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Influences of landscape characteristics on the nesting ecology of female wild turkeys and behavior of raccoons

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INFLUENCES OF LANDSCAPE CHARACTERISTICS ON THE NESTING
ECOLOGY OF FEMALE WILD TURKEYS AND BEHAVIOR OF RACCOONS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The School of Renewable Natural Resources

By
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Abstract

Nest predation is the principle source of reproductive failure in many bird species. Understanding nest predation requires knowledge of interactions between landscape characteristics, and the ecology and behavior of birds and local nest predators. I studied nesting ecology and multi-scale habitat selection of female wild turkeys and the habitat selection and searching behaviors of raccoons, an important nest predator, in a bottomland hardwood forest in Louisiana. My objective was to evaluate the relationships between habitat, wild turkey nest site selection, and raccoon foraging behavior. I used first-passage time (FPT) analysis on nightly foraging tracks of raccoons during the turkey nesting period to test the applicability of the method to a terrestrial predator, determine whether raccoons engage in area-restricted searching (ARS), and to identify areas of concentrated searching activity. Mean turkey home ranges sizes varied from 673ha during pre-incubation to 363ha during brood-rearing. Mature upland forests were selected by turkeys year round. Wild turkeys nested in upland forests ($n = 35$) and openings ($n = 6$) offering understory cover, often close to forest edges. Wild turkey reproduction was characterized by low nesting rates (60%) and average nest success rates (39%), and nest predation was the leading cause of nest failure (34%). Mean raccoon home range sizes ranged from 177ha during breeding to 120ha during summer. Seasonal habitat selection varied, presumably as a response to spatio-temporal changes in food availability. Evidence of ARS was found in 55 of 58 paths analyzed and could be induced by supplemental feeding, validating the assumption that ARS represented foraging activity. ARS was associated with lower elevations and shallow standing water, whereas raccoons moved quickly through upland forest habitats with sparse understory

vegetation. These results suggest that nest predation by raccoons is incidental rather than the result of targeted searching in habitats with similar structure to those selected by wild turkeys for nesting in this system. This represents the first time FPT has been applied to a terrestrial predator and researchers should consider FPT in future studies of habitat use and foraging ecology of terrestrial predators.

Introduction

Nest predation has been identified as a primary cause of nest loss for a variety of bird species (Klett et al. 1988, Patterson et al. 1991, Heske et al. 2001, Rollins and Carroll 2001). Logically, the risk of nest predation is a function of how often potential predators encounter nests. Landscape and habitat features may influence encounter rates by concentrating predator activity in nesting areas. For example, landscape fragmentation may increase predator densities in certain habitats, which may lead to increased nest predation (Oehler and Litvaitis 1996, Dijak and Thompson 2000, Chalfourn et al. 2002), and studies on real and artificial nests have documented increased nest loss associated with high degrees of forest fragmentation or distance to forest edge (Paton 1994, Donovan et al. 1997, Heske et al. 2001). Predation is a complex phenomenon, and accurately assessing the risk of nest predation requires an understanding of the relationships between the nesting ecology of avian species, the behavior of nest predators, and the local landscape.

The nesting ecology and habitat use of wild turkeys (*Meleagris gallopavo*) has been extensively studied in a variety of upland habitats, but published information on bottomland systems, particularly in the lower Mississippi Alluvial Valley, is sparse (but see Wilson et al. 2005a, Wilson et al. 2005b). This is surprising considering bottomland hardwood forests are regarded as high quality turkey habitat (Dickson 2001). Turkeys in bottomland systems face unique conditions such as persistent annual flooding in some areas, so behavior in upland systems may not translate to turkey populations in bottomland systems. The lack of information regarding turkey behavior in bottomland forests represents a considerable gap in the knowledge of wild turkey ecology. A better

understanding of habitat use and nesting ecology in bottomland forests is needed not only to add to the general knowledge of wild turkey ecology, but also to provide important information necessary for proper management of turkey populations in these systems.

The raccoon (*Procyon lotor*) is a generalist mesopredator whose behavioral and dietary plasticity allows it to exploit a wide variety of habitats. Due in part to human alteration of the landscape, and their generalist nature, raccoon populations have experienced dramatic increases since the second half of the last century (Gehrt 2003) and their range is expanding (Gehrt 2003, Larivière 2004). Raccoons are important nest predators of a variety of ground nesting birds, including passerines (Heske et al. 2001, Schmidt 2003), colonial water-birds (Ellis et al. 2007), and game species such as wild turkey (Miller and Leopold 1992), quail (*Colinus virginianus*, Rollins and Carrol 2001), and waterfowl (Urban 1970). Additionally, raccoons are also important furbearers in some regions (Chamberlain and Leopold 2001), and serve as vectors for several diseases that affect humans and domestic animals (Gehrt 2003, Atwood et al. 2009, Rosatte et al. 2010). The potential ecological impacts that raccoons may exert on an area highlights the need for an understanding of the relationships between habitat and raccoon ecology over the wide range of ecosystems they inhabit.

General habitat requirements and life-history characteristics of raccoons are well described and aspects of home range characteristics and habitat use have been detailed in a number of habitat types, including mixed pine forests (Chamberlain et al. 2002, Chamberlain et al. 2003), fragmented agricultural areas (Dijak and Thompson 2000, Beasley et al. 2007a, Beasley et al. 2007b, Barding and Nelson 2008, Attwood et al. 2009), prairies (Fritzell 1978, Henner et al. 2004, Chamberlain et al. 2007), coastal

prairies (Gehrt and Fritzell 1997, Gehrt and Fritzell 1998), freshwater marshes (Urban 1970) and urban environments (Hoffman and Gottschang 1977, Prange et al. 2004, Bozek 2007). Notably, information within bottomland systems is lacking, although raccoons are reported to occur in higher densities in bottomland hardwood forests relative to other habitat types (Johnson 1970, Sonenshine and Winslow 1972; Leberg and Kennedy 1988, Gehrt 2003). Similar to the situation described above for wild turkeys, habitat use and behavior within these systems represents a significant gap in our understanding of raccoon ecology.

Animals live in spatially heterogeneous landscapes where resources are unevenly distributed across the environment in patches of varying scale (Johnson et al. 1992, Fauchald 1999). For example, food resources are normally concentrated in patches within the context of the larger landscape. Predators should respond to this heterogeneity by maximizing the time spent searching within profitable patches offering relatively high prey availability while minimizing time spent searching for prey in less profitable areas (Stephens and Krebs 1986). One way foragers may maximize their time in profitable areas is by altering search strategy as they move through the landscape. Specifically, an organism may move quickly and in a relatively linear fashion through non-profitable areas then adopt a more intensive searching strategy characterized by slower speeds and greater turning angles in response to stimuli, such as the location of a prey item. This behavior is commonly referred to as area-restricted search (ARS). Computer simulations have shown ARS to be an efficient method of locating and remaining in profitable areas when resources are not distributed homogeneously in space (Benhamou 1992, Zollner and Lima 1999). ARS has been observed in a wide variety of taxa in natural and laboratory

settings and may have evolved as an adaptive means of exploiting prey in heterogeneous environments (Scharf et al. 2009).

Studying movements of individuals can provide insights into population-level characteristics (Kareiva and Odell 1987, Johnson et al. 1992, Turchin 1998, Mueller and Fagan 2008), and understanding ARS behavior should be especially useful in working towards identifying links between behavior and habitat. Because organisms should engage in intensive searching in areas that provide valuable resources, identifying habitat characteristics associated with intensive searching should help identify habitat features important to a species in a given landscape. Similarly, identifying habitat characteristics associated with more extensive movements should offer insight into the type of areas an animal is likely to avoid, or potentially the landscape features that serve as movement corridors.

Thanks to recent advances in animal tracking technology, a number of studies have attempted to link movement behavior and habitat in vertebrates. Much of this work has been focused on pelagic marine organisms such as turtles (McCarthy et al. 2010), marine mammals (Freitas et al. 2008) and sea-birds (Pinaud and Weimerskirch 2005, Suryan et al. 2006, Weimerskirch et al. 2007, Hammer et al. 2009, Kappes et al. 2010, Paiva et al. 2010, Scheffer et al. 2010). Similar studies focusing on free-roaming terrestrial vertebrates have been less common (Morales et al. 2004, Frair et al. 2005, Forester et al. 2007, Le Corre et al. 2008), with studies of terrestrial predators comparatively rare (Dickson et al. 2005, Valeix et al. 2010).

By synthesizing the influence of landscape on wild turkey nest site selection as well as raccoon habitat selection and movement behaviors, it should be possible to assess

the relative risk that raccoons pose to wild turkey reproduction in bottomland hardwood systems. For example, risk could be said to be high if turkeys choose to nest in areas that simultaneously concentrate raccoon use (such as foraging habitats in which raccoons engage in ARS, or highly selected habitat types within raccoon home ranges) because the probability of raccoons finding and destroying nests would be high. Conversely, risk could be said to be low if turkeys nest in areas that are not likely to concentrate raccoon use. Because nesting success has been identified as an important parameter influencing turkey population size (Roberts and Porter 1996) and nest predation has been identified as a major cause of nest loss (Hurst et al. 1996), this information can potentially be used to improve wild turkey populations by guiding land management decisions in ways that may reduce nest predation by raccoons.

The specific objectives of the study are as follows:

1. To provide estimates of seasonal space use and to determine habitat selection at multiple spatial scales for adult female wild turkeys in a bottomland hardwood forest.
2. To assess female wild turkey survival and cause specific mortality.
3. To provide estimates of seasonal space use and to determine habitat selection at multiple spatial scales for raccoons in a bottomland hardwood forest.
4. To study and describe wild turkey nesting ecology in a bottomland hardwood system. Specifically, the goals are to determine nest site selection at multiple spatial scales, derive estimates of reproductive parameters, describe nesting phenology, and to assess specific causes of nest mortality.
5. To apply FPT analysis to the nightly movements of raccoons to assess the applicability of the method to a terrestrial mammalian predator and to describe the presence and scale

of ARS behavior, as well as to link habitat characteristics to changes in movement behavior.

6. To use information obtained on wild turkey nest site selection and raccoon habitat use and movement behaviors to assess the risk of raccoons to wild turkey reproduction in a bottomland hardwood forest system.

Study Area Description

I conducted research on a 17,243 ha tract (hereafter Sherburne) of bottomland hardwood forest in Iberville, St. Martin, and Point Coupee parishes, Louisiana, located in the Atchafalaya floodway system. Sherburne included Sherburne Wildlife Management Area (4,767 ha) owned by the Louisiana Department of Wildlife and Fisheries (LDWF), Bayou des Ourses (6,317 ha) owned by the United States Army Corps of Engineers, and the Atchafalaya National Wildlife Refuge (6,159 ha) owned by the United States Fish and Wildlife Service. Additionally, there were approximately 770 ha of private lands interspersed throughout the state and federal lands. Sherburne was bordered on the south by Interstate 10, on the north by Highway 190, on the west by the Atchafalaya River, and the east by the East Protection Guide Levee.

Individual overstory species most commonly found on Sherburne included eastern cottonwood (*Populus deltoids*), willow oak (*Quercus phellos*), nuttall oak (*Q. texana*), water oak (*Q. nigra*), overcup oak (*Q. lyrata*), sweetgum (*Liquidambar styraciflua*), sugarberry (*Celtis laevigata*), green ash (*Fraxinus pennsylvanicus*), black willow (*Salix nigra*), and baldcypress (*Taxodium distichum*). Midstory was composed primarily of boxelder (*Acer negundo*), Drummond red maple (*Acer rubrum drummondii*), black cherry (*Prunus serotina*), red mulberry (*Morus rubra*), Chinese tallow tree (*Triadica sebifera*), and rough-leaf dogwood (*Cornus drummondii*). Understory vegetation was relatively sparse because of shading and annual persistent flooding. Common understory vegetation included rattan vine (*Berchemia scandens*), greenbrier (*Smilax* spp.), blackberry (*Rubus* spp.), bedstraw (*Gallium* spp.), horsetail (*Equisetum hyemale*), trumpet creeper (*Campsis radicans*), Virginia creeper (*Parthenocissus quinquefolia*),

wild carrot (*Daucus cartota*), stinging nettle (*Urtica chamaedryoides*), poison ivy (*Toxicodendron radicans*), southern shield fern (*Thelypteris kunthii*), and elderberry (*Sambucus canadensis*). Wildlife food plots dominated forest openings and were comprised primarily of brown top millet (*Panicum ramosum*), wheat (*Triticum* spp.) and/or sunflowers (*Helianthus* spp.). Sherburne was bisected by a number of rights-of-way (electric and natural gas), which were maintained through mowing and herbicide application. Remaining openings consisted of levees or natural regeneration from forest cuts. Dominant species in these openings were Johnson grass (*Sorghum halepense*), ragweed (*Ambrosia* spp.), black-eyed susan (*Rudbeckia* spp.), rye grass (*Lolium multiflorum*), goldenrod (*Solidago* spp.), beefsteak (*Perilla frutescens*), teaweed (*Sida rhombifolia*), and blackberry.

Due to logging practices of previous landowners (i.e., high-grading), relatively few hard mast producing species were found away from riparian zones or sites where persistent flooding made logging difficult. Although logged extensively in the 1950's, some areas of Sherburne have remained virtually undisturbed since. Forest management practices including group selection cuts, individual selection cuts, clear cuts and shelterwood cuts designed to promote regeneration of dominant canopy species and increase stand diversity have been applied to portions of Sherburne since 1986. Management prescriptions were applied in contiguous sections known as compartments. Recent activity has included 60 ha of clear cut and 244 ha of combined individual/group selection in 2001; 79 ha of individual selection and 25 ha clear cut in 2003; 60 ha of shelterwood cut and 102 ha of combined individual/group selection during 2003-2004; 74 ha of shelterwood cut, 56 ha of individual selection, and 51 ha of combined

individual/group select cut in 2005 (Fred Hagamen, LDWF, personal communication).

In addition, a 99 ha parcel has been maintained to provide a mosaic of early successional habitat primarily for American woodcock (*Scolopax minor*).

Due to construction of levees and water control structures, Sherburne did not experience direct flooding from the Atchafalaya River. River-induced flooding was manifested in the form of back-water flooding moving north from southern areas of the Atchafalaya Basin and varied in severity from year to year. Most seasonal flooding on Sherburne could be attributed to local precipitation during the rainy season (Feb – April). The poorly drained alluvial soils allow surface water to persist for extended periods of time. Additionally, extended flooding was encouraged in some areas by the construction of levees coupled with water control structures designed to hold water during winter and early spring, mimicking natural flood cycles for the Lower Mississippi Alluvial Valley.

Chapter 1: Seasonal Space Use and Habitat Selection of Female Wild Turkeys in a Louisiana Bottomland Forest

Introduction

Central to study of animal ecology is an understanding of how organisms use habitats. In theory, an animal should evaluate and select habitats that best provide the resources necessary for survival and reproduction such as access to food, suitable breeding areas, protection from predators, and the means to meet thermoregulatory requirements. As such it would be expected that certain habitats will be used disproportionately to others relative to their availability based on the quality of resources provided (MacArthur and Pianka 1966, Johnson 1980).

Burt (1943) first described an animal's home range as the space in which an individual conducts their normal daily activities and Samuel et al. (1985) later defined the core area as the area within the home range that receives the most concentrated use. Space use and habitat selection may not be constant for the life of an animal and may vary in response to season, age, population density, and overall habitat quality (Orians and Wittenberger 1991, Pulliam and Danielson 1991, Rosenzweig 1991, Myserud and Ims 1998). Thus, understanding patterns of space use and habitat selection is an important step in understanding the ecology of any species within a given environment.

Habitat selection and space use of female wild turkeys has been extensively studied in a variety of upland landscapes (Everett et al. 1985, Smith and Teitelbaum 1986, Bidwell et al. 1989, Kurzejeski and Lewis 1990, Miller et al. 1999, Thogmartin 2001, Miller and Conner 2007), but similar published information within bottomland systems is sparse (Zwank et al. 1988, Cobb et al. 1993), particularly in the lower Mississippi Alluvial Valley (but see Wilson et al. 2005a). Notably, bottomland

hardwood forests are regarded as high quality turkey habitat (Dickson 2001). Furthermore, although ecological processes are known to operate at varying spatial scales (Wiens 1989) previous studies have focused on habitat selection at one spatial scale, potentially creating misleading inferences about overall selection (Johnson 1980, Orians and Wittenberger 1991). Proper management of wild turkeys requires a working knowledge of space use and habitat selection and wild turkeys in bottomland hardwood forests face unique situations, such as regular flooding, that turkeys in more studied upland habitats do not. As such, the behavior of turkeys in these systems may differ from their upland counter parts, and the information gathered from upland systems may not directly apply to bottomland systems. My objective was to estimate space use and multi-scale seasonal habitat selection for adult female wild turkeys in a bottomland hardwood forest in Louisiana.

