analyses for each period by year using GLMs with the logit function and the covariates selected by GLMMs. I extracted the selection coefficients and the estimated variances of land cover types from the annual GLMs. I used the extracted selection coefficients as the response variables of meta-regressions. Explanatory variables used in the meta-regressions included the means and CVs of the NDVIs of the corresponding periods (i.e., April, March–May, and March–September) and annual mean $|\Delta NDVI|$. I used the mean $|\Delta NDVI|$ as a covariate of inter-year variation in NDVI.

I used restricted maximum likelihood estimators and Knapp and Hartung adjustment for the meta-analysis (Knapp and Hartung 2003). Due to multicollinearity among the covariates, I built single-variable meta-regressions. Regression coefficients were tested at the significance level of 0.05. Meta-analysis models were developed using "metafor" (Viechtbauer 2010).

Table and figures

Table 1 Information of study sites in Tallahala Wildlife Management Area (TWMA), Kemper, Quitman North (QN), Quitman South (QS), Malmaison Wildlife Management Area (MWMA), Caston Creek Wildlife Management Area (CCWMA), and Leaf River Wildlife Management Area (LRWMA)

Site	Long	Lat	Ecoregion	Total forest (%)	Hardwood forest (%)	Data year
TWMA	89°16'W	32°12'N	Mostly forested area. Slope of 0–16%.	81.5	32.5	1984–1995
Kemper	88°31'W	32°47'N	Mostly contiguous forested area. Flat with many streams.	84.1	22.7	1991–1992
QN	90°17'W	34°19'N	Dominated by more agriculture fields than other sites.	16.5	15.7	2009–2010
QS	90°21'W	34°10'N	Dominated by more agriculture field than other sites.	16.5	15.7	2009–2010
MWMA	90°00'W	33°43'N	Within alluvial floodplain of the Yalobusha River. Eastern portion includes primarily loess hills.	48.6	45.2	2004
CCWMA	90°54'W	31°24'N	Within lower thin loess. Southern Mississippi valley silty uplands soil resource area.	75.3	14.3	1999–2000
LRWMA	88°55'W	30°58'N	Moderately rolling topography. Slopes from 0 to 16%.	84.3	26.6	1999–2000

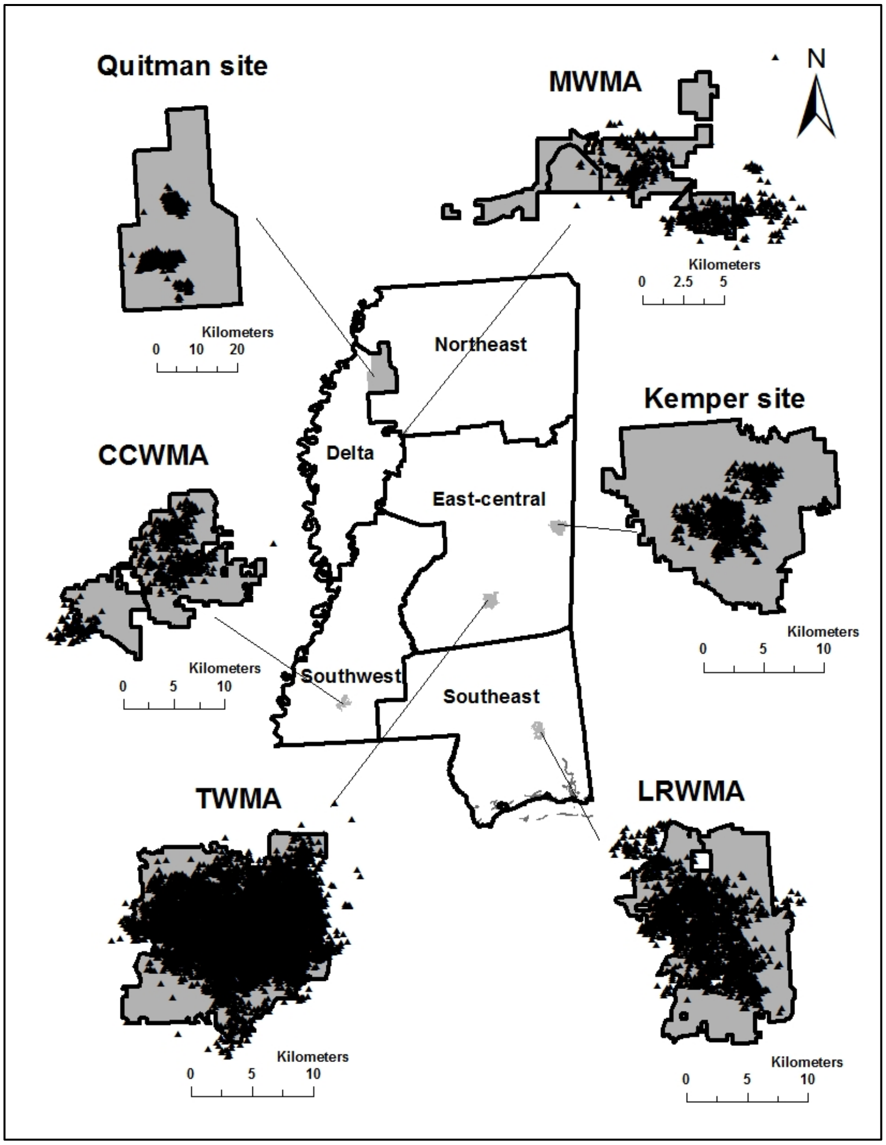

Figure 5 Geographic locations of 7 study sites and boundaries of 5 wild turkey management regions created by Mississippi Department of Wildlife, Fisheries, and Parks in Mississippi, United States. Study sites are Caston Creek Wildlife Management Area (CCWMA), Kemper, Leaf River Wildlife Management Area (LRWMA), Malmaison Wildlife Management Area (MWMA), Tallahala Wildlife Management Area (TWMA), and Quitman (Quitman north and Quitman south). All triangle points represent telemetry locations of wild turkeys. The map was created by ArcMap® 10.4.1 (Environmental Systems Research Institute, California, USA).

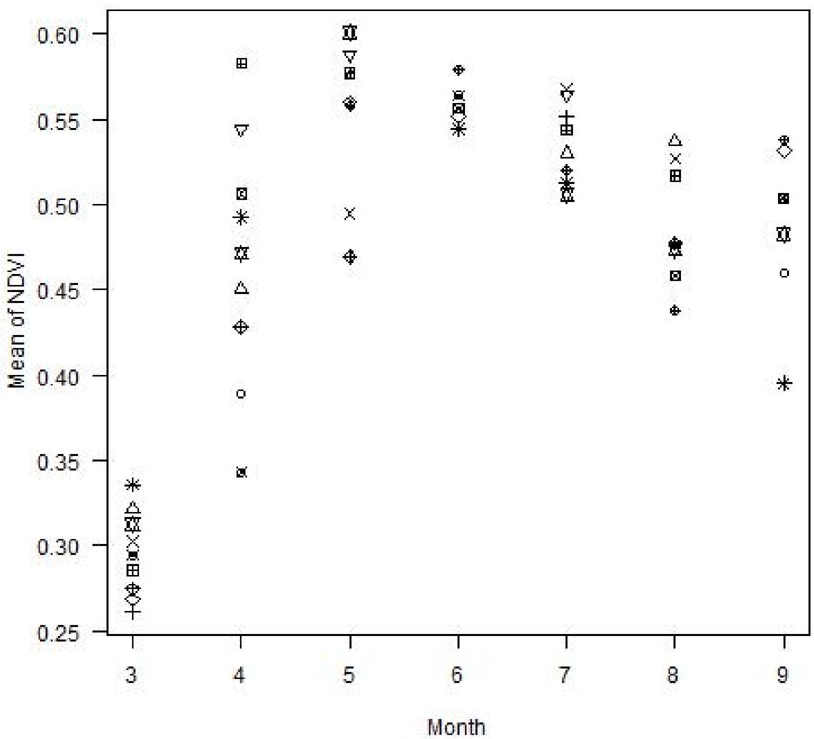

Figure 6 Monthly mean normalized difference vegetation index (NDVI) of March to September in Tallahala Wildlife Management Area from 1984 to 1995. Different shapes of point characters represent different years.