Methods

I captured female wild turkeys with cannon nests at bait sites distributed throughout the study area during summer (June - August) of 2007 and 2008. I established bait sites ($n = 15 - 20$) in forest openings and right-of-ways and baited them with cracked corn. Each bait site was checked twice daily, and capture attempts were planned following the determination of consistent site use by females. We fitted each captured female with a standard serially-numbered leg band and a 75g ($\leq 3\%$ body weight) mortality-sensitive radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota) attached backpack-style. In cases where multiple birds were captured, individuals were placed in appropriate sized boxes until they could be processed. I released all birds at the capture site immediately following processing. Previous

researchers captured females during summers of 2001-2004; they were similarly handled, marked, and released (Wilson et al. 2005a). All capture and handling procedures were covered under Louisiana State University Agricultural Center Institutional Animal Care and Use Protocol number AE2010-09.

I used a hand-held 3-element Yagi antenna and an ATS R4000 receiver (Advanced Telemetry Systems, Isanti, Minnesota) to locate radio-marked females. Locations were obtained by triangulation of azimuth readings taken from 2-5 fixed telemetry stations within a time interval ≤ 20 minutes to minimize error caused by turkey movement. I estimated telemetry error by placing dummy radios ($n = 10$) in the field at the approximate height and orientation of a turkey, and triangulating 20-30 locations on each dummy radio. The individual conducting test triangulations (either a field technician or myself) did not know the exact location of dummy radios during testing. I recorded locations of dummy radios with hand-held GPS and the error was calculated as the distance between each triangulated location and the actual radio location. I used regression analysis to examine the correlation between observer distance and error, and to predict the expected error at a given distance.

I monitored turkeys throughout the year, collecting approximately 3 locations per week for each female from September to early February, and ≥ 1 location daily for the remainder of the year. I used LOCATE III (Pacer; Truro, Nova Scotia, Canada) to obtain Universal Transverse Mercator (UTM) coordinates for all triangulations. When a radio-marked female was visually sighted, its location was recorded on a hand-held GPS. I collected locations from 9 June 2007 - 1 March 2010, and previous researchers collected

locations from 11 February 2002 – 27 August 2004 using the same methods (Wilson et al. 2005a).

I delineated biologically significant seasons based on previous work conducted on the study area; pre-incubation, incubation, brood rearing and fall-winter (Wilson et al. 2005a). Specifically, pre-incubation was defined as the period from 15 February (approximate timing of winter flock break-up) until the onset of incubation, or 9 April for non-reproductive females. Incubation was defined as the onset of incubation until hatch or nest failure for females that successfully achieved nest incubation, or 10 April – 31 May for non- nesting females. Brood-rearing was defined as the period from hatch out or nest failure until 30 September for nesting females, or 1 June – 30 September for non-reproductive females. The fall-winter season covered the time period from 1 October – 14 February for all females.

I imported all triangulated locations into ArcGIS 9 (ESRI, Redlands, California) and converted them to point themes. I calculated kernel density home ranges (95%) and core-use areas (50%) seasonally for each female using the Home Range extension (Rodgers and Carr 1998) in ArcGIS. I chose to use fixed kernel densities as opposed to adaptive kernel to minimize over-estimation of space use (Seaman and Powell 1996). I performed area observation curves on 5 representative turkeys with > 40 locations in a season and determined that home range sizes generally stabilized at ≥ 20 locations; as such, only individuals with ≥ 20 locations in a season were used for analysis.

Additionally, I excluded birds that were monitored for < 75% of a given season. I used a one-way analysis of variance (ANOVA) to test whether home range and core area sizes (ha) were different between seasons. I pooled data from all years for analysis purposes

because sample sizes were low in some seasons and the number of individuals tracked varied considerably between years.

I created a digital land cover of Sherburne in ArcGIS 9 using 2004 digital orthophoto quarter quadrangles (DOQQs) and digital elevation models (DEM's, 5m² resolution) derived from 2003 LIDAR data (available at <http://atlas.lsu.edu>). Because stand-specific information was not readily available for Sherburne, I delineated habitat types into 3 broad categories using visual characteristics of the landscape visible on the DOQQ's, elevation data from the DEM's, and ground truthing. Habitat types included water-influenced forests (forests that experience seasonal flooding and hold standing water for a considerable portion of the year, cypress-tupelo swamps, as well as riparian areas immediately adjacent to waterways), upland forests (bottomland hardwood forests of relatively high elevation not associated with regular flooding, included ridges, natural levees, terraces and higher flats) and openings (right-of-ways, levees, food plots, roads etc.). To delineate upland and water-influenced forests I first generated 0.25m contour lines from DEM's using spatial analyst in ArcGIS. Because the average elevation of Sherburne varies along a north-south gradient, I separated large contour datasets into small enough parcels that a specific elevation value would be hydrologically consistent across the whole parcel. For instance, an elevation of 19m may flood regularly in the north; whereas, 19m may represent the highest point of land in the southern part of the study area. In each parcel I considered the area below the specific elevation contour that represented the highest elevation to regularly flood each year as water-influenced. Determination of this cut-off elevation was made based on personal experience during flood-periods and from cross referencing by overlaying contour data-sets over DOQQ's.

My habitat classifications differ slightly from those of previous work on the area (Wilson 2005a, Grisham 2007) because I collapsed 2 habitat types (water-based forest and lowland forest, see Wilson et al. 2005a) into a single type (water influenced forest). I did this because true cypress-tupelo swamps that comprised the areas originally classified as “water-based forests” were not a prominent habitat type (comprising < 3% of the study area), were not present in the home ranges of a number of animals, were difficult to delineate from surrounding lowland forests even with elevation data, and tended to vary from year to year in size and influence based on flood cycles and precipitation (personal observation). I found it more practical and interpretable to collapse all forest types consistently influenced by water into one category. To compensate for telemetry error, I classified waterways along with water-influenced forested because if a relocation fell within a bayou it was likely that the bird was actually on the bank or near the water (Grisham 2007).

I intersected home ranges, core areas, and point themes with the land cover in ArcGIS to quantify habitat selection across seasons. I used compositional analysis (Aebischer et al. 1993) to examine habitat selection at 3 spatial scales based loosely on the recommendations of Johnson (1980); home ranges vs. habitats available on the study area (1st order), core use areas vs. habitats available in home ranges (2nd order), and individual locations vs. habitat available in home ranges (3rd order). Because compositional analysis requires calculating log-ratios of habitat use, values of zero-use are problematic. Aebischer et al. (1993) originally proposed replacing zero values with a very small positive value (i.e. 0.001); however, substituting such small numbers may potentially inflate type I error rates (Bingham and Brennan 2004) as well as

misclassification error rates (Bingham et al. 2007). Wilson et al. (2005a) determined that no significant difference existed when the values of 0.1, 0.3, and 0.7 were substituted for zero when habitats were not used on Sherburne. Therefore I followed the example of Grisham (2007) and the recommendation of Bingham and Brennan (2004), and used 0.7 to replace zero use and minimize the risk of type I error.

I examined differences of log-ratio habitat use and availability percentages using a multivariate analysis of variance (MANOVA) with season as a main effect to test whether habitat types were used in proportion to their availability (Aebischer et al. 1993). If significant differences between habitat availability and selection were found within a particular spatial scale, I constructed a ranking matrix of *t*-tests to determine order of habitat selection for each season (Aebischer et al. 1993). I pooled data across years due to small sample sizes in some seasons and wide variation in the number of individuals tracked between years.

Results

I estimated 144 seasonal home ranges and core areas for 45 female turkeys from 11 February 2002 – 27 August 2004, and from 1 October 2007 – 30 March 2010. All home ranges included every habitat type, and 107 of 144 core areas included every habitat type (in each case openings were the missing habitat). I failed to locate any incubating turkeys away from their nests, so I considered any individual that incubated a nest for ≥ 5 days ($n = 21$) as reproductively active and excluded them from analysis during the incubation period. Additionally, because females that were known to be reproductively unsuccessful were commonly observed associating with brood flocks during the summer months, I pooled reproductively active and inactive females together

during the brood-rearing season. Regression analysis showed a significant positive correlation between telemetry error and observer distance ($r^2 = 0.52$, $P < 0.001$). Most locations (70%) were taken from a distance $\leq 500\text{m}$, often considerably closer and the expected telemetry error based on the regression equation at a distance of 500m was 111m. I excluded from analysis all estimated locations that were $> 1000\text{m}$ from the closest spot in which an observer took an azimuth reading. The mean number of locations used for seasonal analysis per individual was 45 (range 20-127).

Home range ($F_{3, 140} = 10.89$, $P < 0.001$) and core area ($F_{3, 140} = 6.67$, $P < 0.001$) sizes differed by season, with largest home ranges during preincubation and smallest during brood-rearing. Core areas were largest during preincubation and smallest during incubation (Table 1.1). Female turkeys selected habitats seasonally within their home ranges relative to habitats available across the study area (1st order selection, $F_{2, 139} = 69.18$, $P < 0.001$), within their core areas relative to habitats available within home ranges (2nd order selection, $F_{2, 139} = 11.85$, $P < 0.001$), and used habitats different than availability within their home ranges (3rd order selection, $F_{2, 139} = 9.48$, $P < 0.001$). Upland forest was consistently selected relative to all other habitat types at each spatial scale during all seasons. Water-influenced forests were generally the next most selected habitat type at each spatial scale for most seasons, whereas openings were generally the least selected habitat (Table 1.2).

Table 1.1: Mean seasonal home range and core area size (ha) and associated standard errors (SE) from radio-marked female wild turkeys on Sherburne Wildlife Management Area, Louisiana, from the years 2002-2004, 2007-2010.

Season	n (estimated HR's)	HR \pm SE	CA \pm SE
Preincubation	40	672.26 \pm 55.08	111.79 \pm 11.09
Incubation	15	415.36 \pm 83.84	61.01 \pm 16.19
Brood-rearing	46	362.80 \pm 24.24	67.74 \pm 4.83
Fall-winter	43	430.09 \pm 34.89	81.51 \pm 7.24

Table 1.2: Seasonal and mean ranks (0 = lowest, 2 = highest) of habitat selection across three spatial scales (habitat selection in home ranges vs. habitat availability across study area [1st order], habitat selection in core areas vs. habitat availability across home ranges [2nd order], and habitat used vs. habitat availability across home ranges [3rd order]) based on compositional analysis of female wild turkeys on Sherburne Wildlife Management Area, Louisiana, from the years 2002-2004, 2007-2009.

Habitat	1 st Order					2 nd Order					3 rd Order				
	Season ^a					Season					Season				
	PI	I	BR	FW	Mean	PI	I	BR	FW	Mean	PI	I	BR	FW	Mean
WIF ^b	1	1	0	1	0.75	0	1	1	1	0.75	1	1	1	0	0.75
Upland forest	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Opening	0	0	1	0	0.25	1	0	0	0	0.25	0	0	0	1	0.25

a. Seasons are preincubation (PI), incubation (I), brood-rearing (BR), and fall-winter (FW)

b. water-influenced forest.

Discussion

Space use estimates reported in this study are smaller overall than those previously reported for females on Sherburne (Wilson et al. 2005a). This reflects a difference in methodologies used to estimate home range size between studies rather than an actual decrease in space use over time. Home range estimates for females in the original study years of 2002-2004 were recalculated for this study and were similar to those for females studied in 2007-2010. More importantly, and despite these discrepancies, the general patterns of seasonal space use were similar across study years (see Wilson et al. 2005a).

Space use was greatest during the preincubation period. Due to a combination of consistent yearly flooding on portions of Sherburne and shading from dense canopy cover, understory vegetation is generally sparse, limiting availability of quality nesting areas on portions of the study area. Increased habitat sampling during the preincubation period may be beneficial to nesting success, as females that sample more areas tend to improve their chances of locating high quality nesting sites (Badyaev et al. 1996,

Chamberlain and Leopold 2000). Home range size is often interpreted as a surrogate for habitat quality (Burt 1943, Krzejeski and Lewis 1990, Thogmartin 2001), hence the substantial increase in space use observed during preincubation may be indicative of poor nesting habitat, requiring females to sample a large area to find a suitable nesting location. Cobb et al. (1993) found that space use of female turkeys increased significantly when optimal nesting habitat was flooded in a North Carolina bottomland area.

Space use was least during brood-rearing. Brooding females have been known to restrict their movements to localized areas of high food abundance when broods are young (Miller et al. 1997). I did not partition females into successful and unsuccessful nesters, because reproductively unsuccessful females were often observed associating with brood flocks, a behavior has been observed in other areas (M. Chamberlain, personal communication). Unsuccessful females may associate with brood flocks to reduce the risk of experiencing a mortality event (Jullien and Clobert 2000) or to attempt an adoption event (Mills and Rumble 1991, Metz et al. 2006), and females engaging in this behavior would be restricted to the limited movements of the brood flock. Small home range sizes may also be a function of forest structure and increased food availability during the warmer summer months. Bottomland hardwood forests are productive ecosystems (Conner and Day 1976, Mitsch et al. 1991) and succulent vegetation is widely available on Sherburne during summer, hence adequate brooding habitat is likely abundant enough to allow females to greatly restrict their movements when foraging and protecting broods. A similar trend of reduced space use during the summer in bottomland hardwood forests was observed for male turkeys (Grisham 2007), white-tailed deer (Thayer et al. 2009), and raccoons (see Chapter 3).

Space use during fall-winter was greater than that observed during brood-rearing, but less than that observed during preincubation. Winter habitat use is heavily dependent on the distribution of food resources (Porter 1992) and in some regions space use is least during the winter months (Speake et al. 1975, Bidwell et al. 1989, Kurzejeski and Lewis 1990). During winter turkeys may be forced to concentrate around areas of localized food abundance, for instance, near agricultural lands in northern areas where natural food availability may be limited (Vander Haegen et al. 1989, Kurzejeski and Lewis 1990), or around mast-producing stands in mixed pine/hardwood systems (Bidwell et al. 1989). Past high grading on Sherburne has reduced the distribution of mast producing trees into pockets of abundance, primarily in areas where water made logging difficult, distributed sporadically across the landscape. The observed pattern of increased space use during fall-winter was likely a function of turkeys moving between these pockets of mast producing hardwoods.

Upland forests were selected relative to other habitats at all spatial scales in all seasons in the present study. Earlier work (Wilson et al. 2005a) suggested that other habitat types, particularly cypress-tupelo swamps and riparian areas (water-based forests in Wilson et al. 2005a) were important, especially at the 2nd and 3rd order scales. The discrepancy between studies is likely a result of the differences in the delineation of habitat types. The use of elevation data in the present study allowed for a more hydrologically accurate distinction between upland and lowland forests than in previous studies. Additionally, what constituted water-influenced forests in this study represented 2 separate habitat types in the previous study (water-based and lowland forest) that I did not feel could be accurately separated. Because water-based forests constituted a

particularly small portion of the study area in the Wilson et al. (2005a) study, it stands to reason, given the nature of the analysis, that even a small number of telemetry relocations in these areas would inflate their perceived importance. Water-influenced forests may provide some of the same foraging resources as drier forests when they are not flooded, especially hard-mast in the fall-winter period. Turkeys on Sherburne and other areas have been known to roost in trees over water (Chamberlain et al. 2000, Wilson et al. 2005a, Grisham 2007, personal observation). Although this study was mainly concerned with the day-time habitat use of turkeys, it is plausible that water-influenced forests provide ideal roosting locations.

Females on Sherburne are likely forced to concentrate their nest site selection to upland areas to avoid flooding (Kimmel and Zwank 1985, Zwank et al. 1988, Cobb et al. 1993), contributing to the selection of upland forests during the preincubation and incubation seasons. Preincubation was the only season in which openings were selected relative to water-influenced forests in core areas. All nests located during the study ($n = 42$) were in either upland forests ($n = 36$) or in openings ($n = 6$, see Chapter 4). Nests in forests were often placed close to forest edges (mean distance = 55.8m, see Chapter 4), and several nests were located <1m from a forest edge. Logically, upland forests and openings would be preferentially selected in core use areas relative to their availability across home ranges during a time when females are sampling habitats for potential nest sites.

It is generally accepted that the key to optimal brood habitat is herbaceous ground cover that provides food resources that meet the nutritional needs of developing poults, cover from predators, and is sparse enough as to not impede locomotion and the ability of

the brood female to survey for predators (Healy 1985, Porter 1992, Godfrey and Norman 1999). Upland forests on Sherburne are structurally similar to the preferred brood-rearing areas described by Phalen et al. (1986) in a mixed pine/hardwood system in Mississippi; mature bottomland hardwoods with continuous canopy, sparse understory, and moderate herbaceous ground cover. Juxtaposition of landscape features plays an important role in habitat selection and I contend that the apparent selection for openings at the landscape level (1st order selection) during brood-rearing may be an artifact of the proximity of openings to preferred brood-rearing areas. Phalen et al. (1986) found that openings were only used when they were located close to other highly preferred areas, and Smith and Teitelbaum (1986) found little evidence that openings were a preferentially used habitat type despite the fact that pasture lands comprised centers of activity for almost all radio-marked individuals in their study. Likewise, Pack et al. (1980) found openings to be preferred habitat within oak-hickory forests, but noted most activity occurred under canopy cover and Ross and Wunz (1990) found that females were able to successfully raise broods in forests in Pennsylvania in which natural openings were rare. Most openings found within brood home ranges on Sherburne were comprised of narrow, linear rights-of-way set within the context of the prevailing forest. It is possible that turkeys used these areas because they functioned as convenient travel lanes for leading broods between suitable foraging patches. By early summer, vegetation in openings has grown dense and exceeds 1m in height, which may actually be detrimental to safe and successful brood foraging. Conversely, vegetative structure found within forested habitats provides suitable brood-rearing habitat, allowing broods to stay under canopy cover and reduces the importance of open areas relative to other forest systems.

Several authors have observed a seasonal shift from habitats used during the summer months to primarily forest habitats, particularly hardwood forests, during the fall and winter months (Speake et al. 1975, Everett et al. 1985, Porter 1992, Miller and Conner 2007), and bottomland hardwoods have been specifically identified as being especially preferred (Porter 1992). The selection for forests is widely attributed to the fact that acorns and other hard mast constitute an important part of the wild turkey's diet at this time of year (Eaton 1992, Hurst 1992, Dickson 2001) and likely accounts for the selection of forested habitats over openings observed on Sherburne during fall/winter.

Portions of Sherburne have been under active forest management since 1986. Between 2001 and 2005, approximately 751ha of forest were variously subjected to clearcutting, shelterwood, individual tree harvest, and group selection cutting with an additional 99ha parcel maintained as early successional habitat for American woodcock (see Study Area description). While these management actions seemed to have provided benefit for some wildlife, such as anurans and songbirds (LeGrand 2005), and raccoons (Chapter 3), home ranges of female turkeys rarely encompassed the managed stands, and individual relocations in these areas were extremely rare. This observation was consistent through all stages of the study. I contend that turkey avoidance of the managed stands was related to the consistently dense understory growth associated with the reduction of canopy cover in management plots. Succession was rapid in these plots allowing only a short window of opportunity for use by turkeys. Within 2 growing seasons height of understory vegetation exceeded 2m, and was dominated by woody saplings, particularly within stands managed with clear cutting and group selection (LeGrand 2005). The dense understory growth likely made it difficult for turkeys to efficiently move through, and

possibly increased the chance of predation by affording potential predators ideal ambush opportunities.

Chapter 2: Survival and Cause-specific Mortality of Adult Female Wild Turkeys in a Louisiana Bottomland Hardwood Forest

Introduction

Adult survival has been identified as one of the most important parameters influencing wild turkey abundance (Roberts and Porter 1996). Survival of adult females is particularly important because of their influence on productivity and recruitment, and the associated effects on population dynamics (Vangilder 1992, Roberts and Porter 1996). A working knowledge of demographic parameters such as survival is important in properly managing populations. Survival and cause-specific mortality of female wild turkeys has been studied in a number of locations and habitat types across the species range (Kurzejeski et al. 1987, Roberts et al. 1995, Wright et al. 1996, Miller et al. 1998, Nguyen et al. 2003, Humberg et al. 2009), but information is lacking in bottomland hardwood systems, particularly in the lower Mississippi alluvial valley.

Incubation and brood-rearing activities may increase susceptibility to predation, leading to greater mortality during reproductive periods (Speake 1980, Miller and Leopold 1992, Miller et al. 1998). Several studies have observed seasonal variation in survival with the lowest survival occurring during periods associated with reproductive activity (Vander Haegen et al. 1988, Palmer et al. 1993a, Wright et al. 1996, Hubbard et al. 1999). In addition to increased predation risk, it seems plausible that the physiological costs of nesting and rearing a brood may carry over through the year, potentially affecting survival beyond the reproductive period. As such, reproduction may incur a survivorship cost, and reproductively active females could be expected to exhibit lower rates of survival over the course of a year and differing rates of seasonal survival within a year compared to reproductively inactive females. In Mississippi, Miller et al. (1998) found

no differences in annual survival between reproductively active and inactive females, although nesters were more prone to predation than non-nesters. The authors suspected a high cost of reproduction during the brood-rearing period for females raising young, but did not have sufficient evidence to say so definitively. To my knowledge no other studies have examined the cost of reproduction on both annual and seasonal survival.

My objectives were to estimate annual and seasonal survival rates as well as identify and quantify specific causes of mortality for adult female wild turkeys within a bottomland hardwood system in south-central Louisiana. Additionally, I aimed to determine the consequences of reproduction on annual and seasonal survival for females in this system.

Methods

Female wild turkeys were captured and fitted with mortality sensitive VHF radio transmitters as described in Chapter 1. Turkeys were monitored via radio telemetry throughout the year, with approximately 3 locations gathered weekly for each individual from September to early February, and ≥ 1 location gathered daily for the remainder of the year. Telemetry methodology is described in detail in Chapter 1.

When a mortality signal was detected, I attempted to recover the radio as soon as possible to determine cause of death. Because incubating birds would often activate the mortality signal, I did not investigate mortality signals detected between 1 April and 15 May for 29 days as not to disturb females that may have been nesting. I grouped mortalities into 4 categories based on condition of the carcass and visible sign in the immediate area: bobcat (*Lynx rufus*) predation, canid [either coyote (*Canis latrans*) or domestic dog] predation, predation caused by unknown predators, or unknown. I

classified females as being killed by a bobcat if the carcass was cached, or if bobcat tracks or scat were found near the kill site. I classified females as being killed by canids if canid tracks, scat, or fur were found at the kill site. If predation was evident but no identifiable predator sign was found, or if sign of multiple predators was found, I classified the turkey as being killed by an unknown predator. I classified deaths as unknown when scavengers had destroyed the carcass before recovery, or if there was no obvious sign of predation or injury.

I partitioned the year into 3 biologically meaningful seasons based on observations of female nesting chronology on Sherburne. The nesting season ran from 9 March – 9 May, and was based on back-dating 2 weeks from the earliest recorded nest initiation date until the latest known re-nest initiation date. This period was designed to cover most pre-incubation nest searching, egg laying, and incubation activities. The brood-rearing season was defined as the period 10 May – 30 September, and the fall/winter season was defined as 1 October – 8 March. The biological year ran from 9 March – 8 March.

I used program MARK (White and Burnham 1999) to estimate seasonal and annual survival rates using known fate models with season as the interval. Known fate models in MARK produce survival estimates based on the Kaplan-Meier method (Pollock et al. 1989). I excluded individuals that died within one week of capture from the analysis to remove any bias that may result from capture mortality, and censored any individuals that experienced radio-failure during the interval in which radio contact was lost. For analysis purposes I pooled data across all years. While I am aware of the potential biases that may be associated with pooling across years, this was necessary to

increase sample size within seasons. Because all females were captured during summer (June – August), I did not separate age classes because all individuals were either adults \geq 1 year old or subadults being recruited into the adult population. To determine if survival varied seasonally, I developed 2 candidate models; the first model held survival constant across seasons whereas the second allowed survival to vary across seasons. Akaike's information criterion adjusted for small sample sizes (AIC_c) was used to evaluate and choose the best performing model (Burnham and Anderson 2002).

To assess the influence of reproduction on survival, I estimated seasonal and annual survival in MARK as described above for turkeys in which reproductive activity was known for a given year. As such, females were only introduced into the analysis during the nesting season following the summer in which they were captured. Females that experienced a mortality event or radio-failure between summer capture and 9 March of the following year were excluded from this analysis. I grouped individuals into 2 categories based on reproductive activity within a given year; reproductively active turkeys reached the stage of nest incubation, and reproductively inactive turkeys did not incubate a nest. I developed a set of candidate models to determine how survival was affected by season and reproductive activity. I calculated Akaike's information criterion adjusted for small sample sizes (AIC_c) for each model and used ΔAIC_c and Akaike weights (w_i) to evaluate model performance. I determined the relative importance of each variable (season and reproductive activity) in predicting survival by summing the Akaike weights across all models in which each respective variable occurred (Burnham and Anderson 2002). I present the model averaged seasonal survival estimates for reproductively active and inactive females respectively.

Results

I estimated survival for 54 female turkeys monitored from 11 February 2002 – 27 August 2004, and 8 June 2007 – 9 May 2010. During the study 31 dead females were recovered. Predation accounted for the greatest percentage of observed mortalities (87.1%), and included predation by canids (n = 7), bobcats (n = 5), and unknown predators (n = 15). Cause of death could not be determined for 4 females. In 2 of these cases the carcass showed no obvious signs of injury, and in 2 cases the carcass was destroyed by scavengers. Mean annual survival was 0.58 (SE = 0.06) and there was no evidence of variation in survival among seasons (Table 2.1, Table 2.2).

Table 2.1: Seasonal survival estimates for radio-marked adult female wild turkeys (n=54) on Sherburne Wildlife Management Area, Louisiana during 2002-2004, 2007-2010.

Season ^a	Survival	±SE
Nesting	0.83	0.053
Brood-rearing	0.82	0.042
Fall/winter	0.84	0.046

a. Seasons were nesting, 9 March – 9 May; brood-rearing, 10 May – 30 September, and fall/winter, 1 October – 8 March.

Table 2.2: Results of known-fate survival models^a for radio-marked female wild turkeys during 2002 - 2004, 2007 - 2010 on Sherburne Wildlife Management Area, Louisiana.

Model	K	AIC _c	ΔAIC _c	w _i
Constant Survival	1	175.04	0	0.88
Seasonal Variation	3	179.07	4.03	0.12

a. K = number of parameters, AIC_c = Akaike's Information Criterion adjusted for small sample size, ΔAIC_c = difference in AIC_c relative to smallest value, w_i = AIC_c weight.

Survival estimates were generated for 39 females (25 reproductively active, 14 inactive) in which nesting status was known from the 2002 - 2004, 2008, and 2009 nesting seasons. Reproductively inactive females exhibited greater annual survival (0.49 ± 0.09) than reproductively active females (0.30 ± 0.1). The best approximating model of

survival was the model that solely considered female nesting status (Table 2.3). The second best model considered the effect of season on survival regardless of reproductive activity and showed marginally less support than the best model. The summed model weights for reproductive activity and season were 0.79 and 0.44 respectively, indicating that reproductive activity had greater relative importance in explaining survival.

Reproductively active and inactive females showed similar trends in seasonal survival; with survival estimates for non-nesters ~ 10% greater than for nesters in all seasons (Table 2.4).

Table 2.3: Results of known-fate survival models^a for female wild turkeys of reproductive activity during 2002 - 2004, and 2008 - 2009 on Sherburne Wildlife Management Area, Louisiana.

Model^b	K	AIC_c	ΔAIC_c	w_i
RA	2	131.51	0	0.564
S	3	133.49	1.99	0.209
RA + S	4	133.57	2.07	0.201
RA + S + RAxS	6	137.63	6.12	0.026

a. K = number of parameters, AIC_c = Akaike's Information Criterion adjusted for small sample size, ΔAIC_c = difference in AIC_c relative to smallest value, w_i = AIC_c weight.

b. RA = reproductive activity, S = season (nesting, brood-rearing, fall/winter).

Table 2.4: Model averaged season survival estimates for female wild turkeys with known reproductive status during 2002 - 2004, and 2008 - 2009 on Sherburne Wildlife Management Area, Louisiana based on known-fate survival models.

Season^a	Non-nesters^b	Nesters
	Survival ± SE	Survival ± SE
Nesting	0.80 ± 0.05	0.71 ± 0.09
Brood-rearing	0.75 ± 0.08	0.65 ± 0.09
Fall/winter	0.78 ± 0.07	0.68 ± 0.10

a. Seasons are nesting: 9 March – 9 May; brood-rearing: 10 May – 30 September, and fall/winter: 1 October – 8 March.

b. Non-nesting birds did not nest, nesting birds reached nest incubation.

Discussion

Predation was the primary cause of female mortality on Sherburne, consistent with the literature on the species (Wright et al. 1996, Miller et al. 1998, Hubbard et al. 1999, Hamberg et al. 2009) and previous work on the area (Wilson et al. 2005b). Bobcats and coyotes were responsible in all cases in which a predator could be identified. Bobcats and coyotes are often cited as important predators of wild turkeys throughout their range (Speake 1980, Miller and Leopold 1992, Chamberlain et al. 1996, Wright et al. 1996). Feral dogs were present on Sherburne, but not in large numbers and were rarely found far from areas inhabited by humans, hence it is likely that all mortalities attributed to canids were caused by coyotes. Bobcats and coyotes appear to represent the most important predators on Sherburne; especially considering that other common predators of adult wild turkeys in the South (e.g., great horned owls *Bubo virginianus*) were rare or absent on the study area. In some locations, hunting (legal and illegal) has been shown to be an important cause of female mortality (Kimmel and Kurzejeski 1985, Vangilder and Kurzejeski 1995, Wright et al. 1996); however, there is no legal either-sex fall hunting season on Sherburne, and there was no evidence of poaching during this study.

Annual survival was well within the range of that reported in the literature (range 0.288 [Nguyen et al. 2003] – 0.777 [Hamburg et al. 2009]), and similar to previous findings on the study area (Wilson et al. 2005b). Survival was nearly identical across seasons when all individuals were considered for analysis. An earlier study on Sherburne found lowest survival during the nesting and brood-rearing seasons (Wilson et al. 2005b). The discrepancy between previous work and my findings can likely be attributed to

differences in delineations of seasons, as well as differences in sample size and study duration. The longer time frame and larger sample size represented in the present study may have acted to give a more accurate picture of survival over time. Additionally, I was able to delineate seasons based on the more informed understanding of the annual cycle of female turkeys that additional years of radio-tracking provided.

While variation in seasonal survival has been reported in some locations (Vander Haegen et al. 1988, Palmer et al. 1993*a*, Wright et al. 1996, Hubbard et al. 1999, Nguyen et al. 2003) it is not a universally observed characteristic across the species range (Kurzejeski et al. 1987, Roberts et al. 1995, Miller et al. 1998, Hamberg et al. 2009). Comparing survival rates among studies is tenuous, as there is no standard in defining seasons, and as such, seasonal delineations can vary considerably among studies. Nonetheless, the overall lack of consistency in seasonal variation across studies seems to indicate that variation in survival among seasons is influenced by site-specific local parameters such as the local predator community, habitat characteristics, and landscape structure and their influence on predation risk at certain time periods (Chamberlain et al. 1996, Thogmartin and Schaeffer 2000), or climate (Healy 1992), among others. My findings suggest that local conditions on Sherburne during the study period facilitated consistent survival probabilities for females through time. These results should be interpreted with the forethought that all years were combined for analysis due to sample size constraints for some years of the study. It is conceivable that survival within seasons may vary among years based on temporal changes in biotic and abiotic factors, and such variation may not have been detected in this study.

My findings suggest that reproduction incurs a cost to survival, as reproductive activity was the best predictor of survival between reproductively active and inactive females. While mortalities directly associated with reproductive activities did not result in different seasonal survival rates between reproductive classes, reproduction did lead to overall lower survival rates over time. Wild turkeys do not begin incubation until the entire clutch has been laid (Eaton 1992) and nests can be depredated or destroyed prior to incubation. Unfortunately there was no way of differentiating between females that had lost a nest prior to incubation and females that simply did not attempt to nest, meaning some individuals that had lost nests during egg laying may have been classified as reproductively inactive. I do not believe this influenced my results however, because none of these individuals engaged in the incubating and brood-rearing behaviors that would theoretically be expected to increase the mortality potential of reproductively active females.

It is believed that females are more likely to experience mortality events while engaged in reproductive activities that may leave them vulnerable to predation, specifically while incubating and early in the brood-rearing process (Speake 1980, Vander Haegen et al. 1988, Palmer et al. 1993a, Miller et al. 1995, Miller et al. 1998). My findings do not directly support this notion. Reproductively active females exhibited reduced survival relative to reproductively inactive females during all seasons, but seasonal trends were identical for reproductive classes. If increased predation due to reproductive activities was solely responsible for the observed difference in annual survival, I would have expected to see reduced survival during one or both of the reproductive seasons (nesting and brood-rearing) for reproductively active females,

whereas survival should have remained relatively constant for reproductively inactive females during these times.