CHAPTER III

RESULTS

Study 1: Spatial variation in space use by eastern wild turkeys

I included 16, 20, 14, 16, 33, 15, and 18 birds and 2,068, 2,492, 1,342, 4,672, 3,972, and 3,510 telemetry locations in the analyses of order-III habitat selection for TWMA, Kemper, MWMA, CCWMA, LRWMA, QN, and QS, respectively. In single-variable analyses, the GLM of daily movement scale had the lowest AICc value for total and hardwood forests. Therefore, daily movement scale was supported as the optimal spatial scale of order-III habitat selection for both total and hardwood forest (Table 2).

The best GLMMs of total forest and hardwood forest included random slopes of total and hardwood forest proportions, respectively, and random intercept (Table 3). Variance estimates (σ^2) of random slope of hardwood forest proportion ($\sigma^2 = 0.28$) was greater than that of total forest proportions ($\sigma^2 < 0.01$). Inclusion of the random slopes in the best model suggested a possibility of functional responses of order-III habitat selection to availability of forests. However, in the linear models regressing individual selection coefficients against within-home-range forest proportions, functional responses of order-III habitat selection were not supported for either forest type (total forest: β = 0.01; *SE* = 0.01, t = 0.18, p = 0.86; hardwood forest: β = -0.15; *SE* = 0.10, t = -1.48, p = 0.14).

In the meta-analysis of the selection coefficients of bootstrapped GLMs, selection coefficients of total forest proportion were related inversely to within-home-range total forest proportion (β = -5.55, *SE* = 0.84, *t* = -6.59, p ≤ 0.01; Table 4, Figure 7). On the other hand, selection coefficients of hardwood forest proportion were not related to within-home-home hardwood proportions (β =-1.46, *SE* = 0.84, *t* = -1.74, p = 0.08; Table 4).

Study site was included in the best model of hardwood coefficients (Table 4). In the heterogeneity test among study sites, total and hardwood selection coefficients were significantly heterogeneous among study sites, possibly suggesting that other factor(s) might also influence total and hardwood forest selection by wild turkeys (total forest: *Q* = 44.86, *v* = 6, p ≤ 0.01; hardwood forest: *Q* = 35.76, *v* = 6, p ≤ 0.01; Figure 8).

Study 2: Temporal variation in space use by eastern wild turkeys

I obtained 226 April centroids from 191 birds, 318 March–May centroids from 260 birds, and 361 March–September centroids from 277 birds over 12 years. Proportions of agriculture, forest, and 'other' cover types were highly correlated with one another (|r| > 0.7). In single-variable GLM analyses of all three periods, annual movement scale was supported as the optimal spatial scale for agriculture, developed area, forest, open field, and 'other' (Table 5). Therefore, I used forest, developed area, and open field land covers at annual movement scales in the GLMMs of order-II habitat selection for April, March–May, and March–September.

Among GLMMs for determining land cover types selected by wild turkeys, the model containing forest, developed area, and open field was the best model for April, March–May, and March–September order-II habitat selection (Table 6). Forest proportion was related positively to resource selection probability (April: β = 0.43, *SE* = 0.15, *z* = 2.84, p ≤ 0.01; March–May: β = 0.62, *SE* = 0.14, *z* = 4.59, p ≤ 0.01; March–

September: β = 0.62, SE = 0.13, z = 4.80, $p \leq 0.01$). Proportion of open field was also related positively to resource selection probability (April: β = 0.50, SE = 0.11, z = 4.36, $p \leq 0.01$; March–May: β = 0.56, SE = 0.10, z = 5.77, $p \leq 0.01$; March–September: β = 0.54, SE = 0.09, z = 5.92, $p \leq 0.01$). On the other hand, proportion of developed areas was related inversely to probability of habitat selection (April: β = -1.00, SE = 0.17, z = -5.86, $p \leq 0.01$; March–May: β = -0.88, SE = 0.15, z = -5.83, $p \leq 0.01$; March–September: β = -0.81, SE = 0.14, z = -5.95, $p \leq 0.01$). Sex was included in a competing model of March–May and March–September (ΔAICc < 2), but the coefficients of sex were not significant (March–May: β = -0.12, SE = 0.19, z = -0.66, p = 0.51; March–September: β = -0.09, SE = 0.18, z = -0.50, p = 0.62). Therefore, I included forest, developed area, and open field in the meta-analysis of April, March–May, and March–September order-II habitat selection.

In the meta-regression of order-II habitat selection, April mean NDVI was related inversely to selection coefficients of forest in April (β = -10.05, SE = 2.30, t = -4.36, $p \leq 0.01$; Figure 9A). The CV of NDVI were related positively to selection coefficient of open field from March to May (β = 17.63, SE = 5.93, t = 2.97, p = 0.02; Figure 9B) although one value affecting the positive slope was observed by a diagnostic test. None of mean NDVI, CV of NDVI, and |ΔNDVI| was related to selection coefficients of developed land cover (p > 0.05).

Tables and figures

Table 2 Single-variable generalized linear models of order-III habitat selection of forests by wild turkeys in Caston Creek Wildlife Management Area (1999–2000), Quitman (2009–2010), Kemper (1991–1992), Leaf River Wildlife Management Area (1999–2000), Malmaison Wildlife Management Area (2004), and Tallahala Wildlife Management Area (1991–1992)

Movement scale	AICc[a]	ΔAICc[b]	Coefficient[c]	AICc	ΔAICc	Coefficient
	Total forest[d]			Hardwood forest[e]		
Annual	26767.67	16.73	-0.017	26767.79	27.87	-0.007
Season	26767.66	16.73	0.017	26767.20	27.28	0.059
Daily	26750.93	0.00	0.197	26739.93	0.00	0.302

[a]AICc is Akaike Information Criteria corrected for small sample size.
[b]ΔAICc is the difference in AICc from the best model.
[c]Coefficient is the selection coefficient of each land cover type.
[d]Total forest includes deciduous, evergreen, and mixed forest and woody wetland.
[e]Hardwood forest includes deciduous forest and woody wetland.

Table 3 Generalized linear mixed models of order-III habitat selection of forests by wild turkeys in Caston Creek Wildlife Management Area (1999–2000), Quitman (2009–2010), Kemper (1991–1992), Leaf River Wildlife Management Area (1999–2000), Malmaison Wildlife Management Area (2004), and Tallahala Wildlife Management Area (1991–1992)

Model[a]	K[b]	logLik[c]	AICc[d]	ΔAICc[e]	w_i[f]
Total forest[g]					
fop + (fop | site/id)	8	-13309.0	26633.94	0.00	0.731
fop + (fop | site/id) + (1 | yr)	9	-13309.0	26635.95	2.00	0.269
fop + site + (fop | id)	11	-13344.4	26710.83	76.89	0.000
fop + (1 | site/id)	4	-13359.2	26726.47	92.53	0.000
fop + (fop | id)	5	-13373.5	26756.94	122.99	0.000
1 + (1 | site/id)	3	-13381.9	26769.80	135.86	0.000
Hardwood forest[h]					
hwp + (hwp | site/id)	8	-13304.8	26625.51	0.00	0.731
hwp + (hwp | site/id) + (1 | yr)	9	-13304.8	26627.51	2.00	0.269
hwp + (hwp | id)	5	-13331.4	26672.81	47.3	0.000
hwp + site + (hwp | id)	11	-13356.0	26733.95	108.44	0.000
hwp + (1 | site/id)	4	-13366.4	26740.81	115.30	0.000
1 + (1 | site/id)	3	-13381.9	26769.80	144.29	0.000

[a]Model terms are forest proportion (fop), hardwood proportion (hwp), study site (site), bird identity (id), and year (yr). Proportions of forests were computed at daily movement scales.
[b]K is number of parameter.
[c]logLik is Log-likelihood value.
[d]AICc is Akaike Information Criteria corrected for small sample size.
[e]ΔAICc is the difference in AICc from the best model.
[f]w_i is model weight.
[g]Total forest includes deciduous, evergreen, and mixed forest and woody wetland.
[h]Hardwood forest includes deciduous forest and woody wetland.