Future work may do well to distinguish between reproductively inactive females, females that reach nest incubation but fail to hatch any young (due to nest destruction, abandonment, or adult mortality), and females that successfully hatch young. There is evidence based on observations made during this study as well as others (Speake 1980, Palmer et al. 1993*a*, Miller et al. 1998) that mortality risk during the brood-rearing season is greater for females that successfully hatch a brood. In the present study, 3 females that successfully hatched young were killed by predators within 5 days of hatching; a time before poults could fly and in which the female was forced to roost with her young on the ground. Unsuccessfully nesting females should functionally behave as reproductively inactive females during this time and not face such risks associated with caring for a brood. Reproduction does seem to incur a survival cost for females, yet clearly more work must be done to determine the exact mechanisms by which survival and reproduction are related and investigations into the nature of this relationship represent an interesting course for future research.

Chapter 3: Seasonal Space Use and Habitat Selection of Adult Raccoons in a Louisiana Bottomland Hardwood Forest

Introduction

The raccoon is a generalist mesopredator whose behavioral and dietary plasticity allows it to exploit a wide variety of habitats. Due in part to human alteration of the landscape and their generalist nature, raccoon populations have experienced dramatic increases since the second half of the last century (Gehrt 2003). Currently, raccoons are found in nearly every habitat type across North America and their range is expanding (Gehrt 2003, Larivière, 2004). Raccoons are often implicated as important nest predators of a variety of ground nesting birds and reptiles, including passerines (Heske et al. 2001, Schmidt 2003), colonial water-birds (Ellis et al. 2007), game species such as wild turkey and quail (Miller and Leopold 1992, Rollins and Carrol 2001), and turtles (Burke et al. 2005). Additionally, raccoons are regionally important furbearers (Chamberlain and Leopold 2001), and serve as vectors for several diseases that affect humans and domestic animals (Gehrt 2003, Atwood et al. 2009, Rosatte et al. 2010). Given the potential ecological impacts raccoons may exert on an area, an understanding of the relationships between habitat and raccoon ecology over the wide range of ecosystems they inhabit is important.

The general habitat requirements and life-history characteristics of raccoons are well described. Aspects of home range characteristics and habitat use have been described in a number of habitat types across the continent including mixed pine forests (Chamberlain et al. 2002, Chamberlain et al. 2003), fragmented agricultural areas (Dijak and Thompson 2000, Beasley et al. 2007^a, Beasley et al. 2007^b, Barding and Nelson 2008, Attwood et al. 2009), prairies (Fritzell 1978, Henner et al. 2004, Chamberlain et al.

2007), coastal prairies (Gehrt and Fritzell 1997, Gehrt and Fritzell 1998), freshwater marshes (Urban 1970) and urban environments (Hoffman and Gottschang 1977, Prange et al. 2004, Bozek 2007). These studies reveal space use to vary based on gender, season, weather, population density, landscape structure, and the distribution and availability of food and den sites. Common to studies of habitat selection across ecosystems is the importance of forest habitats (particularly hardwoods) and proximity to water. Not surprisingly, raccoons are reported to occur in higher densities in bottomland hardwood forests relative to other habitat types (Johnson 1970, Sonenshine and Winslow 1972; Leberg and Kennedy 1988, Gehrt 2003). Despite this knowledge, information regarding raccoon space use and habitat selection in bottomland hardwood systems is scarce (but see Fisher 2007).

It is recognized that an animal's habitat selection may occur at levels along a spatial gradient (Johnson 1980, Orians and Wittenberger 1991), and several studies have demonstrated this trait in raccoons (Pedlar et al. 1997, Chamberlain et al. 2002, Chamberlain et al. 2003, Beasley et al. 2007a, Bozek et al. 2007). My objective was to describe space use and multi-scale seasonal habitat selection for adult raccoons in a bottomland hardwood forest in Louisiana.

Methods

I trapped raccoons using wire-cage traps from 15 December 2007 – 10 March 2008, and from 14 January – 21 February 2009. I placed traps in areas that seemed like good raccoon habitat or in areas that contained abundant raccoon sign. I conscientiously trapped across the landscape to ensure that radio-marked individuals occurred throughout the study area. I baited traps with various combinations of fish, corn, and pastries and

checked all traps daily within 4 hours of sunrise. I anesthetized raccoons with ketamine hydrochloride at a rate of 10mg/kg of estimated body mass (Bigler and Hoff 1974) and recorded the gender of each individual and estimated age based on tooth wear (Grau et al. 1970) and overall body characteristics. I fitted all individuals ≥ 1 year old with a 50g mortality-sensitive radio collar (Advanced Telemetry Systems, Isanti, Minnesota) and released all raccoons at their respective capture sites following processing and recovery.

I used a hand-held 3-element Yagi antenna and an ATS R4000 receiver (Advanced Telemetry Systems, Isanti, Minnesota) to locate radio-marked individuals. Locations were obtained by triangulation of azimuth readings taken from 2-5 fixed telemetry stations within a time interval ≤ 20 minutes to minimize error caused by raccoon movement. Approximately 90% of all triangulations were based on 3 or 4 azimuth readings. Telemetry stations were spatially referenced points located throughout the study area along roads, ATV trails, and gas/powerline rights-of-way. I estimated telemetry error by triangulating 20-30 locations on dummy radios ($N = 10$) placed in the field at the approximate height and orientation of a raccoon on the ground. The individual conducting test triangulations (either a field technician or myself) did not know the exact location of dummy radios during testing. I recorded locations of dummy radios using hand-held GPS and the error was calculated as the distance between each triangulated location and the actual radio location. I used regression analysis to examine the correlation between observer distance and error, and to predict the expected error at a given distance.

I monitored raccoons throughout the year, and collected locations using two telemetry techniques. Systematic telemetry consisted of locating each animal once a day

approximately three times per week with locations recorded throughout the diel period to ensure an accurate representation of raccoon space use during day and night-time periods. Sequential telemetry (focal runs) consisted of triangulating a location on a single raccoon every 20 minutes for a period lasting from 4-12 hours. Focal runs were conducted between the hours of sunrise and sunset during March, April, and May of 2008 and 2009, coinciding with the nesting season of wild turkeys on the study area. I used locations gathered through focal runs to supplement locations gathered during the breeding season by extracting a single location from each focal run every four hours. Four hours allowed enough time for a raccoon to traverse its entire home range and was considered long enough to ensure independence between locations. I used LOCATE III (Pacer; Truro, Nova Scotia, Canada) to obtain Universal Transverse Mercator (UTM) coordinates for all triangulations. If a radio-marked individual was visually sighted, its location was recorded on a hand-held GPS. I collected locations on raccoons from 1 March 2008 – 1 March 2010.

I separated the year into three biologically meaningful seasons; breeding, summer, and fall-winter. Specifically, the breeding season was defined as the period from 1 February – 31 May, summer as the period from 1 June – 30 September, and fall-winter as the period from 1 October – 31 January (Chamberlain et al. 2003). We imported all triangulated locations into ArcGIS 9 (ESRI, Redlands, California) and converted them to point themes. I calculated fixed kernel density home ranges (95%) and core-use areas (50%) seasonally for each raccoon using the Home Range extension tool in ArcGIS. I chose to use fixed kernel densities as opposed to adaptive kernel to minimize over-estimation of space use (Seaman and Powell 1996). I performed area-observation curves

on 5 representative raccoons with > 40 locations in a season and determined that home range sizes generally stabilized at ≥ 18 locations; as such, only individuals with ≥ 18 locations in a season were used for analysis. I used a one-way analysis of variance (ANOVA) to test for variation in space use across seasons.

I created a digital land cover of Sherburne in ArcGIS 9 using 2004 digital orthophoto quarter quadrangles (DOQQs) and digital elevation models (DEMs, 5 m² resolution) based off 2003 LIDAR data (available at <http://atlas.lsu.edu>). Habitat types were delineated into four broad categories based off visual characteristics of the landscape on the DOQQ's, elevation data from the DEM's, forest management history, and personal ground truthing. Habitat types included water-influenced forests, upland forest, managed forests, and openings. Water-influenced forests included relatively low elevation forests that experienced seasonal flooding and held standing water for a portion of the year, cypress-tupelo swamps, and riparian areas immediately adjacent to waterways. Upland forests included forests of relatively high elevation not associated with regular flooding, including ridges, natural levees, terraces and higher flats. Managed forests included upland forests that had been subjected to forest management practices since 2000, and were characterized by reduced canopy cover and dense understory growth. Openings included rights-of-way, levees, foot plots, and roads. I delineated upland and water-influenced forests as described in Chapter 1. To compensate for telemetry error, waterways were classified as water-influenced forest because if a relocation fell within a bayou it was likely that the raccoon was actually on the bank or near water.

I intersected home ranges, core areas, and point themes with the land cover in ArcGIS to quantify habitat selection across seasons. I used compositional analysis (Aebischer et al. 1993) to examine habitat selection at three spatial scales; home ranges vs. habitats available on the study area (1st order), core use areas vs. habitats available in home ranges (2nd order), and individual locations vs. habitat available in home ranges (3rd order, Chamberlain et al. 2003). The study area habitat availability was defined in each year by calculating the mean distance of the longest axis of each breeding season home range (2008 = 1995 m, 2009 = 1941 m), then buffering each home range in each respective year by that amount and merging the buffered home ranges together. Thus, study area habitat availability was different in each year of the study.

Because compositional analysis requires calculating log-ratios of habitat use, values of zero-use are problematic. Aebischer et al (1993) originally proposed replacing zero values with a very small positive value (i.e. 0.001); however, substituting such small numbers may potentially inflate type I error rates (Bingham and Brennan 2004) as well as misclassification error rates (Bingham et al. 2007). When a habitat type was not represented in a raccoon's space use at a given scale I substituted a value of 0.7 as suggested by Bingham and Brennan (2004) to minimize the risk of type I error. We examined differences of log-ratio habitat use and availability percentages using a multivariate analysis of variance (MANOVA) with season as a main effect. If significant differences between habitat availability and selection were found within a particular spatial scale, a ranking matrix of *t*-tests was constructed to determine order of habitat selection for each season.

Results

I trapped 49 raccoons, 4 of which were too young to collar, and 4 of which experienced radio failure within 2 weeks of release. I estimated 128 seasonal home ranges and core areas for 41 raccoons (37 male, 4 female) from 1 March 2008 – 28 February 2010. Because I only radio-tracked 4 females, both sexes were combined for analysis. A regression analysis showed a significant positive correlation between telemetry error and observer distance ($r^2 = 0.55$, $P < 0.001$). Most locations (90%) were taken from a distance ≤ 400 m, often considerably closer and the expected telemetry error based on the regression equation at that distance was 86.5m. I excluded from analysis all estimated locations that were > 400 m from the closest spot in which an observer took an azimuth reading. The mean number of locations used for seasonal analysis was 37 (range 18-83).

Home range ($F_{2, 125} = 8.45$, $P < 0.001$) and core area ($F_{2, 125} = 7.17$, $P = 0.001$) sizes differed among seasons, with greatest space use during the breeding season and the least during summer (Table 3.1). Raccoons selected different habitats seasonally within home ranges relative to availability across the study area (1st order selection; $F_{3, 118} = 74.26$, $P < 0.001$). Openings were consistently selected by raccoons when establishing their home ranges. However, the composition of core use areas did not differ from the composition of habitats selected when establishing home ranges (2nd order selection; $F_{3, 118} = 1.88$, $P = 0.137$). Raccoons used habitats different than availability within their home ranges (3rd order selection; $F_{3, 118} = 56.52$, $P < 0.001$), using water-influenced forests most during the breeding season, managed forests during summer, and upland forests during fall-winter (Table 3.2).

Table 3.1: Mean seasonal home range (HR) and core area (CA) size (ha) plus associated standard errors from radio-marked raccoons on Sherburne Wildlife Management Area, Louisiana, 2008 -2010

Season ^a	n (home ranges)	HR ± se	CA ± se
Breeding	48	175.67 ± 9.91	33.15 ± 1.91
Summer	46	120.28 ± 7.64	22.54 ± 2.00
Fall-winter	34	148.19 ± 13.04	27.18 ± 2.42

a. Breeding: 1 February – 31 May; summer: 1 June – 30 September; fall-winter: 1 October – 31 January.

Table 3.2: Seasonal and mean ranks (0 = lowest, 3 = highest) of habitat selection across two spatial scales (habitat selection in home ranges vs. habitat availability across study area [1st order], and habitat used vs. habitat availability across home ranges [3rd order]) based on compositional analysis of raccoons on Sherburne Wildlife Management Area, Louisiana, 2008-2010

Habitat Type	1 st Order Selection				3 rd Order Selection			
	Season ^a				Season			
	<i>B</i>	<i>S</i>	<i>FW</i>	<i>Mean</i>	<i>B</i>	<i>S</i>	<i>FW</i>	<i>Mean</i>
Water-influenced Forest	1	0	1	0.67	3	1	1	1.67
Upland Forest	2	2	2	2.00	2	2	3	2.33
Managed Forest	0	1	0	0.33	1	3	2	2.00
Opening	3	3	3	3.00	0	0	0	0

a. Seasons are breeding (B) 1 February – 31 May, summer (S) 1 June – 30 September, and fall-winter (FW) 1 October – 31 January.

Discussion

Raccoons maintained larger home ranges and core areas during the breeding season. Because male raccoons mate promiscuously (Gehrt 2003) they may be expected to increase their range during breeding to increase reproductive success by increasing encounters with females. Conversely, space use was least during summer, a period when soft mast and invertebrates are abundant and relatively ubiquitous, allowing raccoons to fulfill energetic requirements without extensive movements. Previous research in northern latitudes has reported a reduction in winter space use, primarily attributed to raccoons reducing their activities during the coldest time periods (Stuewer 1943, Glueck et al. 1988, Kamler and Gipson 2003, Prange et al. 2004). This behavior is not typically

observed in southern locations (Gehrt and Fritzell 1997, Chamberlain et al. 2003, Fisher 2007), presumably because the mild winters and lack of extreme temperature fluctuations maintain adequate food resources and allow raccoons to stay active during winter (Gehrt and Fritzell 1997). My findings are consistent with this trend as raccoons on Sherburne increased their home ranges during fall-winter relative to summer. As vegetation senesced and hard mast disappeared later in fall, raccoons likely had to expand their ranges to meet foraging demands.

My findings suggest that openings are important to raccoons when selecting and establishing their home ranges. While raccoons have been reported to use agricultural fields for foraging in a number of studies (Ellis 1964, Greenwood 1982, Chamberlain et al. 2007, Atwood et al. 2009), agricultural fields were not present on Sherburne. Openings on Sherburne were dominated by road ways, gas and power right-of-ways, wildlife food plots, and hunting camps. Raccoons have been reported to use forest edges for foraging and travel (Pedlar et al. 1997, Dijack and Thompson 2000, Barding and Nelson 2008) and Oehler and Litvaitis (1996) found raccoons in New Hampshire to be more abundant in landscapes offering a variety of cover-types. Most home ranges selected by raccoons on Sherburne incorporated several different patches of forest separated by openings. If raccoons are selecting home ranges that offer them access to several forest patches and/or concentrating around forest edges, then it is plausible that openings would be an important home range characteristic during all seasons, despite the fact that openings are less important to raccoons at smaller spatial scales.

That no 2nd order selection was detected (i.e., habitats within core areas did not differ compared to availability within home ranges) suggests that raccoons maintained

core areas that were essentially microcosms of their respective home ranges, at least at the resolution at which I delineated habitats. This suggests that patterns of habitat selection exhibited by raccoons on Sherburne led to the creation of home ranges sufficiently heterogeneous such that core areas were not proportionally different from home ranges as a whole. Stated differently, raccoons may have established home ranges in such a way that differential selection of core areas within home ranges was unnecessary.

Habitat selection within home ranges (3rd order) varied across seasons. Raccoons are true generalist foragers known to change their foraging patterns to exploit food items that are most prevalent at a given time (Stuewer 1943, Baker et al. 1945, Johnson 1970, Fleming 1976). I know that raccoons denned in all forest types based on locations of inactive raccoons during day-light hours and occasional walk-ins on dens, and since standing water was widely available in the form of bayous and ephemeral pools I assume that raccoons were not limited by these resources and that habitat selection observed at the 3rd order reflects a response to spatio-temporal variation in food availability. Water-influenced forests were important during the breeding season (February - May), at the height of seasonal flooding on Sherburne. Raccoons use these forests to forage on abundant invertebrates (e.g., crawfish) and vertebrates (e.g., reptiles and amphibians) found in shallow water pools which represent a readily available food source at a time when soft mast are not yet available.