Table 4 Meta-regressions of order-III habitat selection by wild turkeys in Caston Creek Wildlife Management Area (1999–2000), Quitman (2009–2010), Kemper (1991–1992), Leaf River Wildlife Management Area (1999–2000), Malmaison Wildlife Management Area (2004), and Tallahala Wildlife Management Area (1991–1992)

Model[a]	K[b]	logLik[c]	AICc[d]	ΔAICc[e]	w_i[f]
Total forest[g]					
Proportion	3	-469.71	945.58	0.00	1.00
Site	8	-472.46	961.92	16.34	0.00
Null	2	-487.53	979.13	33.55	0.00
Hardwood forest[h]					
Site	8	-336.91	690.82	0.00	1.00
Proportion	3	-350.26	706.68	15.86	0.00
Null	2	-351.74	707.56	16.74	0.00

[a]Resource selection coefficient for each bird was calculated by generalized linear model. Model terms are proportions of total or hardwood forest within home range delineated by 95% minimum convex polygon (Proportion) and study site (Site).
[b]K is number of parameters.
[c]logLik is Log-likelihood value.
[d]AICc is Akaike Information Criteria corrected for small sample size.
[e]ΔAICc is the difference in AICc from the best model.
[f]w_i is Akaike weight.
[g]Total forest includes deciduous, evergreen, and mixed forest and woody wetland.
[h]Hardwood forest includes deciduous forest and woody wetland.

Table 5 Single-variable generalized linear models of order-II habitat selection by wild turkeys during the periods of April, March to May, and March to September in Tallahala Wildlife Management Area, 1984–1995

Movement scale	ΔAICc[a]	Coefficient[b]	ΔAICc	Coefficient	ΔAICc	Coefficient
	April[c]		March–May[c]		March–September[c]	
Agriculture						
Annual	0.00	-20.09	0.00	-22.16	0.00	-23.19
Seasonal	32.76	-7.36	43.06	-11.24	51.56	-11.73
Daily	40.64	-4.16	68.63	-4.86	87.92	-3.34
Developed area						
Annual	0.00	-2277.97	0.00	-2112.48	0.00	-2018.13
Seasonal	24.88	-1491.39	42.11	-1125.01	53.18	-939.31
Daily	71.86	-243.82	77.09	-322.56	78.03	-427.48
Forest[d]						
Annual	0.00	9.55	0.00	11.02	0.00	11.07
Seasonal	22.99	4.42	36.32	5.53	38.04	5.89
Daily	36.31	1.70	59.44	2.35	75.51	1.78
Open field[e]						
Annual	0.00	15.44	0.00	16.92	0.00	14.92
Seasonal	6.67	5.43	15.05	2.51	14.12	2.49
Daily	9.68	0.52	14.62	-1.58	14.91	0.43
Other area[f]						
Annual	0.00	-96.29	0.00	-107.36	0	-102.07
Seasonal	18.42	-49.53	42.27	-47.35	44.62	-45.60
Daily	39.67	-14.01	69.96	-11.92	66.27	-17.52

[a]ΔAICc is the difference in AICc from the best model.
[b]Coefficient is the selection coefficient of each land cover type.
[c]Centroids of April, March–May, and March–September home range were computed by averaging Universal Transverse Mercator coordinates of all relocations by bird within the corresponding periods.
[d]Forest includes deciduous forest, evergreen forest, mixed forest, and woody wetland.
[e]Open area includes bare ground uncovered by green vegetation.
[f]Other area includes all the land cover types not being aforementioned.

Table 6 Generalized linear mixed models of order-II habitat selection by wild turkeys during the periods of April, March to May, and March to September in Tallahala Wildlife Management Area, 1984–1995

Model[a]	K[b]	logLik[c]	AICc[d]	ΔAICc[e]	*wi*[f]
April[g]					
fop + dvp + opp + (1 | id)	5	-260.87	531.87	0.00	0.72
sex + fop + dvp + opp + (1 | id)	6	-260.87	533.93	2.05	0.26
dvp + opp + (1 | id)	4	-265.12	538.32	6.45	0.03
fop + dvp + (1 | id)	4	-271.16	550.40	18.53	0.00
yr + fop + dvp + opp + (1 | id)	15	-260.01	551.13	19.25	0.00
yr + sex + fop + dvp + opp + (1 | id)	16	-259.98	553.22	21.34	0.00
fop + opp + (1 | id)	4	-283.14	574.37	42.50	0.00
March–May[g]					
fop + dvp + opp + (1 | id)	5	-366.63	743.35	0.00	0.69
sex + fop + dvp + opp + (1 | id)	6	-366.41	744.95	1.60	0.31
yr + fop + dvp + opp + (1 | id)	15	-365.28	761.33	17.99	0.00
yr + sex + fop + dvp + opp + (1 | id)	16	-364.97	762.82	19.47	0.00
dvp + opp + (1 | id)	4	-378.11	764.29	20.94	0.00
fop + dvp + (1 | id)	4	-384.95	777.96	34.61	0.00
fop + opp + (1 | id)	4	-387.65	783.36	40.02	0.00
March–September[g]					
fop + dvp + opp + (1 | id)	5	-420.98	852.04	0.00	0.71
sex + fop + dvp + opp + (1 | id)	6	-420.85	853.82	1.78	0.29
yr + fop + dvp + opp + (1 | id)	16	-419.59	871.94	19.90	0.00
yr + sex + fop + dvp + opp + (1 | id)	17	-419.57	874.01	21.97	0.00
dvp + opp + (1 | id)	4	-433.48	875.01	22.97	0.00
fop + dvp + (1 | id)	4	-440.38	888.81	36.77	0.00
fop + opp + (1 | id)	4	-442.29	892.65	40.60	0.00

[a]Model terms are forest proportion (fop), developed area proportion (dvp), open field proportion (opp), bird identity (id), sex, year (yr); April and March–May centroids of wild turkeys were not available in 1990. Proportions of land covers were computed at the annual movement scale.
[b]K is number of parameters.
[c]logLik is log-likelihood value.
[d]AICc is Akaike Information Criteria corrected for small sample size.
[e]ΔAICc is the difference in AICc from the best model.
[f]w_i is Akaike weight.
[g]Centroids of April, March–May, and March–September home range were computed by averaging Universal Transverse Mercator coordinates of all relocations by bird within the corresponding periods.