Raccoons are known to shift diet from invertebrates during the cold months to soft mast during the warmer months (Johnson 1970, Gehrt 2003). During summer, raccoons selected managed forests within their home ranges. The dense understory

growth associated with these forests provided an abundance of soft mast, particularly blackberries and elderberries, throughout the summer. Upland forests were the next most selected habitat type at this time of the year and were likely important for raccoons that did not have managed forests available within their home ranges. Blackberries and elderberries occur in upland forests on Sherburne and are particularly prominent along forest edges; I frequently observed raccoons foraging in elderberry thickets along forest edges during peak berry abundance. Raccoon diets during fall and winter are dominated by remaining soft mast with an increasing reliance on hard mast, particularly acorns (Johnson 1970). The observed selection for upland forests during fall-winter likely reflects exploitation of these resources.

My findings highlight the importance of landscape heterogeneity to raccoons and the importance of evaluating habitat selection at multiple spatial scales. Raccoons altered their habitat selection on a seasonal basis, tracking the temporal changes in food availability across habitats. Raccoons are habitat generalists, and my results suggest that they select habitats differently across various spatial scales within bottomland hardwood systems, presumably to allow them to exploit resources that vary spatially and temporally.

Chapter 4: Nesting Ecology of Wild Turkeys in a Bottomland Hardwood Forest

Introduction

Reproductive success is an important factor influencing wild turkey population dynamics (Vangilder 1992, Roberts and Porter 1996). Reproductive output for a given area may be a function of the quality of available nesting habitat. As a ground nester, wild turkey nests are susceptible to nest predators, a notion supported by the large number of studies identifying predation as the primary cause of nest failure (Vander Haegen et al. 1988, Still and Baumann 1990, Palmer et al. 1993*b*, Miller et al. 1998, Paisley et al. 1998, Thogmartin and Johnson 1999). Predation risk likely plays a large role in wild turkey nest site selection, especially at small spatial scales. For example, one characteristic associated with turkey nests across the entire species range is the presence of well developed, ground-level vegetation, providing visual cover in the immediate vicinity of the nest (Porter 1992). Dense vegetation may reduce visual clues to terrestrial predators (Bowman and Harris 1980) and dense screening cover was associated with reduced mammalian predation on Merriam's turkey nests in South Dakota (Lehman et al. 2008). Turkeys may choose to place their nests in such areas as a means of predator defense, and a lack of such protection may translate into increased predation risk.

Animals are known to respond to habitat characteristics at a range of spatial scales (Wiens 1989, Orians and Wittenberger 1991), and landscape factors at larger scales likely also influence nest site selection. Thogmartin (1999) found that turkeys selected large habitat patches and avoided areas with a high degree of edge density in a highly fragmented landscape, whereas Lazurus and Porter (1985) suggested that nest site selection may be partially influenced by proximity to suitable brood-rearing habitat. The

availability of quality nesting habitat, offering qualities such as nest protection and close proximity to foraging areas, should influence reproductive parameters such as nest initiation and success. An understanding of nest site selection is important because it identifies the habitat and landscape characteristics important to turkey nesting, and can guide land management decisions aimed at increasing wild turkey production.

Wild turkey reproduction has been widely studied in a variety of habitats (Lazarus and Porter 1985, Ransom et al. 1987, Day et al. 1991, Paisley et al. 1998, Thogmartin 1999, Nguyen et al. 2003), but information regarding reproduction and nest site selection in bottomland hardwood forest systems is noticeably lacking (but see Wilson 2005*b*). Bottomland systems are widely recognized as high quality turkey habitat (Dickson 2001), hence the lack of information available on nesting ecology in these systems represents a substantial gap in our understanding of wild turkey ecology. My goals were to study nest site selection at a variety of spatial scales in a bottomland hardwood system in Louisiana, primarily to identify the habitat and landscape characteristics associated with nesting. Additionally, I describe reproductive parameters and identify causes of nest failure.

Previous work on Sherburne indicated low nesting rates (Wilson 2005*b*), suggesting that a large portion of the population likely has their clutch destroyed prior to initiating incubation. This combined with the large home ranges observed during pre-incubation (Chapter 1), suggest a scarcity of quality nesting habitat. Understory vegetation on Sherburne is generally sparse due to annual flooding and overstory shading, which may reduce the availability of suitable nesting locations. Flooding presents an additional threat to nesting success on Sherburne. I hypothesized that turkeys would choose to nest in patches of denser ground-level vegetation relative to

what was generally available, and in areas of relatively higher elevation less prone to flooding.

Methods

Female wild turkeys were captured and fitted with mortality-sensitive VHF radio transmitters as described in Chapter 1. I tracked birds throughout the year via radio telemetry. To insure that all nesting related activity was detected, I triangulated ≥ 1 location daily for each turkey beginning on 15 February and continued through the end of the nesting season (March – June) in each year. I studied nesting ecology during the nesting seasons 2008-2010, whereas previous researchers collected data during the 2002-2004 nesting seasons using the same methods described below (see Wilson 2005*b*).

I assumed a bird to have initiated incubation when it was found in the same location for 2 consecutive days. Since incubation would often trigger the mortality sensor in the VHF transmitters, I treated any consistent mortality signals discovered from 1 April – 15 May as an incubating bird and did not walk in on the radio for 30 days to avoid accidentally flushing turkeys that may have been incubating a nest. Once I determined a turkey to be incubating, I approached the nest to within a distance of ~15m and placed flagging tape on the vegetation surrounding the nest site. On each piece of flagging I recorded a compass bearing toward the incubating bird and used this information to later help locate the nest. In addition to the nests of radio-marked birds, several nests were located incidentally by WMA staff and other researchers working on the study area.

Once incubation had been terminated and the female had left the nest site (due to successful hatching or nest failure), or after 32 days had passed since the first known date

of incubation, I located the nest and recorded its location with a hand-help GPS unit. I considered a nest successful if ≥ 1 egg hatched and unsuccessful otherwise. I used clues at the nest site to determine the cause of nest failure. I considered a nest abandoned if the nest was undisturbed and a full clutch of eggs was found intact and considered a nest to have been destroyed by floods in cases where the nest site was inundated by water. I considered a nest to have been destroyed by predators if the nest site was trampled, eggs were destroyed at the nest site, eggs were found carried away from the nest site and destroyed, or if the nest was found to be empty and incubation lasted < 27 days. I considered a female to have been killed by a predator during incubation if the carcass of the female was found at, or within the immediate vicinity of the nest. Nests that were suspected of being abandoned due to observer interference were censored from estimates of nesting success.

I calculated reproductive parameters in each year based on those identified by Vangilder (1992). Specifically, I defined nesting rate as the percentage of females alive on 23 March of each year that were known to reach incubation. I chose 23 March because that was the earliest incubation start date recorded on Sherburne. I defined the renesting rate in each year as the percentage of females that renested following the failure of their first nesting attempt, excluding those females who were killed while incubating their initial nest. Since wild turkeys do not begin incubation until the entire clutch has been laid (Eaton 1992) and I was not able to detect nests until incubation began, it is possible that estimates of nesting rates are biased low as some nests may have been destroyed prior to incubation. Nesting and renesting success was defined as the percentage of initial and renests that successfully hatched ≥ 1 egg respectively. Nests

that were suspected of observer-induced abandonment were excluded. I calculated female success in each year as the percentage of females alive on 23 March that successfully hatched ≥ 1 egg in that nesting season.

Because all females were captured during summer (June – August), I did not separate age classes because all individuals were adults by the first nesting season in which they were studied. I report reproductive parameters for each nesting season independently, pooled for each of the 2 study periods (2002-2004, and 2008-2010), and pooled for all study years combined. I used Fisher's exact test to test for differences in the pooled nesting rate, initial nesting success, and female success between the first (2002-2004) and second (2008-2010) 3 year study periods.

Landscape-level Nesting Habitat Selection

To study nest site selection at the landscape level, I first imported and converted the UTM coordinates of all nests into a point theme in ArcGIS 9 (ESRI, Redlands, California). For each nest I generated a random location within the study area. Because turkeys may respond to different landscape characteristics at varying scales (Johnson 1980, Wiens 1989), I created spatial buffers of 200m, 400m, and 800m around each nest and random point, and intersected these buffers with a digital landcover of Sherburne. Habitats were delineated into 4 broad types; open water, upland forest, water-influenced forest, and openings. A detailed description of each habitat type and the process by which the digital landcover was created is presented in Chapter 1. At each spatial scale the percentage of each habitat type within each buffered area was calculated, and the Shannon-diversity index was calculated to provide a measure of habitat diversity. Because wild turkeys have been reported to nest close to edges between forest habitats

and openings (Speake et al. 1975, Everett et al. 1985, Campo et al. 1989, Seiss et al. 1990), I calculated edge density within each buffered area as the total length (m) of all edge between forest habitats and openings divided by the total area (ha) of each buffered zone.

I used principal components analysis (PCA) as a variable reduction tool and because of multicollinearity between variables. I retained principal components based on the results of a scree plot and developed a suite of logistic regression models to differentiate between nest sites and random locations using the retained components as variables. When interpreting components I considered only variables that loaded on a single component with a value ≥ 0.5 following an orthogonal matrix transformation. I used a Hosmer-Lemeshow goodness-of-fit test to assess model fit and calculated Akaike's information criterion adjusted for small sample sizes (AIC_c) for each model and used ΔAIC_c and Akaike weights (w_i) to evaluate model performance (Burnham and Anderson 2002). I determined the relative importance of each principle component in determining between random and nest sites by summing the Akaike weights across the models in which each component occurred (Burnham and Anderson 2002).

Micro-habitat Nest Site Selection

To study selection at the level of the nest site I measured habitat characteristics within 10m of each nest. I estimated canopy cover by taking readings with a spherical densiometer (Lemmon 1956) directly over the nest and at a distance of 10m from the nest in each of the 4 cardinal directions. I then averaged each canopy cover reading to provide a value for the nest site. I estimated lateral visual obstruction for each nest by taking minimum (VO_{min}), average (VO_{avg}), and maximum (VO_{max}) readings of a

Robel pole (Robel et al. 1970) placed at the nest center from a distance of 10m in each of the 4 cardinal directions, and averaged the 4 readings of each measurement to provide a value for the nest site. I used a 1m² Daubenmire frame (Daubenmire 1959) to quantify ground cover composition as the percentage of water, open ground, grasses, forbs, ferns, vines, debris, and woody vegetation present within each frame. Ground cover measurements were taken at the nest and at a distance of 10m in each of the 4 cardinal directions and averaged to provide a single value for each nest. I recorded the habitat type each nest was located in and the distance from the nest to the nearest forest edge. For each nest site a random site was chosen within 100-500m of the nest, and the same characteristics were measured as described above. This allowed comparison of the habitat within the immediate area of nest placement to that of other locations that each nesting female could have sampled prior to nesting. Habitat characteristics of each nest site and its associated random site were recorded on the same day, ≤ 5 days following the day in which I determined the nest was no longer active.

I developed a suite of 27 logistic regression models designed to discriminate between nest sites and random sites relative to microhabitat characteristics assumed to be important to wild turkeys when selecting nest sites. I used a Hosmer-lemeshow goodness-of-fit test to assess model fit. I calculated Akaike's information criterion adjusted for small sample sizes (AIC_c) for each model and used Δ AIC_c and Akaike weights (w_i) to evaluate model performance (Burnham and Anderson 2002). Using the top 10 performing models I determined the relative importance of each habitat variable in distinguishing between random and nest sites by summing the Akaike weights across the models in which each variable occurred (Burnham and Anderson 2002).

Results

A total of 47 nests were discovered across 6 nesting seasons, 35 nests belonged to radio-marked birds and 12 nests were found opportunistically. Data on the date on which incubation was initiated were available from radio-marked turkeys during the 2008-2010 nesting seasons. Continuous incubation of initial nesting attempts occurred within a relatively narrow time frame from late March through early April during 2008 and 2009, but considerably later during 2010 (Table 4.1). The average length of incubation for successful nests was 28.6 days ($n = 8$, range 26 – 33 days). Three nests were likely abandoned due to observer disturbance and were censored when estimating nesting success. Of the remaining 32 nests whose fates were known, 12 (37.5%) were successful in hatching ≥ 1 egg, 11 nests (34.38%) were destroyed by predators, 4 nests (12.5%) failed due to predation of the incubating hen, 4 nests (12.5%) were destroyed by flooding, and 1 nest (3.13%) was abandoned. All nests lost to flooding were during the 2002 nesting season. Nest predation accounted for most (55%) nest failures.

Table 4.1: Mean dates and ranges of the onset of incubation for initial nesting attempts of female wild turkeys on Sherburne WMA, Louisiana, 2008-2010.

Year	<i>n</i>	Mean date	Range
2008	4	2 April	30 March – 5 April
2009	11	31 March	23 March – 7 April
2010	5	22 April	16 April – 25 April

All reproductive parameters varied considerably among years (Table 4.2). Nesting rate ranged from 12.5% - 100% and averaged 60% across the study (Table 4.2). Pooled nesting rates were approximately 20% higher during the 2008-2010 nesting seasons than during the 2002-2004 seasons (Table 4.2), but the proportion of females initiating incubation was similar between these time periods (Fisher's exact test, $P = 0.23$). The

overall nesting success rate for initial nesting attempts was 39.9% (Table 4.2). Success of initial nests was not significantly different between the 2 time periods (Fisher's exact test, $P = 1.0$). Four turkeys (26.7%) attempted to renest following the failure of their initial nest, but only 1 renest attempt was successful (Table 4.2). Overall, hen success was 24% (Table 4.2), and tended to be higher during the 2008-2010 time period, although the difference was not statistically significant (Fisher's exact test, $P = 0.73$).

Table 4.2: Reproductive parameters of wild turkeys nesting on Sherburne WMA, Louisiana, during the 2002-2004 and 2008-2010 nesting seasons. Numbers in parentheses correspond to the number of nesting attempts or successful nesting attempts.

Year	<i>n</i>	Nesting rate	1 st nest success	Renest rate	Renest success	Female success
2002	6	83% (5)	20% (1)	0%	N/A	20% (1)
2003	8	12.5% (1)	0%	0%	N/A	0%
2004	5	60% (3)	66.7% (2)	100% (1)	0%	40% (2)
Pooled	19	47.4% (9)	33.3% (3)	14.3% (1)	0%	15.8% (3)
2008	4	100% (4)	25% (1)	50% (1)	0%	25% (1)
2009	17	70.6% (12)	60% (6)	50% (2)	33.3% (1)	41.2% (7)
2010	10	50% (5)	20% (1)	0%	N/A	10% (1)
Pooled	31	67.7% (21)	42.1% (8)	30% (3)	25% (1)	29% (9)
All Years	50	60% (30)	39.3% (11)	26.7% (4)	20% (1)	24% (12)

Following PCA of landscape-level variables of 41 nests and associated random locations, I chose to retain 3 principal components for use in developing logistic regression models. All 3 components had eigenvalues > 1 and cumulatively accounted for 76% of the variance. Component 1 included edge density, as well as the percentage of upland and water-influenced forest within buffered areas at all 3 spatial scales. Component 2 consisted of the percentage of openings within buffered areas at all spatial scales, and landscape diversity estimates at the 400m and 800m scales. Component 3 consisted of the percentage of open water within buffered areas at all spatial scales and landscape diversity at the 200m scale. All models had adequate goodness-of-fit based on

Hosmer-Lemeshow statistics (all P -values > 0.05). The 2 best performing models ($\Delta AICc < 4$, combined $w_i = 0.87$) both included principal components 1 and 2 (Table 4.3), and both components had large summed model weights (Table 4.4) indicating they were considerably more important in distinguishing between nesting locations and random locations relative to other model parameters. Turkeys chose to nest in landscapes characterized by high edge density, and comprised of greater proportions of upland forest and forest openings compared to what was generally found throughout the study area (Table 4.5). Turkeys avoided water-influenced forests when selecting nesting areas (Table 4.5), and all nests were placed in either upland forests ($n = 35$) or openings ($n = 6$). Additionally, habitat diversity at the larger spatial scales (400m and 800m) appeared important to turkeys when selecting nesting areas; this is probably a by-product of the selection for high edge densities and openings, which only comprised 2.36% of the study area.

Microhabitat characteristics were measured for 40 nests and random locations (Table 4.6). An examination of the correlations between microhabitat characteristics indicated high correlation existed between visual obstruction measurements, so only one visual obstruction measure (VOavg) was retained for construction of models to avoid multicollinearity issues. All models I evaluated had adequate goodness-of-fit based on Hosmer-Lemeshow statistics (all P -values > 0.05). Two of the top 10 performing models were relatively well supported, carrying a cumulative w_i of 0.63 with $\Delta AICc$ values < 3 (Table 4.7). The percent open ground (BG) found within 10m of nests and random sites was a common variable in all of the top 10 performing models (Table 4.7). Examination of summed model weights based on the top 10 models indicated that percent open ground

Table 4.3: Results of logistic regression models^a developed to differentiate between nests ($n = 41$) and random locations ($n = 41$) based on principal components^b of landscape features measured at 3 spatial scales (200m, 400m, and 800m) for the 2002-2004, and 2008-2010 nesting seasons on Sherburne WMA, Louisiana.

Model	K	AICc	ΔAICc	w_i
C1 + C2 + C1xC2	4	72.33	0.00	0.4918331403
C1 + C2 + C3	4	72.84	0.51	0.3807486755
C1 + C2	3	76.94	4.61	0.0490480683
C1 + C3	3	77.05	4.72	0.0464000624
C1 + C3 + C1xC3	4	78.76	6.43	0.0197694835
C1	2	79.72	7.39	0.0122005694
C2	2	115.56	43.23	0.0000000002
C2 + C3	3	115.74	43.40	0.0000000002
C3	2	115.81	43.48	0.0000000002
C2 + C3 + C2xC3	4	118.21	45.88	0.0000000001

a. Model = Principle components used in each model, K = number of parameters, AIC_c = Akaike's Information Criterion adjusted for small sample size, Δ AIC_c = difference in AIC_c relative to smallest value, w_i = AIC_c weight.

b. C1 = edge density, % upland forest, and % water-influenced forest at all spatial scales, C2 = % openings at all spatial scales and landscape diversity at 400m and 800m, C3 = % open water at all spatial scales and landscape diversity at 200m.

Table 4.4: Summed model weights of principle components used in logistic regression models differentiating nest sites from random locations based on landscape level habitat characteristics for the 2002-2004 and 2008-2010 nesting seasons, Sherburne WMA, Louisiana.

Principal Component	Summed model weight
C1	0.9999999994
C2	0.9216298845
C1xC2	0.4918331403
C3	0.4469182218
C1xC3	0.0197694835
C2xC3	0.0000000001

(BG) along with distance to nearest edge (EDGE) and visual obstruction (VOavg) were most important in distinguishing between random and nests sites relative to other habitat variables (Table 4.8). Compared to random sites, turkeys tended to place their nests at sites with little bare ground, close to forest edges, and in locations with greater visual obstruction (Table 4.6).

Table 4.5: Mean \pm standard error for habitat characteristics measured within 200m, 400m, and 800m buffered areas around wild turkey nest locations (n = 41) and random locations (n = 41) from the 2002-2004, and 2008-2010 nesting seasons on Sherburne WMA, Louisiana.

Variable	Nests	Random
200m Buffer		
Edge density ^a	55.87 \pm 4.21	16.54 \pm 4.48
%Water	3.45 \pm 0.99	1.07 \pm 0.38
%Water-based forest	8.94 \pm 2.42	50.07 \pm 5.74
%Upland forest	76.35 \pm 3.95	44.62 \pm 5.33
%Open	11.26 \pm 3.32	4.25 \pm 2.16
Diversity index	0.49 \pm 0.04	0.47 \pm 0.05
400m Buffer		
Edge density	46.76 \pm 1.91	15.82 \pm 3.72
%Water	3.35 \pm 0.65	0.99 \pm 0.26
%Water-based forest	13.51 \pm 2.50	49.33 \pm 4.94
%Upland forest	74.50 \pm 3.14	46.31 \pm 4.51
%Open	8.64 \pm 2.07	3.37 \pm 1.39
Diversity index	0.62 \pm 0.04	0.58 \pm 0.04
800m Buffer		
Edge density	38.08 \pm 1.33	15.64 \pm 2.48
%Water	2.84 \pm 0.35	1.28 \pm 0.21
%Water-based forest	17.71 \pm 2.21	47.62 \pm 3.96
%Upland forest	73.45 \pm 2.29	48.43 \pm 3.61
%Open	6.00 \pm 1.03	2.67 \pm 0.63
Diversity index	0.70 \pm 0.03	0.69 \pm 0.04

a. Length (m) of all edges between forest habitats and openings/Area (ha).

Table 4.6: Means \pm SE of habitat characteristics measured at wild turkey nests ($n = 40$) and random points ($n = 40$) during the 2002-2004, and 2008-2010 nesting seasons on Sherburne WMA, Louisiana.

Variable	Nests	Random points
	Mean \pm SE	Mean \pm SE
% Canopy Cover	77.8 \pm 5.43	85.2 \pm 4.27
Visual obstruction ^a (m)-min	0.79 \pm 0.056	0.51 \pm 0.068
Visual obstruction (m)-avg	0.95 \pm 0.045	0.73 \pm 0.062
Visual obstruction (m)-max	1.2 \pm 0.044	1.03 \pm 0.06
Ground Cover^b		
% Grass	15.5 \pm 5.0	7.7 \pm 3.35
% Woody	5.6 \pm 0.91	3.1 \pm 0.71
% Forb	15.3 \pm 2.00	15.8 \pm 2.37
% Vine	19.9 \pm 3.00	17.7 \pm 2.74
% Fern	23.8 \pm 3.9	18.6 \pm 3.6
% Open ground	4.2 \pm 0.92	22.2 \pm 4.1
% Debris	15.1 \pm 2.49	12.29 \pm 2.31
%Water	0 \pm 0	2.08 \pm 0.92
Distance to edge (m)	55.8 \pm 8.59	86.6 \pm 12.8

a. Visual obstruction measured using a Robel pole.

b. Ground cover composition estimates obtained by use of a 1m² Daubenmire frame.

Table 4.7: Ten highest ranking logistic regression models^a differentiating between nests and random points based on microhabitat characteristics during the 2002-2004 and 2008-2010 nesting seasons, Sherburne WMA, Louisiana.

Model ^b	K	AIC _c	Δ AIC _c	w_i
VOavg + OG + WOOD + EDGE	5	88.09	0.00	0.4836111511
EDGE + OG + VOavg	4	90.55	2.46	0.1416869274
EDGE + OG	3	91.16	3.07	0.1044053769
OG + WOOD	3	91.76	3.67	0.0773454055
CC + VOavg + OG + EDGE	5	92.89	4.80	0.0439161080
CC + VOavg + OG + DEB	5	93.11	5.01	0.0394597505
VOavg + OG + CC + EDGE	5	93.26	5.16	0.0365536548
EDGE + OG + EDGE x OG	4	93.69	5.60	0.0294478201
VOavg + OG	3	94.17	6.07	0.0232262052
OG	2	94.43	6.34	0.0203476005

a. Model = Habitat variables used as parameters in each model, K = number of parameters, AIC_c = Akaike's Information Criterion adjusted for small sample size, Δ AIC_c = difference in AIC_c relative to smallest value, w_i = AIC_c weight.

b. Habitat variables are average visual obstruction (VOavg), % ground cover = open ground (OG), % ground cover = woody vegetation (WOOD), distance to nearest forest/opening edge (EDGE), % ground cover = debris (DEB), and canopy cover (CC).

Table 4.8: Summed model weights for variables in the top 10 performing models developed to discriminate between nest sites and random points based on microhabitat habitat characteristics during the 2002-2004 and 2008-2010 nesting seasons, on Sherburne WMA, Louisiana.

Variable	Summed model weight
OG	1.0000000000
EDGE	0.8790807887
VOavg	0.7684537969
WOOD	0.5609565566
CC	0.0804697628
DEB	0.0394597505

Discussion

As expected, turkeys on Sherburne selected topographically higher areas for nesting; all nests were placed predominantly in upland forests or openings. Water-influenced forests were avoided at the landscape scale, which corresponds to habitat selection observed during the pre-incubation period (Chapter 1). Several advantages may come from nesting in upland areas. Flooding can seriously impact turkey nesting (Kimmel and Zwank 1985), and given the flood-prone nature of bottomland forests, nesting in upland sites offers the best chance of avoiding nest loss from flooding. Upland areas on Sherburne also provided more ground level vegetative cover than those areas that experience regular inundation. Proximity to quality brood-rearing habitat may play an important role in nest site selection (Porter 1992). Upland forests on Sherburne appear to provide the qualities associated with good brood-rearing habitat and are the preferred habitat type of female turkeys during the brood-rearing season (Chapter 1); thus the proximity to brood-rearing habitat may be an additional benefit of nesting in upland forests.

A proclivity for nesting close to edges has been widely reported for wild turkeys (Hillestad 1970, Speake et al. 1975, Everett et al. 1985, Campo et al. 1989, Seiss et al.

1990, Still and Baumann 1990), a pattern that was evident on Sherburne as well. Turkeys chose to nest in areas with relatively high edge densities at all landscape scales studied. The mean distance of nest placement from the nearest edge was 55.8m, with 80% of nests located within 100m of a forest edge. Turkeys may choose to nest near right-of-ways and roads (the predominant openings on Sherburne) because they can be used as travel lanes and offer incubating females foraging opportunities near the nest.

Potential predators such as raccoons and coyotes are known to concentrate in areas offering high landscape heterogeneity and to make use of edge areas (Chapter 3, Dijak and Thompson 2000, Kays et al. 2008), which may cause nests placed close to edges to face increased predation risk. Thogmartin (1999) found turkeys in a highly fragmented forest in Arkansas avoided nesting in edge habitats, presumably as a response to high predator densities. Landscape structure appears to influence the severity of edge effects on nest predation, with more pronounced effects generally observed in highly fragmented landscapes (Paton 1994, Donovan et al. 1997, Keyser et al. 1998, Stephens et al. 2003). Turkeys must balance the trade-off between the perceived advantages of nesting in edge habitats, such as proximity to foraging and brood-rearing areas, and predation risk. Sherburne is characterized by large swaths of continuous forest with relatively low fragmentation. Success of initial nesting attempts (39.3%) was well within the range of that reported for adult eastern wild turkeys in the literature (range: 16% [Paisley et al. 1998] - 66.7% [Swanson et al. 1995]). It would appear that on Sherburne the potential risks of nesting in edge habitats are outweighed by the benefits.

As is commonly reported, the presence of ground level vegetation was important to nesting turkeys (Hon et al. 1978, Everett et al. 1985, Campo et al. 1989, Still and

Baumann 1990, Day et al. 1991, Chamberlain and Leopold 1998). The concealment such cover provides likely serves as a predator defense mechanism (Lehman et al. 2008). Despite the fact that understory vegetation is rather sparse on Sherburne, turkeys consistently choose to nest in patches that offered ground level cover within the immediate vicinity of the nest, and avoided nesting in areas consisting largely of bare ground. Nests in openings were in locations that had not been recently mowed and were dominated by dense grass cover. Nests in forests were placed within a range of vegetative cover types, including southern shield fern (*Thelypteris kunthii*), vines such as green brier (*Smilax* spp.), blackberry (*Rubus* spp.), various woody shrubs, and within the debris of fallen trees.

Nests in forests were commonly associated with small breaks in the canopy caused by fallen trees. These isolated openings allowed understory vegetation to flourish, and also provided cover in the form of debris from the fallen trees themselves. Hurricane Gustav impacted Sherburne in the fall of 2008, causing an estimated 30% reduction in canopy cover across the area (Louisiana Department of Wildlife and Fisheries, unpublished data). The following nesting season (2009) was characterized by high nesting rates, and the highest observed female success rate for the study. Periodic natural disturbances, such as hurricanes, that cause spot reductions in canopy over a wide area appear to create quality nesting habitat, and may be an important element maintaining turkey populations in bottomland systems. Interestingly, there is little evidence that applied forest management techniques, such as shelterwood and group harvests, that reduced canopy cover served to provide nesting habitat on a long term basis. Only 2 nests were found within forest stands that had been managed with these harvests; both

nests were found during the 2004 nesting season in a shelterwood treatment that had been cut the previous fall. As mentioned in Chapter 1, succession occurs rapidly in these stands, and after 2 growing seasons understory vegetation is too dense to be of use by turkeys. Given the rapid rate of succession that occurs in forest openings in bottomland systems, suitable nesting habitat likely only exists within a single growing season of canopy disturbance. Thus, I offer that natural periodic disturbances create an abundance of ephemeral, high quality nesting habitat over a broad area, and that temporary increases in reproductive output likely follow such events. Further investigation into the effects of major natural disturbances on turkey reproduction in southern bottomland hardwood forests may prove valuable for predicting pulses in hen success and recruitment.

Reproductive parameters varied considerably across years as is commonly reported in other areas (Vangilder et al. 1987, Roberts et al. 1995, Miller et al. 1998, Thogmartin and Johnson 1998). The overall nesting rate of 60% in this study is among the lowest reported for adult eastern wild turkeys (reported range: 63.4% [Miller et al. 1998] - 100% [Vander Haegen et al. 1988]). This number is likely biased low because nests that were destroyed prior to incubation could not be detected, but this bias is present in all wild turkey studies. Because the overall success rate of initial nesting attempts on Sherburne falls well within the normal range for adult eastern wild turkeys, it is the low nesting rate that seems to account for the overall low rate of female success. Female success is probably a more accurate indicator of total reproductive output than nesting rates since clutches that are destroyed prior to incubation can not be detected, and at 24% this is among the lowest reported (range: 19.5% [Thogmartin and Johnson 1999] – 82.8% [Vangilder 1992]) for adult eastern wild turkeys.

I contend that the low reproductive output observed on Sherburne results from a scarcity of quality nesting habitat. The lack of quality nesting habitat likely results in some females being forced to place nests in sub-optimal habitat that increases the risk of nest destruction. This would account for the low nesting rates observed, as most individuals likely lost their clutches to predators prior to incubation and observer detection. A number of individuals for which a nesting attempt was never discovered exhibited behaviors associated with nesting; namely, concentrated activity in a small area over a narrow time frame. Additional evidence of poor nesting habitat is provided by significant increases in home range sizes observed during the pre-incubation period relative to other times of the year, suggesting that females may be sampling a large area during the nest site selection process. While an increase in space use at this time may have been a result of increased foraging range in response to a lack of foraging resources during an energetically expensive time of year, the general productivity of Sherburne and significantly smaller home ranges observed during all other seasons makes this alternative hypothesis unlikely.

Despite female success rates similar to those in areas with declining turkey populations (Miller et al. 1998, Thogmartin and Johnson 1999), harvest rates on Sherburne do not indicate any negative population trends on Sherburne (Louisiana Department of Wildlife and Fisheries 2010). Despite low reproductive rates the turkey population does not show evidence of any population declines. While nesting habitat may be poor, upland forest areas on Sherburne appear to provide quality brood-rearing habitat (Chapter 1). Thus, a habitat mediated trade-off may exist, in which low reproduction as a result of poor nesting habitat is compensated for by high poult survival

due to quality brood-rearing habitat. In this scenario, the number of poult produced may be low, but a substantial percentage of poult that do hatch are recruited into the adult population. Clearly, a better understanding of the relationship between habitat, reproduction, and recruitment in bottomland hardwood systems is needed, and presents an interesting avenue of future ecological research.

Chapter 5: The Use of First-passage Time to Identify Area-restricted Search Behavior in Raccoons

Introduction

Animals live in spatially heterogeneous landscapes where resources are unevenly distributed across the environment in patches of varying scale (Johnson et al. 1992, Fauchald 1999). For example, food resources are normally concentrated in patches within the context of the larger landscape. Predators should respond to this heterogeneity by increasing the time spent within profitable patches that offer relatively high prey availability and minimizing time spent searching for prey in less profitable areas (Stephens and Krebs 1986).

One way foragers may maximize their time in profitable areas is by altering their search strategy as they move through the landscape. Specifically, an organism may move quickly and in a relatively linear fashion through non-profitable areas, then adopt a more intensive searching strategy characterized by slower speeds and greater turning angles in response to stimuli, such as the location of a prey item. This behavior is commonly referred to as area-restricted search (ARS) and studies using computer simulations have shown it to be an efficient method of locating and remaining in profitable areas, especially when resources are not distributed homogeneously in space (Benhamou 1992, Zollner and Lima 1999). ARS likely evolved as an adaptive means of exploiting prey in heterogeneous environments (Scharf et al. 2009) and has been observed in a wide variety of taxa in natural and laboratory settings, including insects (Kareiva and Odell 1987, Crist and MacMahon 1991), copepods (Leising and Franks 2002), birds (Smith 1974, Nolet and Mooij 2002, Paiva et al. 2010), spiders (Patt and Pfannenstiel 2009), fish (Mikio et al. 1994, Hill et al. 2000), as well as terrestrial and marine mammals (Lode

2000, Frair et al. 2005, Freitas et al. 2008). A number of methods have been used to characterize and model ARS behavior based on movement paths, including modeling of correlated and random walks (Kareiva and Shigesada 1983, Bergman et al. 2000, Morales et al. 2004), analysis of fractal dimension (Crist et al. 1992, Nams 2005), state space modeling (Forester et al. 2007), first-passage time analysis (Fauchald and Tveraa 2003), path sinuosity (McCarthy et al. 2010), and tortuosity (Valeix et al. 2010).