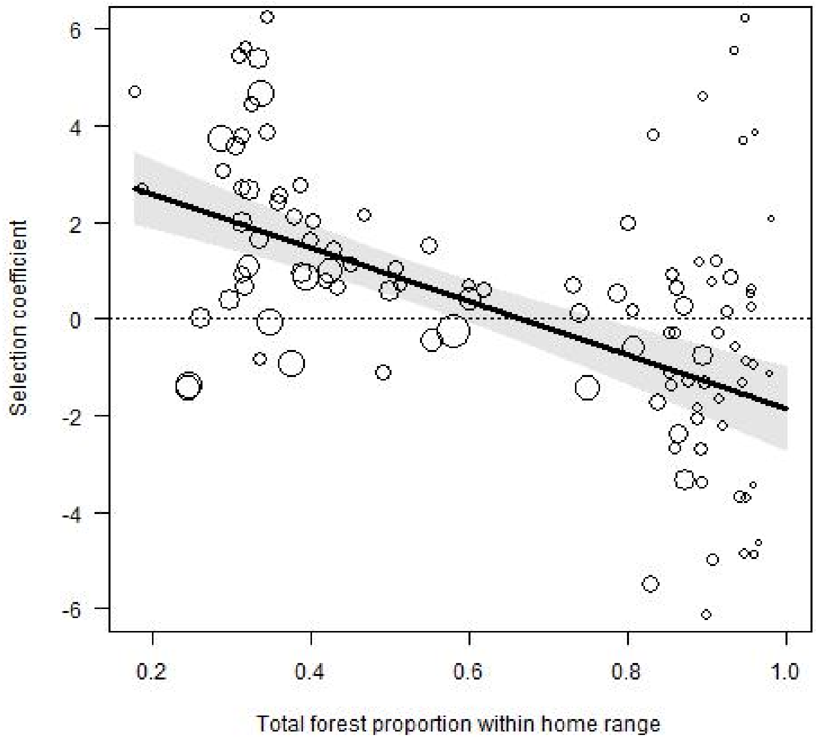

Figure 7 Functional responses of order-III habitat selection to total forest availability within home ranges by wild turkeys of Caston Creek Wildlife Management Area (1999–2000), Quitman (2009–2010), Kemper (1991–1992), Leaf River Wildlife Management Area (1999–2000), Malmaison Wildlife Management Area (2004), and Tallahala Wildlife Management Area (1991–1992). The size of points represents the precision of coefficient estimation. Gray polygon represents 95% confidence interval.

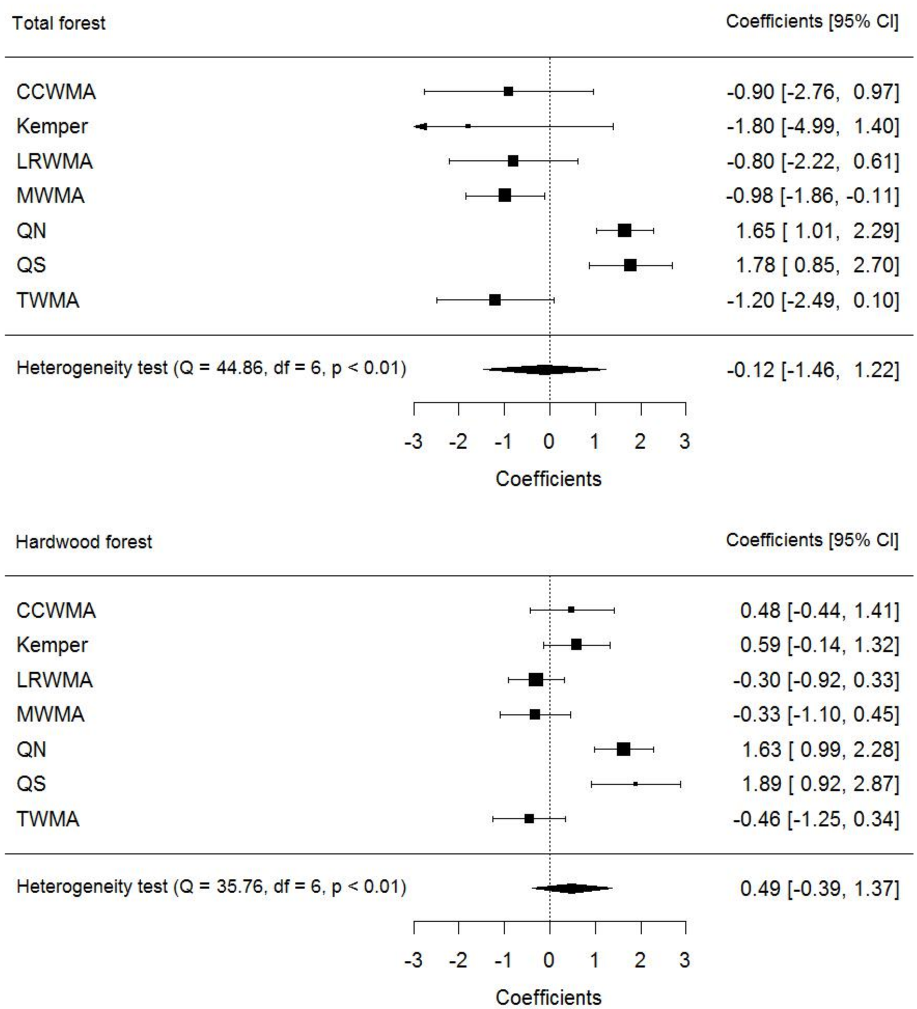

Figure 8 Heterogeneity test of order-III habitat selection of total and hardwood forests by wild turkeys of Caston Creek Wildlife Management Area (CCWMA, 1999–2000), Quitman (Quitman north[QN] and Quitman south [QS], 2009–2010), Kemper (1991–1992), Leaf River Wildlife Management Area (LRWMA, 1999–2000), Malmaison Wildlife Management Area (MWMA, 2004), and Tallahala Wildlife Management Area (TWMA, 1991–1992). Error bars represent 95% confidence intervals. Q is Cochran's Q statistic for heterogeneity test.

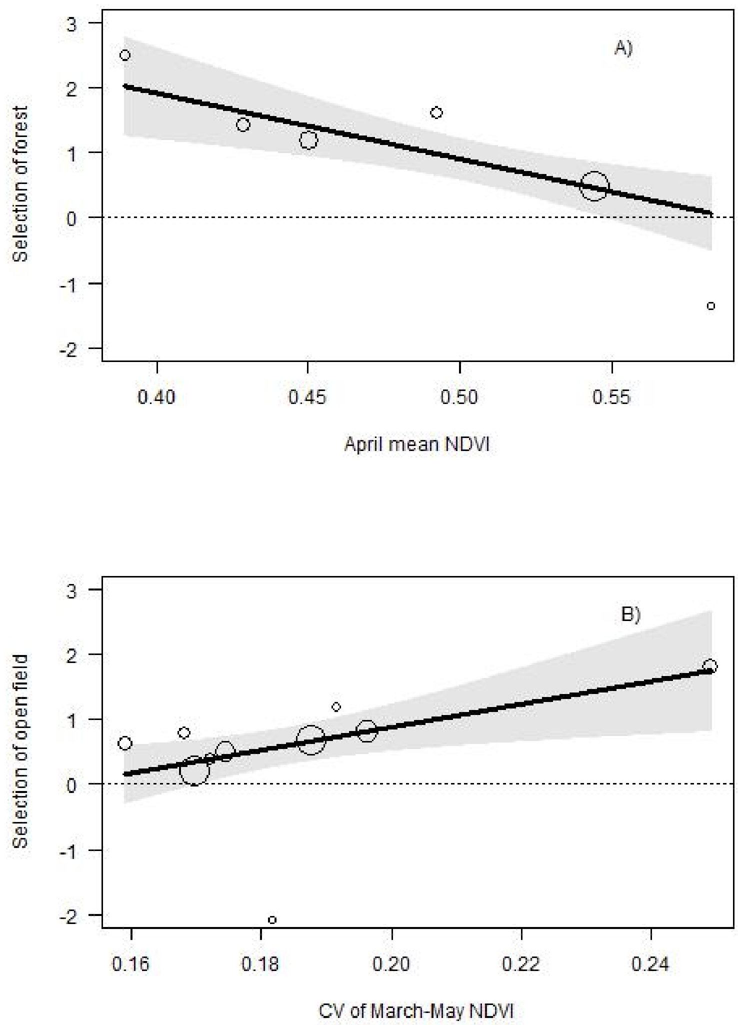

Figure 9 Meta-regression of the effects of (A) the normalized difference vegetation index (NDVI) on order-II habitat selection of forest during April and (B) Coefficient of variation (CV) of NDVI on order-II habitat selection of open field from March to May by wild turkeys in Tallahala Wildlife Management Area, 1984–1995. The size of points reflects the precision of coefficient estimation. Gray polygon represents 95% confidence intervals. In (B), an influential value which affected positive slope was observed by a diagnostic test.

CHAPTER IV

DISCUSSION

Study 1: Spatial variation in space use by eastern wild turkeys

I found that wild turkeys used both total and hardwood forests at a daily movement scale for order-III habitat selection. I suggest that meta-analysis models can be better models for testing the functional responses in order-III habitat selection than GLMMs. My results supported the prediction that wild turkeys exhibited negative functional responses in order-III habitat selection of total forests to increasing total forest availability within the home range. However, I did not find functional responses to hardwood forests. My results also supported the prediction that wild turkeys displayed region-specific variation in order-III habitat selection of both total and hardwood forests (Table 4).

Testing the optimal spatial scale by which organisms select land cover types is of crucial importance for understanding the spatial extent of habitat selection on heterogeneous landscapes. Understanding the appropriate spatial scale for habitat selection helps wildlife managers develop the landscape configuration with different land cover types to improve habitat quality (Laforge et al. 2015a, 2015b). The size of the optimal spatial scale for each land cover type may differ depending on types of animal activities (Laforge et al. 2015b). Laforge et al. (2015b) indicated that white-tailed deer selected cover at a smaller spatial scale than deer selected areas with food. I observed that wild turkeys selected forests at a small spatial scale (i.e., daily movement scale). Not only food and loafing, forests provide cover to wild turkeys when encountering predators (Fleming and Porter 2015). Thus, wild turkeys' order-III habitat selection for forests at the small spatial scale may be indicative of anti-predatory responses.

My study also applied a new method with meta-analysis and bootstrapping for assessing functional responses in order-III habitat selection by wild turkeys. To estimate individual variation in order-III habitat selection for land cover types, GLMMs are a commonly recommended method (Gillies et al. 2006, Hebblewhite and Merrill 2009). GLMMs can handle unequal sample sizes between individuals and account for individual variation in behaviors. However, GLMMs cannot account for estimation uncertainties and data heterogeneities, resulting from different data collection methods and different observers among different studies. On the other hand, meta-analysis considers the parameter estimation uncertainties of the original studies and data heterogeneities to draw robust inferences (Schwarzer et al. 2015). In addition, I used bootstrapping methods in meta-analyses to mitigate the effects of spatial autocorrelation among telemetry locations and to standardize sample sizes among individuals. In my study, GLMMs did not detect negative functional responses to either total or hardwood forests. However, meta-analyses revealed that individual variation in total forest selection by wild turkeys among the 7 sites may result from negative functional responses to increasing total forest availability within the home range.

Considering functional responses is critically important for evaluating habitat selection because functional responses may mask habitat selection patterns due to changing resource availability (Mysterud and Ims 1998). The behavioral mechanism of functional responses in habitat selection is ascribed to the trade-off between multiple habitats under constant habitat preferences and varying habitat availability (Van Moorter et al. 2013). Wild turkeys might exhibit the functional responses in habitat selection when the turkeys experienced a trade-off between foraging and antipredator (Godvik et al. 2009). Wild turkeys in Quitman, where most parts of landscapes were covered by agricultural fields, might select forests more intensely for cover from predation, while wild turkeys in TWMA, where most landscapes were forested, might select other habitats over forests for food resources or other reasons (e.g., breeding behavior). Niedzielski and Bowman (2014) suggested a possibility of functional responses to several land cover types (e.g., deciduous forest, conifer forest, and mixed forest) in wild turkeys, demonstrating that strength of order-III habitat selection changed at different times of a year (i.e., temporally varying resource availability). Other avian species, such as little owls (*Athene noctua*) and greater sage-grouse (*Centrocercus urophasianus*), were also found to modulate the strength of habitat selection as a function of resource availability, weather, and seasons (Sunde et al. 2014, Sandford et al. 2017).

However, I also observed regional difference in turkey habitat selection to total forest. Animals can modify their space use pattern according to the environmental variation (Scheiner 2013). For instance, the frequency of prescribed burning largely can change the pattern of wild turkey habitat selection because the fire creates the early successional forest, which is preferred by wild turkeys (Miller and Conner 2007, Little et al. 2016). In my study, I missed the detail within total forest which could vary wild turkey habitat selection at the population level. Therefore, unstudied region-specific factors could be also related to turkey habitat selection to total forest.

Wild turkeys did not show functional responses to hardwood forest availability but exhibited region-specific variation in hardwood selection (Table 4, Figure 8). Amounts of hardwood forests varied from 19% to 35% among 5 WTMRs, whereas amounts of total forest differed from 19% to 60%, with the Mississippi Delta having about 19% of land covered by hardwoods or forests (Davis 2016). It is possible that hardwood forests were a limiting habitat component in all the 5 regions; thus, the amount of hardwood forests on landscapes was too low to exhibit functional responses, unlike relatively abundant total forests (about 1.7 to 2.7 times hardwood forest amounts, Table 2.1 of Davis 2016).

Other reasons could be the difference in hardwood species composition among study sites. At Mississippi, the regions with different soil types, elevation, and frequency of flooding create different forest types (Hurst and Dickson 1992, MDWFP 2012). Therefore, it is possible that such varying forest types result in different hardwood species composition among sites. In fact, some dominant hardwood species were different among study sites (e.g., pecan, black gum, and dogwood; Seiss 1989, Jones 2001, Holder 2006, Miller and Conner 2007, Marable 2012). Such difference in food availability could change the degrees of turkey's preference to hardwood forest among study sites.

Temporal mismatch of the study period from when turkeys use hardwood forests might also cause region-specific differences in habitat selection without functional responses. My study period is during March to August, but wild turkeys mainly consume hardwood mast (e.g. acorns) from autumn to winter season (Hurst 1992, Barnett and Barnett 2008). Because turkeys might less likely use hardwood mast during March to

August than during autumn to winter season, many of the selection coefficients to hardwood forest could be insignificant to exhibit functional responses.

In conclusion, my approach provided three insights for wild turkey habitat selection: 1) daily movement scale as the optimal spatial scale of order-III habitat selection by wild turkeys; 2) negative functional responses of total forest selection; and 3) region-specific variation in habitat selection for both total and hardwood forests. I recommend using meta-analyses to assess functional responses in habitat selection in the future study. Researchers may also need to consider amounts of hardwood forests within study sites and the reproductive status of wild turkeys when investigating functional responses to hardwood forest availability.

Study 2: Temporal variation in space use by eastern wild turkeys

I found that wild turkeys used annual movement scale for order-II habitat selection of agriculture, developed area, forest, open field, and other land cover types. My results supported the prediction that wild turkeys reduced the selection of forests as mean NDVI increased in April. However, wild turkeys increased selection of open fields during March to May as spatial heterogeneity of green biomass increased. On the other hand, my results did not support the prediction that wild turkeys avoided temporally variable habitat types.

Wild turkeys selected home range locations at a spatially larger scale than that of order-III habitat selection as shown in my study 1. Placement of home ranges on landscapes (i.e., order-II habitat selection) may be the combined outcomes of annual activities (e.g., spring dispersal, nesting, brooding, and wintering), whereas habitat use within home ranges (i.e., order-III habitat selection) may correspond to daily activities (e.g., foraging, roosting, and loafing). This finding represents a case where spatial scales of behaviors are connected to their temporal scales. DeCesare et al. (2012) demonstrated that the larger extents of habitat selection by woodland caribou (*Rangiferr tarandus caribou*) could correspond to larger spatial scales of habitat availability, as suggested by Johnson's hierarchical habitat selection (Johnson 1980). Therefore, spatial scale-dependent habitat selection should be considered in future studies of mobile birds.