Studying the movements of individuals can provide insights into population-level characteristics (Kareiva and Odell 1987, Johnson et al. 1992, Turchin 1998, Mueller and Fagan 2008), and understanding ARS behavior should be especially useful in working towards identifying links between behavior and habitat. Because organisms should engage in intensive searching in areas that provide valuable resources, identifying the habitat characteristics associated with intensive searching should likewise identify the habitat features that are important for a species in a given landscape. Similarly, identifying the habitat characteristics associated with more extensive movements should offer insight into the type of areas an animal is likely to avoid, or potentially the landscape features that serve as corridors of rapid movement through the environment.

Advances in radio, satellite, and GPS telemetry have made the historically challenging task of collecting accurate data on movements of wild free-ranging vertebrates feasible. In recent years, a number of studies using telemetry have attempted to link movement behavior and habitat in vertebrates. A great deal of this work has been focused on pelagic marine organisms such as turtles (McCarthy et al. 2010), marine mammals (Freitas et al. 2008) and especially sea-birds (Pinaud and Weimerskirch 2005, Suryan et al. 2006, Weimerskirch et al. 2007, Hammer et al. 2009, Kappes et al. 2010,

Paiva et al. 2010, Scheffer et al. 2010). Similar studies focusing on free-roaming terrestrial vertebrates have been less common (Morales et al. 2004, Frair et al. 2005, Forester et al. 2007, Le Corre et al. 2008), with studies of terrestrial predators comparatively rare (Dickson et al. 2005, Valeix et al. 2010). I used the method of first-passage time analysis (FPT) introduced by Fauchald and Tveraa (2003), which identifies the scale and location in which an organism engages in ARS, to analyze the nightly movement paths of raccoons collected through radio-telemetry, and subsequently link changes in searching behavior to habitat features.

The raccoon is a primarily nocturnal, generalist mesopredator whose behavioral and dietary plasticity allows it to exploit a wide variety of habitats. Raccoons are known to modulate their diet through the year to take advantage of seasonally abundant food resources (Gehrt 2003). During late winter and spring, when hard-mast of the previous fall has been exhausted and before the soft-mast of summer is available, raccoons in the southeastern portion of North America feed primarily on invertebrates, especially crayfish (Baker et al. 1945, Johnson 1970, Gehrt 2003). Invertebrate prey is certainly not distributed evenly across the landscape; crayfish for example are a primarily aquatic organism and their availability to raccoons is limited to areas providing water shallow enough to allow raccoons to capture them. It could therefore be hypothesized that intensive searching should be associated with areas providing abundant invertebrate prey, such as those offering shallow water and abundant crayfish. The fine scale movements of raccoons have never been investigated in this manner, but observations describing long movements interrupted by periods of concentrated activity in confined areas associated

with foraging support the hypothesis that raccoons engage in ARS (Urban 1970, Hoffmann and Gottschang 1977, Greenwood 1982).

My objectives were to apply FPT analysis to the nightly foraging paths of raccoons within a bottomland hardwood forest system to determine if raccoons engage in ARS, describe the scale at which raccoons concentrate their intensive searching activities, and assess the success of applying FPT analysis to understanding behavior of a terrestrial predator. This represents the first time (to my knowledge) this technique has been applied to a terrestrial vertebrate predator. Secondly, I tested the hypothesis that ARS is linked to habitat characteristics by comparing the habitat characteristics of areas along movement paths in which raccoons exhibit intensive searching to areas in which raccoons exhibit more extensive movements. If intensive searching is related to prey resources whose availability is habitat-specific, then habitat associated with intensive searching should differ from habitats in which raccoons exhibit linear movements.

Methods

Raccoon Movement Data Collection

Raccoons were captured, fitted with radio-collars and released as described in Chapter 3. I used sequential telemetry (hereafter focal runs) to obtain movement paths for individual raccoons during a single night. A focal run consisted of triangulating a focal animal's position from 3-4 locations at 20 minute intervals over the course of a night. I used LOCATE III (Pacer; Truro, Nova Scotia, Canada) to obtain Universal Transverse Mercator (UTM) coordinates for each triangulated location. I began all focal runs within an hour of sun-set and continued to track the focal animal until an hour after sunrise or until it reached its day-time den and ceased movements the following morning,

which normally occurred within an hour of sunrise. The goal was to obtain a complete movement path representing the raccoon's nightly movements. I terminated a focal run if the signal was lost on an animal or my ability to triangulate an accurate location was otherwise compromised for ≥ 40 minutes (2 sequential locations were missed). In 8 cases the focal raccoon temporarily became inactive for short periods (1-3hr) in the middle of the night; in such instances I separated the nightly movements into 2 separate paths for analysis purposes (from dusk until temporary den, and from temporary den until dawn). I was able to distinguish active raccoons from inactive raccoons based on radio signal modulation; animals that were moving transmitted a wavering signal whereas inactive animals transmitted a steady signal (Greenwood 1982, personal observation). I conducted focal runs during spring (March – May) 2008-2010

First-passage Time Analysis

I used the method of FPT analysis introduced by Fauchald and Tveraa (2003) to detect and characterize area-restricted search behavior along individual movement paths. First-passage time is defined as the time required for an animal to cross a circle of a given radius (Johnson et al. 1992). The analysis begins by interpolating time and location at set intervals along each path and placing circles of a given radius (r) around each interpolated location. The FPT for each point is measured by the time lag between the first crossing of the circle back along the path and the first crossing of the circle forward along the path. As the radii of the circle increases so does mean FPT as each circle encompasses a greater number of turns and loops in the path (i.e. the time a raccoon spends within each circle will increase as circle size increases), but this increase in FPT will not be equal for each point. Intensively searched areas will experience a greater

increase in FPT as circles around points in these areas will encompass a greater number of turns coupled with decreased speed, compared to areas in which raccoons are traveling at a faster speed and turning less often. As such, the variance in log FPT (FPT is log transformed to make variance independent of the magnitude of mean FPT) will increase as r increases, until the point that r matches the scale of the intensively searched area. At this point, differences in FPT between intensively and non-intensively searched areas will begin to decrease, resulting in a decrease in variance of log FPT. The value of r that gives the maximum variance in log FPT represents the spatial scale in which the raccoon concentrated its searching activities [referred to Area Restricted Search (ARS) scale].

To determine the specific sections of the movement path associated with intensive search behavior, the FPT for the value of r that gives the maximum variance in log FPT is plotted against time along the path. Stated differently, the FPT for the value of r that gives the maximum variance in log FPT is plotted for each sequentially interpolated location along the path. The proportion of the timeline associated with a rapid increase in FPT represents that part of the path in which the animal was engaged in intensive searching behavior. For this analysis I interpolated locations at 1m intervals along each path and measured FPT for circles starting with an r of 10m, and increasing in 10m increments up to 500m. Large-scale activities may mask smaller scale behaviors (Fauchald and Tveraa 2003). Because my objective was to determine the most biologically significant scale in which raccoons were concentrating their foraging activities, I investigated any intensively searched areas with an $r \geq 60\text{m}$ for nested areas of concentration by re-running the analysis using just the portion of the path that fell

within that intensively searched area (Fauchald and Tveraa 2003). I conducted all FPT analysis using software R version 2.12.2 (R Development Core Team 2010).

FPT analysis is sensitive to telemetry error (Pinaud 2008); if telemetry error increases as the focal animal's distance from the observer increases, then the noise associated with this error may lead to an artificial inflation of ARS scale. I calculated telemetry error as described in Chapter 3 and based on those results determined the expected error at an observer distance of 300m to be 60m. To reduce the impacts of telemetry noise on my results, I excluded from analysis paths in which the estimated locations of ≥ 3 sequential triangulations were ≥ 300 m from the closest location in which an azimuth reading was taken. To examine the relationship between telemetry error and the predicted scale of searching behavior, I calculated the distance from the center of each intensively searched area to the nearest location where I recorded an azimuth and used regression analysis to test for relationships between observer distance and scale of the search area. Because telemetry error is positively correlated with observer distance (Chapter 3), I offer that distance should act as a suitable proxy for telemetry error. If the scale of search behavior as determined by FTP analysis is influenced by telemetry error, I would expect to find a positive correlation between observer distance and scale of ARS behavior.

Validation of Area Restricted Search behavior

To test whether the detection of search behavior represented an actual change in behavior on the part of the focal animal and was not simply the by-product of telemetry noise, during early spring 2010 I created an artificial food patch in an area simultaneously occupied by 5 radio-marked raccoons. If a focal raccoon entered the food patch and

began feeding and searching for food within the patch (i.e. engaging in search behavior), analyzing that raccoon's movement path should allow detection of search behavior for the time period associated with the raccoon's time within the patch. The artificial food patch was a 40m × 40m grid, with food items placed at every 10m intersection of the grid and at the center of the patch (Figure 5.1). Food items consisted of a mixture of corn, pastries, fish, and fruit and were placed in aluminum tins that facilitated their easy placement and removal. To help eliminate the possibility that raccoons may have been using this area for other purposes, the food patch was placed in a dry area that raccoons had showed no obvious affinity for based on movements recorded in the previous year, and in which no obvious natural food resources were present. The artificial patch was not active on all nights, and food was made available on a schedule that facilitated tracking of raccoons on nights in which no artificial food was available. To validate telemetry locations within the patch, I placed a Lotek SRX-DL (Lotek Wireless, Newmarket, Ontario) data logging telemetry receiver in the center of the patch and programmed it to scan through the frequencies of the 5 raccoons at 10 minute intervals and record their presence or absence. I used a radio in the same frequency bandwidth to adjust the receiver settings so that radio signals would only be detected when a raccoon was within the food patch itself. This allowed me to validate triangulations within the food patch with the corresponding information collected by the data logger during the same time period.

Habitat Analysis

To assess the link between habitat and ARS behavior, I compared habitat associated with intensive searching activity to that associated with more extensive

movements. I identified intensively searched areas based on the results of FPT analysis and measured habitat characteristics within each area. To measure habitat associated with extensive movements, I selected a point along a movement path in which the raccoon was traveling at a high rate of speed; normally this point fell between the 2 successive locations that were the greatest distance apart. I sampled habitat characteristics in an area centered on this point by creating a sample plot with the same r as the intensively searched portion of the path.

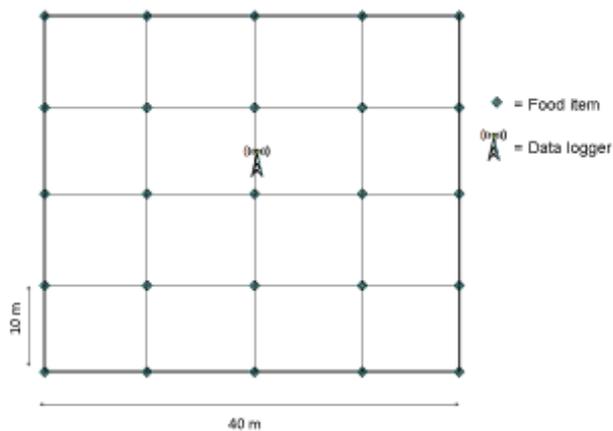


Figure 5.1: Layout of artificial food patch placed on Sherburne WMA, Louisiana, during the spring of 2010 to validate the relationship between the detection of ARS behavior and actual raccoon foraging.

I measured 18 structural and vegetative habitat characteristics that may have influenced raccoon foraging opportunities (Table 5.1). I used a 5m² Daubenmire frame (Daubenmire 1959) to quantify ground cover composition as the percentage of water, open ground, grasses, forbs, ferns, vines, debris, and woody vegetation present within each frame. Ground cover measurements were taken at the center of the plot and at 10m intervals along 4 transects radiating out from the plot center in each of the 4 cardinal directions. The exact number of frame measurements taken in each plot varied in

accordance with the scale of ARS activity, and all estimates were averaged to provide a mean value for each cover type for each sample plot. Vegetation density was estimated using a Robel pole (Robel et al. 1970) to measure vertical obstruction. Measurements of minimum (VO min), average (VO avg), and maximum (VO max) visual obstruction were taken at 10m increments starting from the plot center and radiating out along the 4 transect lines. All values were averaged to provide a mean value for the entire plot. Canopy cover was estimated at plot center and at 10m increments along the 4 transect lines using a spherical densiometer (Lemmon 1956), and the estimates were averaged to give a mean value for each plot. Because coarse woody debris (CWD) may provide raccoons with invertebrate forage and/or impede movements, I counted the number of pieces of CWD with diameter $> 10\text{cm}$ within 5m of each transect line. I separated all CWD into one of 2 size categories; $10 - 30.5\text{cm}$ and $> 30.5\text{cm}$. To calculate CWD density, I divided the amount of CWD in each size category by the total number of transect meters sampled in each plot. For example, in a plot with a spatial scale of $r = 30\text{m}$ there would be 4 transect lines 30m in length totaling 120m of transect lines; the density of CWD $> 30.5\text{cm}$ in this case would be calculated as total number of pieces of CWD $> 30.5\text{cm} / 120$.

I calculated tree density within plots by counting the number of trees with DBH $\geq 10\text{cm}$ within 5m of each transect line and dividing by the total number of transect meters as described above for CWD. Additionally, I calculated the density of sugarberry (*Celtis laevigata*) and oak (*Quercus* spp.) trees of DBH $\geq 10\text{cm}$ respectively. Raccoons on Sherburne forage on the fruit of sugarberry trees (personal observation), which ripens during winter, leaving residual berries during early spring. Residual oak mast also may

have provided forage during early spring. To calculate an index of available water, I measured the total length of each of 4 transect lines that crossed standing water and divided that total by the total number of transect meters as described above for estimating CWD density.

Table 5.1: Abbreviations and descriptions of 18 habitat variables measured along raccoon movement paths within areas of ARS as identified by FPT analysis and within sample plots of areas representative of extensive straight-line movement during March-May 2008-2009, on Sherburne WMA, Louisiana.

Variable	Description
H ₂ O	Value derived by measuring the total # of meters of each of 4 transect lines radiating from plot center at 90° angles that fell over standing water, divided by the combined length of all transects within a plot.
Tree	Density of all trees with DBH > 10cm within 5m of 4 transect lines radiating from plot center at 90° angles.
Sugar	Density of sugarberry trees with DBH > 10cm within 5m of 4 transect lines radiating from plot center at 90° angles.
Oak	Density of oak trees with DBH > 10cm within 5m of 4 transect lines radiating from plot center at 90° angles.
CWD (10-30.5)	Number of pieces of coarse woody debris with diameter 10-30.5cm within 5m of 4 transect lines radiating from plot center at 90° angles divided by the total length of all transects.
CWD (>30.5)	Number of pieces of coarse woody debris with diameter >30.5cm within 5m of 4 transect lines radiating from plot center at 90° angles divided by the total length of all transects.
CC	Value derived from averaging all canopy cover measurements within each plot.
<u>Vegetation Density</u>	Visual obstruction as measured by Robel pole readings (in m) taken from a distance of 10m, averaged across all readings within a plot.
VO min	Minimum level of visual obstruction
VO avg	Average level of visual obstruction
VO max	Maximum level of visual obstruction
<u>Ground Cover</u>	% of each ground cover type within a 5m ² Daubenmire frame averaged across all frame measurements within each plot.
%H ₂ O	Water
%Deb	Debris
%Fern	Ferns
%Vine	Vines
%Forb	Forbs
%Woody	Woody vegetation
%Grass	Grass
%Open	Open Ground

I used principle component analysis (PCA) as a variable reduction tool because of multicollinearity between variables. I retained principle components with eigenvalues >1 . When interpreting principle components I considered all variables that loaded on only a single component with a loading value ≥ 0.50 following an orthogonal matrix transformation. Using the retained principle components as independent variables, I developed a suite of logistic regression models to differentiate between ARS zones as identified by FPT analysis and areas associated with extensive straight-line movements. I tested each model for goodness-of-fit using a Hosmer-Lemeshow goodness-of-fit test. I calculated Akaike's information criterion adjusted for small sample sizes (AIC_c) for each model and used ΔAIC_c and Akaike weights (w_i) to evaluate model performance (Burnham and Anderson 2002). Using the top 10 models, I determined the relative importance of each principle component in predicting intensive searching activity by summing the Akaike weights across the models in which each component occurred (Burnham and Anderson 2002).

Results

I collected 61 nightly trajectories from 16 (12 male, 4 female) raccoons, including 9 paths from 9 March – 5 May 2008, 33 paths from 28 February – 4 May 2009, and 19 paths from 22 February – 22 April 2010. The mean number of locations collected per night was 32 (range 19-37). I excluded 3 movement paths from analysis because ≥ 3 successive relocations were estimated at a distance $\geq 300\text{m}$ from the closest location in which I took an azimuth reading, which would have resulted in unacceptable telemetry error.