The inverse relationship between wild turkey order-II habitat selection of forest and mean April NDVIs may indicate the negative functional responses of order-II habitat selection to the timing of nesting. In April, female wild turkeys may nest and hatch eggs, while males may follow females' movement for mating opportunities (Miller et al. 2000, Barnett and Barnett 2008). Well-grown vegetation in April can provide wild turkeys with concealment at nesting sites (Hurst 1992, Badyaev 1995, Nguyen et al. 2004). In my study, wild turkeys were less selective to forested area in a year of well-grown vegetation. Turkeys could have already started nesting and stayed closer to the other fields to rear offspring, such as forest opening (Pollentier et al. 2017). On the other hand, when the vegetation growth is less, turkeys might delay their reproductive activity and select hardwood forests as turkeys stayed during winter (Niedzielski and Bowman 2016). Such an adaptive phenotypic plasticity by environmental change is supported by great tits (*Parus major*), which delayed laying date with decreasing spring temperature (Charmantier et al. 2008).

Wild turkeys placed home ranges overlapping increasing amount of open fields during April, March to May, and March to September, possibly because young birds needed invertebrates in open fields as a food resource during nesting and brood-rearing seasons (Hurst 1992, Jones et al. 2005, Streich et al. 2015). In addition, I found that the selection of open field by wild turkeys was related positively to the CVs of the NDVI in March to May. The CV of the NDVI may index the vegetative heterogeneity of landscapes. At TWMA, 95% of the landscape was forested. Wild turkeys extensively use open fields when available, and increases in forest edges enhance wild turkey abundance in Mississippi (Davis 2016). Spatial variation in the NDVI may represent variation in the spatial juxtaposition of forests and small forest opening (i.e., open fields) at TWMA. Wild turkeys could increase the selection of open field intermixed with forest covers (i.e., positive functional responses; Mysterud and Ims 1998, Laforge et al. 2015a, van Beest et al. 2016). However, an influential values found by diagnostic test existed in the positive slope. So further research is necessary for this relationship.

In contrast to my hypothesis, wild turkeys did not change the positions of home ranges according to temporal variation in the NDVI, with |ΔNDVI| being unrelated to order-II habitat selection of any land cover types. A possible cause of this inconsistency is that turkeys are a generalist in terms of habitat use and an omnivore in terms of diet (Hurst 1992). In other words, wild turkeys could be very malleable and can adapt to inter-year changes in local condition. The other problem is the sparse data of |ΔNDVI| images. I could not derive NDVI images for all months of annual seasons because of clouds. The more precise |ΔNDVI| values might have allowed me to detect the effects of |ΔNDVI| on order-II habitat selection by wild turkeys.

My study 2 investigated how spatiotemporal changes in vegetative greenness, a surrogate of food availability, may influence order-II habitat selection by wild turkeys. However, I did not investigate demographic consequences of variation in order-II habitat selection. Several studies found that wild turkeys had lower survival probabilities during nesting and breeding seasons (Roberts et al. 1995, Miller et al. 1998, Hubbard et al. 1999). In the nesting and breeding seasons, I found that order-II habitat selection by wild turkeys was related inversely to the mean NDVIs. Marable (2012) found that the amount of spring precipitation could be related inversely to survival of wild turkeys. Precipitation in April substantially affects vegetative growth. Hence, understanding the effect of variation in habitat selection on the demographic rates of wild turkeys will help wild turkey biologists determine pathways, through which environmental factors, such as precipitation and NDVI, determine movements of wild turkeys, leading to variation in the demographic rates in the end.

In conclusion, my findings provide three insights into the spatiotemporal use of wild turkeys: 1) annual movement scale as optimal spatial scale of order-II habitat selection for agriculture, developed area, forest, open field, and other land cover types; 2) negative functional responses in order-II habitat selection of forest land cover to increasing mean NDVIs in April; and 3) positive functional responses in open field selection to increasing the spatial CVs of NDVI in March to May. Future work needs to investigate how inter-year variation in habitat selection by wild turkeys could affect the demographic rates.

Synthesis

I demonstrated that the extents of habitat selection by wild turkeys (i.e., order-II and order-III) corresponded to annual and daily movement scales, respectively. I also observed that wild turkeys exhibited functional responses in both order-II and III habitat selection to spatiotemporally varying forest resource availability. Wild turkeys selected more forested areas when the availability of forest within home ranges or mean April NDVIs were lower. However, selection of forests by wild turkeys decreased as forest availability within home ranges or mean April NDVIs increased. Wild turkeys did not show functional responses to hardwood forest availability, possibly due to limited hardwood availability at my study sites, missing information on hardwood species composition, and temporal mismatch of my study period from intense turkey habitat use to hardwoods. Last, order-II habitat selection of open fields was related positively to the CVs of NDVI in March to May, suggesting that wild turkeys could increase selection of open fields when landscapes were heterogeneous.

Management implications

This is the first study that tested functional responses in turkey habitat selection to total forest. My results suggest that wild turkeys requires 60–80% total forests for habitat component within the home ranges (Figure 7). As Davis (2016) suggested, wild turkey managers need to create heterogeneous landscapes, especially as the threshold of 60–80% total forests from my study, for improving wild turkey habitat quality.

Many different studies have demonstrated wild turkeys' affinity for hardwood forests (McKinney 2013, McShea et al. 2015, Davis 2016). However, my results suggest that wild turkey selection of hardwoods can vary from place to place. The difference I found in selection intensity could be a result of conditions unique to individual sites; features related to the surrounding landscape (Miller 1997, Inglis 2001, Jones 2001, Holder 2006, Miller and Conner 2007, Marable 2012), within-stand differences such as tree species composition (Hurst 1992), or the synergistic effects of both could all influence the relative importance hardwood stands play in meeting the biological requirements of wild turkeys at a given location. Therefore, there cannot be one general wild turkey hardwood management applied to any regions.

REFERENCES

Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49:340–346.

Badyaev, A. V. 1995. Nesting habitat and nesting success of eastern wild turkeys in the Arkansas Ozark highlands. The Condor 97:221–232.

Bailey, R. W. 1976. Live-trapping wild turkeys in North Carolina. North Carolina Wildlife Resources Commission Publication, Raleigh, North Carolina, USA.

Barnett, S. W., and V. S. Barnett. 2008. The Wild Turkey in Alabama. The Alabama Department of Conservation and Natural Resources, Division of Wildlife and Freshwater Fisheries, Montgomery, Alabama, USA.

Bartoń, K. 2016. MuMIn: Multi-model inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models Using lme4. Journal of Statistical Software 67:1–48.

van Beest, F. M., P. D. McLoughlin, A. Mysterud, and R. K. Brook. 2016. Functional responses in habitat selection are density dependent in a large herbivore. Ecography 39:515–523.

Bell, A. M., S. J. Hankison, and K. L. Laskowski. 2009. The repeatability of behaviour: a meta-analysis. Animal Behaviour 77:771–783.

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

Butler, A. B., G. Wang, and K. D. Godwin. 2015. Using avid hunter and brood surveys to predict hunter success and assess regulatory changes in spring gobbler seasons. Proceedings of the National Wild Turkey Symposium 11:225–235.

Byrne, M. E., and M. J. Chamberlain. 2015. Using behavior and space use of raccoons to indirectly assess the nature of nest predation. Proceedings of the National Wild Turkey Symposium 11:283–293.

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.

Chamberlain, M. J., B. D. Leopold, and L. W. Burger. 2000. Characteristics of roost sites of adult wild turkey females. Journal of Wildlife Management 64:1025–1032.

Charmantier, A., R. H. Mccleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, and B. C. Sheldon. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320:800–804.

Charnov, E. l. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129–136.

Cochran, W. W., and R. D. Lord. 1963. A radio-tracking system for wild animals. Journal of Wildlife Management 27:9–24.

Conley, M. D., J. G. Oetgen, J. Barrow, M. J. Chamberlain, K. L. Skow, and B. A. Collier. 2015. Habitat selection, incubation, and incubation recess ranges of nesting female Rio Grande wild turkeys in Texas. Proceedings of the National Wild Turkey Symposium 11:117–126.

Davies, N. B., J. R. Krebs, and S. A. West. 2012. Introduction to behavioural ecology. Fourth edition. Wiley-Blackwell, Chichester, West Sussex, UK.

Davis, A. M. 2016. Landscape ecology of eastern wild turkeys in Mississippi. Thesis, Mississippi State University, Mississippi State, Mississippi, USA.

DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. Mcdermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, L. E. Morgantini, M. Wheatley, and M. Musiani. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22:1068–1083.

Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Animal Behaviour 30:1183–1192.

Dreibelbis, J. Z., K. L. Skow, J. B. Hardin, M. J. Peterson, N. J. Silvy, and B. A. Collier. 2015. Nest habitat selection by Rio Grande wild turkeys on the edwards plateau of Texas. Proceedings of the National Wild Turkey Symposium 11:107–116.

Eriksen, B., J. Cardoza, J. Pack, and H. Kilpatrick. 1993. Procedures and guidelines for rocket-netting wild turkeys. NWTF Technical Bulletin No 1. National Wild Turkey Federation. Edgefield, South Carolina, USA.

Eriksen, R. E., T. W. Hughes, T. A. Brown, M. D. Akridge, K. B. Scott, and C. S. Penner. 2015. Status and distribution of wild turkeys in the United States: 2014 status. Proceedings of the National Wild Turkey Symposium 11:7–18.

Fleming, K. K., and W. F. Porter. 2015. Comparison of landscape, patch, and local habitat effects on risk of predation of artificial wild turkey nests. Proceedings of the National Wild Turkey Symposium 11:271–282.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey, USA.

Fretwell, S. D., and H. L. Lucas Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds - I. Theoretical development. Acta Biotheoretica 19:16–36.

Frost, C. C., J. Walker, and R. K. Peet. 1986. Fire-dependent savannas and prairies of the Southeast: original extent, preservation status, and management problems. Pages 348–357 *in* D. L. Kulhavy and R. N. Conner, editors.Wilderness and natural areas in the eastern United States: a management challenge. Center for Applied Studies, School of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Geffen, E., R. Hefner, D. W. Macdonald, and M. Ucko. 1992. Habitat selection and home range in the blanford's fox, *vulpes cana*: Compatibility with the resource dispersion hypothesis. Oecologia 91:75–81.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Godvik, I. M. R., L. E. Loe, J. O. Vik, V. Veiberg, R. Langvatn, and A. Mysterud. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology 90:699–710.

Godwin, K. D. 1991. Habitat use, home range size, and survival rates of wild turkey gobblers on Tallahala Wildlife Management Area. Thesis, Mississippi State University, Mississippi State, Mississippi, USA.

Goslee, S. C. 2011. Analyzing remote sensing data in R : The landsat package. Journal of Statistical Software 43:1–25.

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

Groepper, S. R., S. E. Hygnstrom, B. Houck, and S. M. Vantassel. 2015. Real and perceived damage by wild turkeys: A literature review. Proceedings of the National Wild Turkey Symposium 11:371–377.

Healy, W. M. 1992. Behavior. Pages 46–65 *in* J. G. Dickson, editor.The wild turkey: Biology and management. Stackpole, Mechanisburg, Pennsylvania, USA.

Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology 45:834–844.

Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445–3454.

Hedges, L. V., and I. Olkin. 1985. Statistical methods for meta-analysis. Academic Press, San Diego, California, USA.

Herfindal, I., J. P. Tremblay, B. B. Hansen, E. J. Solberg, M. Heim, and B. E. Sæther. 2009. Scale dependency and functional response in moose habitat selection. Ecography 32:849–859.

Hijmans, R. 2016. raster: Geographic data analysis and modeling. R package version 2.5-8.

Hirzel, A. H., J. H. Ausser, and D. C. Hessel. 2002. Ecological-Niche Factor Analysis: How to compute habitat-suitability maps without absence data? Ecology 83:2027–2036.

Hobbs, N. T. 2003. Challenges and opportunities in integrating ecological knowledge across scales. Forest Ecology and Management 181:223–238.

Holder, B. D. 2006. Survival, habitat use, and nest-site characteristics of wild turkeys in central Mississippi. Thesis, Mississippi State University, Mississippi State, Mississippi, USA.

Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345–354.

Hubbard, M. W., D. L. Garner, and E. E. Klaas. 1999. Factors influencing wild turkey hen survival in southcentral Iowa. Journal of Wildlife Management 63:731.

Hurst, G. A. 1992. Foods and feeding. Pages 66–83 *in* J. G. Dickson, editor.The wild turkey: Biology and management. Stackpole, Mechanicsburg, Pennsylvania, USA.

Hurst, G. A., and J. G. Dickson. 1992. Eastern turkey in southern pine-oak forests. Pages 265–285 *in* J. G. Dickson, editor.The wild turkey: Biology and management. Stackpole, Mechanicsburg, Pennsylvania, USA.

Inglis, J. E. 2001. Reproductive ecology and survival of eastern wild turkey hens in a managed longleaf pine system in southeastern Mississippi. Thesis, Mississippi State University, Mississippi State, Mississippi, USA.

Johnson, D. D. P., R. Kays, P. G. Blackwell, and 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.

Jones, B. C. 2001. Wild turkey reproductive ecology on a fire-maintained national forest in Mississippi. Thesis, Mississippi State University, Mississippi State, Mississippi, USA.

Jones, B. C., J. E. Inglis, and G. A. Hurst. 2005. Wild turkey brood habitat use in relation to prescribed burning and red-cockaded woodpecker management. Proceedings of the National Wild Turkey Symposium 9:209–215.

Kennamer, J. E., M. Kennamer, and R. Brenneman. 1992. History. Pages 6–17 *in* J. G. Dickson, editor.The wild turkey: Biology and management. Stackpole, Mechanicsburg, Pennsylvania, USA.

Knapp, G., and J. Hartung. 2003. Improved tests for a random effects meta-regression with a single covariate. Statistics in Medicine 22:2693–2710.

Knowlton, F. F., E. D. Michael, and W. C. Glazener. 1964. A marking technique for field recognition of individual turkeys and deer. Journal of Wildlife Management 28:167–170.

Laforge, M. P., R. K. Brook, F. M. van Beest, E. M. Bayne, and P. D. McLoughlin. 2015a. Grain-dependent functional responses in habitat selection. Landscape Ecology 31:855–863.

Laforge, M. P., E. Vander Wal, R. K. Brook, E. M. Bayne, and P. D. McLoughlin. 2015b. Process-focussed, multi-grain resource selection functions. Ecological Modelling 305:10–21.

Lambert, E. P., W. P. Smith, and R. D. Teitelbaum. 1990. Wild turkey use of dairy farm-timberland habitats in southeastern Louisiana. Proceedings of the National Wild Turkey Symposium 6:55–64.

Leclerc, M., E. Vander Wal, A. Zedrosser, J. E. Swenson, J. Kindberg, and F. Pelletier. 2016. Quantifying consistent individual differences in habitat selection. Oecologia 180:697–705.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Little, A. R., M. J. Chamberlain, L. M. Conner, and R. J. Warren. 2016. Habitat selection of wild turkeys in burned longleaf pine savannas. Journal of Wildlife Management 80:1280–1289.

Macdonald, D. W., and D. D. P. Johnson. 2015. Patchwork planet: the resource dispersion hypothesis, society, and the ecology of life. Journal of Zoology 295:75–107.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: Statistical design and analysis for field studies. Second edition. Kluwer Academic Publisher, Dordrecht, the Netherlands.

Marable, K. 2012. Movement, space use, and cause-specific mortality of translocated wild turkeys in the Mississippi Delta. Thesis, Mississippi State University, Mississippi State, Mississippi, USA.

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

Matthiopoulos, J., J. Fieberg, G. Aarts, H. L. Beyer, J. M. Morales, and D. T. Haydon. 2015. Establishing the link between habitat selection and animal population dynamics. Ecological Monographs 85:413–436.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.

McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31:1161–1175.

McKinney, M. R. 2013. Microhabitat use by translocated wild turkeys in the Mississippi Delta. Thesis, Mississippi State University, Mississippi State, Mississippi, USA.

McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010. Considering ecological dynamics in resource selection functions. Journal of Animal Ecology 79:4–12.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. American Naturalist 97:133–140.

McShea, W. J., W. M. Healy, and P. Van Deusen. 2015. Trends in mast availability for wild turkeys in eastern forests. Proceedings of the National Wild Turkey

Symposium 11:61–78.

MDWFP. 2012. Spittin' & Drummin' 2012 Mississippi Wild Turkey Report. Jackson, Mississippi, USA.

Miller, D. A. 1997. Habitat relationships and demographic parameters of an eastern wild turkey population in central Mississippi. Dissertation, Mississippi State University, Mississippi State, Mississippi, USA.

Miller, D. A., L. W. Burger, B. D. Leopold, and G. A. Hurst. 1998. Survival and cause-specific mortality of wild turkey hens in central Mississippi. Journal of Wildlife Management 62:306–313.

Miller, D. A., and L. M. Conner. 2005. Seasonal and annual home ranges of female eastern wild turkeys in a managed pine landscape in Mississippi. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 59:89–99.

Miller, D. A., and L. M. Conner. 2007. Habitat selection of female turkeys in a managed pine landscape in Mississippi. Journal of Wildlife Management 71:744–751.

Miller, D. A., G. A. Hurst, and B. D. Leopold. 1999. Habitat use of eastern wild turkeys in central Mississippi. Journal of Wildlife Management 63:210–222.

Miller, D. A., B. D. Leopold, G. A. Hurst, and P. D. Gerard. 2000. Habitat selection models for eastern wild turkeys in central Mississippi. Journal of Wildlife Management 64:765–776.

Moorcroft, P. R. 2012. Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. Journal of Mammalogy 93:903–916.

Van Moorter, B., C. M. Rolandsen, M. Basille, and J. M. Gaillard. 2016. Movement is the glue connecting home ranges and habitat selection. Journal of Animal Ecology 85:21–31.

Van Moorter, B., D. Visscher, S. Benhamou, L. Börger, M. S. Boyce, and J. M. Gaillard. 2009. Memory keeps you at home: A mechanistic model for home range emergence. Oikos 118:641–652.

Van Moorter, B., D. Visscher, I. Herfindal, M. Basille, and A. Mysterud. 2013. Inferring behavioural mechanisms in habitat selection studies getting the null-hypothesis right for functional and familiarity responses. Ecography 36:323–330.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79:1435–1441.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and 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.

Nguyen, L. P., J. Hamr, and G. H. Parker. 2004. Nest site characteristics of Eastern Wild Turkeys in central Ontario. Northeastern Naturalist 11:255–260.

Niedzielski, B., and J. Bowman. 2014. Survival and cause-specific mortality of the female eastern wild turkey at its northern range edge. Wildlife Research 41:545–551.

Niedzielski, B., and J. Bowman. 2016. Home range and habitat selection of the female eastern wild turkey at its northern range edge. Wildlife Biology 22:55–63.

Palmer, W. E. 1990. Relationships of wild turkey hens and their habitat on Tallahela Wildlife Management Area. Thesis, Mississippi State University, Mississippi State, Mississippi, USA.

Pelham, P. H., and J. G. Dickson. 1992. Physical characteristics. Pages 32–45 *in* J. G. Dickson, editor.The wild turkey: Biology and management. Stackpole, Mechanicsburg, Pennsylvania, USA.

Pettorelli, N. 2013. The normalized difference vegetation index. First edition. Oxford University Press, Great Clarendon Street, Oxford, UK.

Pettry, D. E. 1977. Soil resource areas of Mississippi. Mississippi Agricultural and Forestry Experiment Station, Invormation Sheet 1278, Mississippi State University, Mississippi State, Mississippi, USA.

Phalen, P. S. 1986. Reproduction, brood habitat use, and movement of wild turkey hens in East-Central Mississippi. Thesis, Mississippi State University, Mississippi, USA.

Pollentier, C. D., R. S. Lutz, and D. Drake. 2017. Female wild turkey habitat selection in mixed forest-agricultural landscapes. Journal of Wildlife Management 81:487–497.

Porter, W. F. 1992. Habitat requirements. Pages 202–213 *in* J. G. Dickson, editor.The wild turkey: Biology and management. Stackpole, Mechanicsburg, Pennsylvania, USA.

Porter, W. F., E. Lansing, C. A. Stewart, and C. J. Parent. 2015. Summary of the 11th National Wild Turkey Symposium. Proceedings of the National Wild Turkey Symposium 11:407–410.

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, S. D., J. M. Coffey, and W. F. Porter. 1995. Survival and reproduction of female wild turkeys in New York. Journal of Wildlife Management 59:437–447.

Rosenzweig, M. L. 1981. A theory of habitat selection. Ecology 62:327–335.

Rouse, J. W., R. H. Haas, and J. A. Schell. 1974. Monitoring the vernal advancement and retrogradation (greenwave effect) of natural vegetation. Texas A & M University, College Station, Texas, USA.

Sánchez-Clavijo, L. M., J. Hearns, and P. F. Quintana-Ascencio. 2016. Modeling the effect of habitat selection mechanisms on population responses to landscape structure. Ecological Modelling 328:99–107.

Sandford, C. P., M. T. Kohl, T. A. Messmer, D. K. Dahlgren, A. Cook, and B. R. Wing. 2017. Greater sage-grouse resource selection drives reproductive fitness under a conifer removal strategy. Rangeland Ecology and Management 70:59–67.

Scheiner, S. M. 2013. The genetics of phenotypic plasticity: XII: Temporal and spatial heterogeneity. Ecology and Evolution 3:4596–4609.

Schwarzer, G., J. R. Carpenter, and G. Rücker. 2015. Meta-analysis with R. Springer, New York, USA.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management:739–747.

Seiss, R. S. 1989. Reproductive parameters and survival rates of wild turkey hens in east-central Mississippi. Thesis, Mississippi State University, Mississippi State, Mississippi, USA.

Signer, J., N. Balkenhol, M. Ditmer, and J. Fieberg. 2015. Does estimator choice influence our ability to detect changes in home-range size? Animal Biotelemetry 3:1–9.

Smith, D. R., G. A. Hurst, J. D. Burk, and B. D. Leopold. 1990. Use of loblolly pine plantations by wild turkey hens in east-central Mississippi. Proceedings of the National Wild Turkey Symposium 6:61–66.

Streich, M. M., A. R. Little, M. J. Chamberlain, L. M. Conner, and R. J. Warren. 2015. Habitat characteristics of eastern wild turkey nest and ground-roost sites in 2 longleaf pine forests. Journal of the Southeast Association of Fish and Wildlife Agencies 2:164–170.

Sunde, P., K. Thorup, L. B. Jacobsen, and C. Rahbek. 2014. Weather conditions drive dynamic habitat selection in a generalist predator. PLoS ONE 9:1–12.

Tardy, O., A. Massé, F. Pelletier, J. Mainguy, and D. Fortin. 2014. Density-dependent functional responses in habitat selection by two hosts of the raccoon rabies virus variant. Ecosphere 5:1–16.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. Journal of Statistical Software 36:1–48.

Weinstein, M. D. 1994. Experimental designs for estimating wild turkey population size and reproduction using bait size counts and radio-telemetry. Thesis, Mississippi State University, Mississippi, USA.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7:81–120.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Williams Jr., L. E., D. H. Austin, and J. Peoples. 1967. Progress in capturing turkeys with drugs applied to baits. Proceedings of the Southeastern Association of Game and Fish Commissioners 20:219–226.

Zar, J. H. 2010. Biostatistical analysis. Fifth edition. Prentice-Hall, New Jersey, USA.