I found evidence of ARS behavior in 55 of 58 (94.8%) paths analyzed (Fig 5.2), whereas 3 paths showed no clear peak in variance of log FPT. In 31 instances in which a peak in variance of log FPT occurred at $r \geq 60\text{m}$, a subsequent FPT analysis of the portion of the path that fell within these areas revealed nested smaller scale areas of intensive searching on 24 occasions (Fig 5.3). The scale of ARS zones ranged from $r = 20\text{m}$ - 100m , with a mean of 42.6m . The average time spent in intensive searching behavior was 108.3 min . Most paths (70.9%) only contained a single bout of ARS activity, although 2 bouts were identified in 13 paths, and 3 bouts were identified in 3 paths. Regression analysis revealed a significant positive relationship ($r^2 = 0.19$, $P < 0.001$) between observer distance and the spatial scale on which ARS was detected.

FPT analysis detected ARS behavior associated with the use of the artificial food patch during the 2010 season in 9 of 10 instances in which a tracked raccoon encountered the patch when food was available (Fig 5.4); and in all cases raccoon locations within the vicinity of the food patch were validated by cross referencing with the stationary data logger. Raccoons would visit the patch site on nights in which no food was offered, but analysis of movement paths and recordings of the data logger indicated raccoons did not remain in the patch or engage in ARS behavior when supplemental food was unavailable. The spatial scale (r) associated with the peak in variance of log FPT for raccoons foraging within the food patch ranged from $20\text{m} - 80\text{m}$, with a mean value of 41.3m . The dimensions of the food patch were $40\text{m} \times 40\text{m}$, thus this analysis tended to slightly over-estimate the size of the patch in which raccoons were foraging.

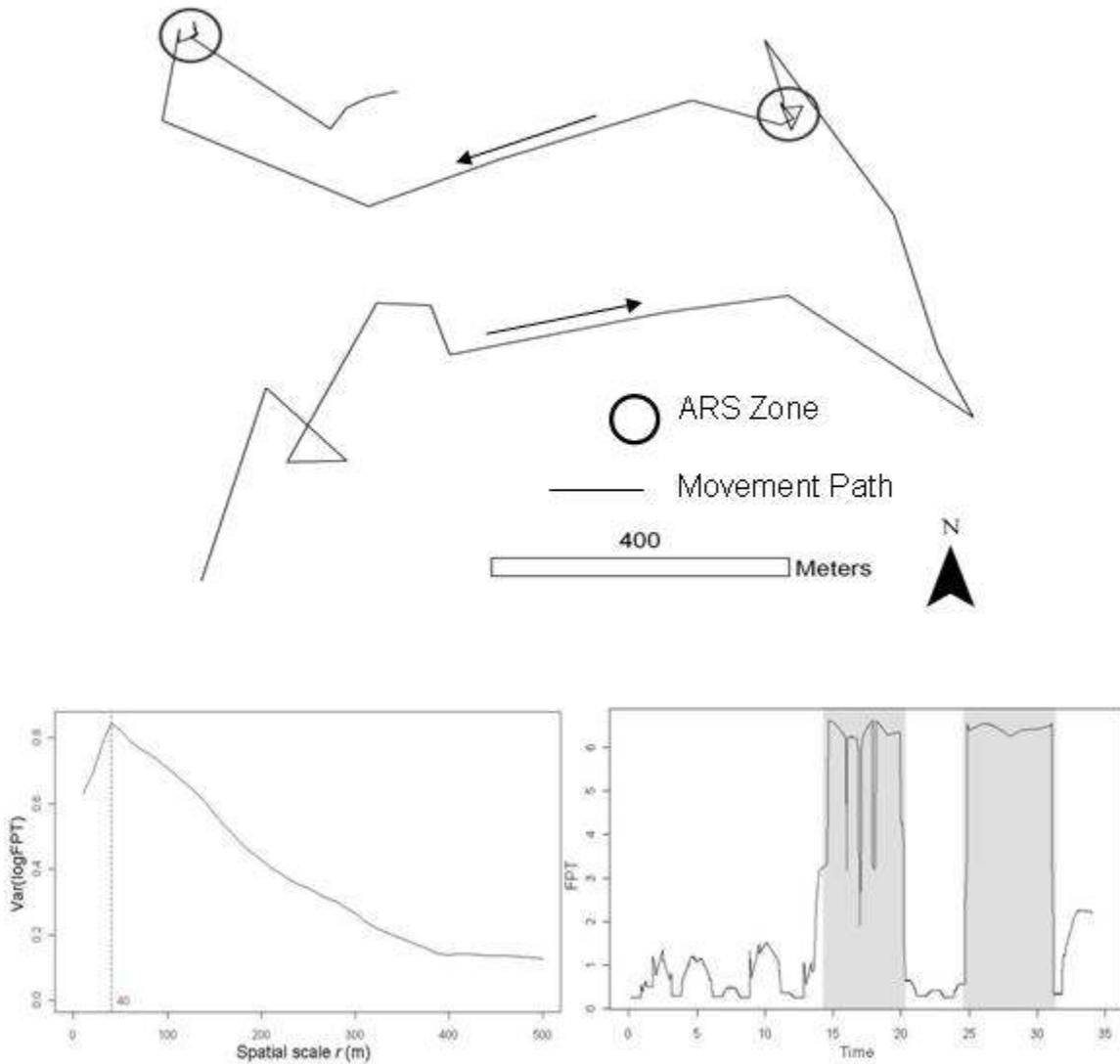


Figure 5.2: Movement path of raccoon 1633 on the night of 21 April, 2008. The open circles represent zones of area-restricted search (ARS) and arrows indicate direction of travel. The bottom left insert shows the plot of the variance in log transformed first-passage time as a function of spatial scale r , showing a peak of variance corresponding to a scale (r) of ARS occurring at 40m. The bottom right insert shows the plot of first-passage time as a function of time; the 2 shaded peaks in first-passage time correspond to the time along the path were ARS occurs.

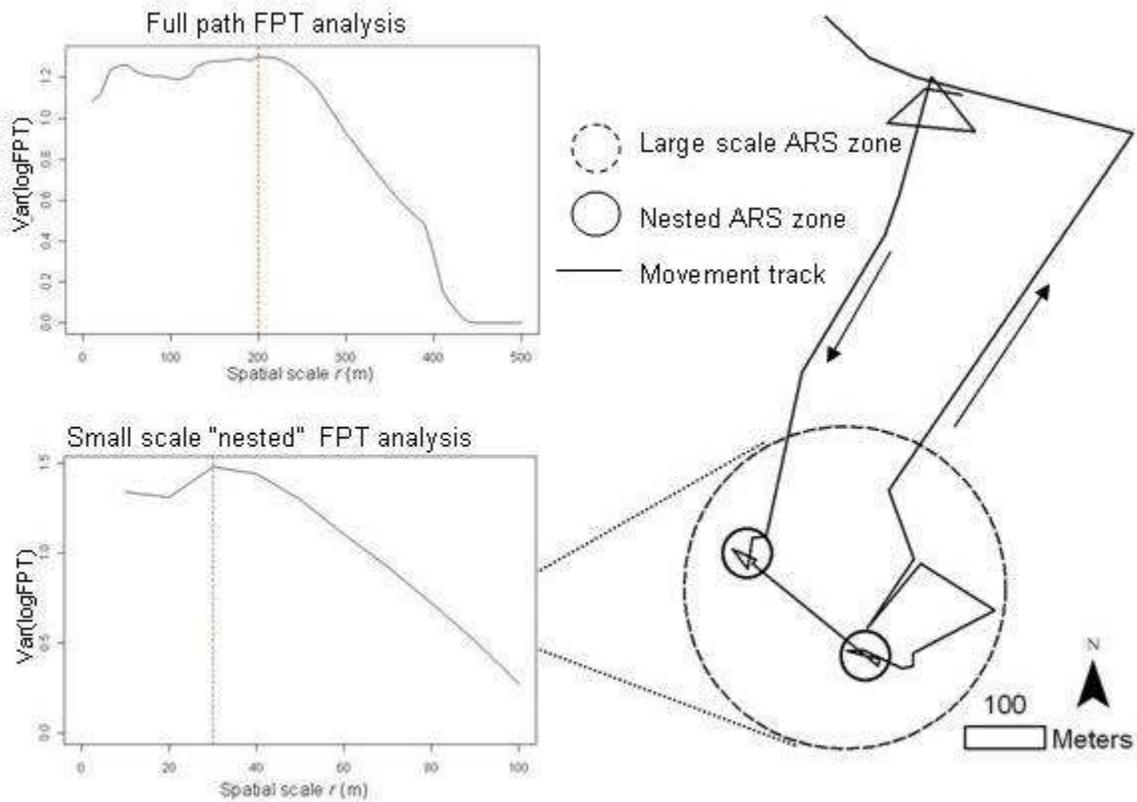


Figure 5.3: Movement path of raccoon 1903 on the night of 9 March, 2009 illustrating small scale area restricted search (ARS) zones (solid open circles) nested within a larger scale ARS zone (dashed open circle). Arrows indicate direction of travel. The top insert shows the plot of the variance in log transformed first passage time (FPT) based on analysis of the entire path, with a peak in variance occurring at a spatial scale (r) of 200m. The bottom insert is a plot of the variance in log FPT based on FPT analysis of the portion of the path within the large scale ARS zone showing a peak in variance indicating ARS at a scale of 30m.

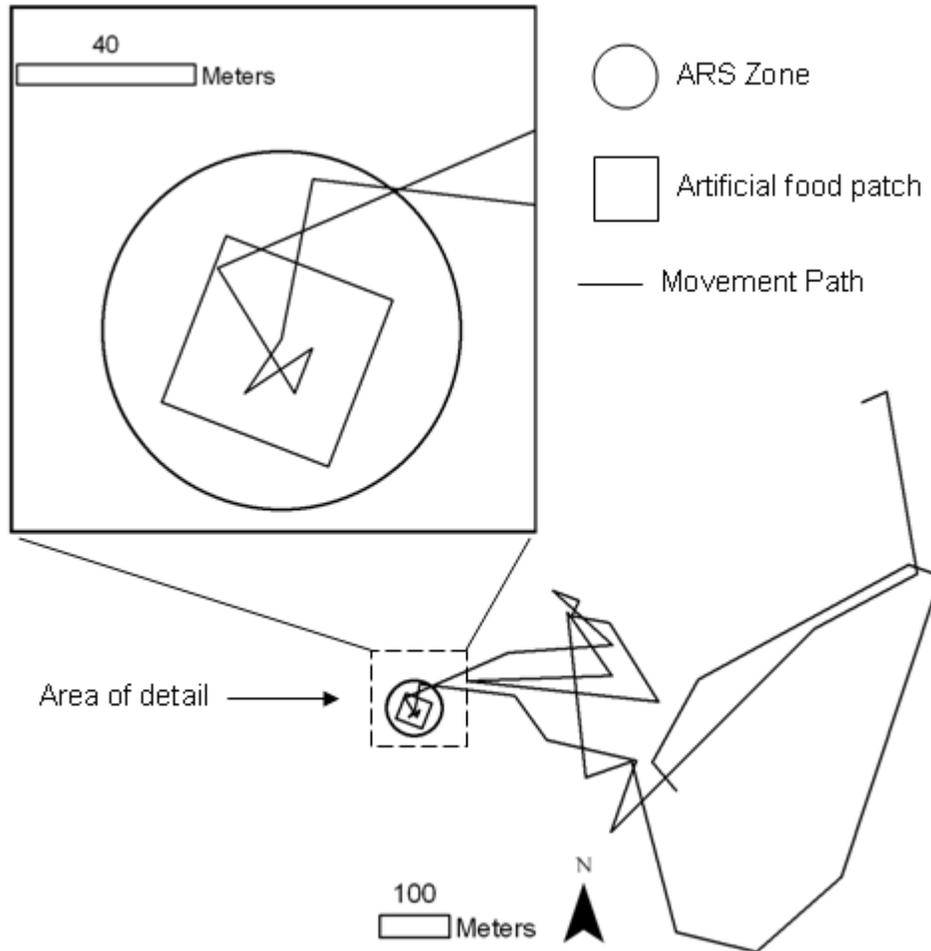


Figure 5.4. Movement path of raccoon 1723 on the night of 25 February, 2010, illustrating ARS behavior in the vicinity of an artificial food patch. The open circle represents an ARS zone of $r = 40\text{m}$. The open box represents an artificial food patch with dimensions $40\text{m} \times 40\text{m}$.

I measured habitat variables associated with 40 ARS zones as identified by FPT analysis, as well as 40 sample plots located along movement paths associated with rapid straight-line movements (Table 5.2). Based on PCA analysis, I retained 6 components with eigenvalues >1 , cumulatively accounting for 72.7% of the total variance, for use in creating a suite of logistic regressions models (Table 5.3). Of the 19 models I evaluated, all had adequate goodness-of-fit based on Hosmer-lemeshow statistics (all P-values > 0.05). Three models were strongly supported with ΔAICc values < 4 and comparatively high model weights (Table 5.4). Common to all 3 of the top models were principle

components 1, 2, and 5 (Table 5.4), which could be said to represent vegetation density, standing water, and degree of canopy closure respectively (Table 5.3). The summed model weights for each of these 3 principle components were quite large, indicating that these components had relatively high importance in distinguishing between intensive and extensive searching behavior in raccoons compared to the remaining components (Table 5.5). Raccoons tended to restrict their searching activities in areas containing ample amounts of standing water and relatively dense vegetation and to move quickly through forest openings and areas with relatively open understory (Table 5.2).

Table 5.2: Mean \pm SE values for all habitat variables measured along raccoon movement paths within areas of ARS (n = 40) as identified by FPT analysis and within sample plots of areas representative of extensive straight-line movement (n = 40) during February-May 2008-2009, on Sherburne WMA, Louisiana.

Variable	ARS	Straight-line movement
H ₂ O	0.29 \pm 0.032	0.03 \pm 0.008
Tree	0.17 \pm 0.007	0.21 \pm 0.02
Sugar	0.03 \pm 0.004	0.03 \pm 0.004
Oak	0.01 \pm 0.004	0.02 \pm 0.003
CWD (10-30.5)	0.51 \pm 0.062	0.28 \pm 0.036
CWD (>30.5)	0.20 \pm 0.025	0.10 \pm 0.018
CC	96.5 \pm 0.27	88.6 \pm 4.16
<u>Vegetation Density</u>		
VO min	0.52 \pm 0.04	0.36 \pm 0.03
VO avg	0.82 \pm 0.04	0.63 \pm 0.04
VO max	1.23 \pm 0.04	1.12 \pm 0.03
<u>Ground Cover</u>		
%H ₂ O	24.69 \pm 2.64	3.36 \pm 0.94
%Deb	13.26 \pm 1.13	13.77 \pm 1.47
%Fern	3.73 \pm 0.92	4.69 \pm 1.06
%Vine	17.6 \pm 1.63	15.36 \pm 1.19
%Forb	10.78 \pm 0.98	13.16 \pm 1.4
%Woody	12.12 \pm 0.82	13.04 \pm 0.92
%Grass	2.13 \pm 0.49	5.52 \pm 2.84
%Open	15.29 \pm 1.67	33.45 \pm 2.34

Table 5.3: Variables with meaningful loading values (> 50) and the % of variance accounted for, for each of 6 principle components retained following PCA analysis of habitat variables measured along raccoon movement paths within areas of ARS (n = 40) as identified by FPT analysis and within sample plots of areas representative of extensive straight-line movement (n = 40) during February-May 2008-2010, on Sherburne WMA, Louisiana. Variables that loaded in >1 component were excluded.

Component	Variables	Variance accounted for (%)
1	VO min, VO avg, VO min, %Vine	19.3
2	H2O, %H2O	15.8
3	CWD (10-30.5), CWD (>30.5), %Debris,	12.9
4	Sugar, %Forb	10.5
5	Tree, CC, %Grass	8.2
6	Oak, %Fern	6

Table 5.4: Ten highest ranking logistic regression models^a differentiating between habitats associated with ARS and extensive straight-line movements of raccoons based on nightly movement paths recorded during February-May 2009-2010, on Sherburne WMA, Louisiana.

Model	K	AICc	Δ AICc	w_i
C1 C2 C3 C5	5	52.10	0.00	0.466913
C1 C2 C5	4	53.11	1.02	0.281036
C1 C2 C3 C4 C5	6	54.52	2.42	0.139194
C1 C2 C3 C4 C5 C6	7	57.57	5.47	0.030330
C1 C2 C3	4	57.85	5.75	0.026311
C1 C2	3	57.88	5.79	0.025872
C2 C5	3	58.65	6.55	0.017648
C1 C2 C3 C4	5	60.42	8.32	0.007280
C2	2	62.01	9.91	0.003285
C2 C3	3	62.88	10.78	0.002132

a. Model = Principle components used in each model, K = number of parameters, AIC_c = Akaike's Information Criterion adjusted for small sample size, Δ AIC_c = difference in AIC_c relative to smallest value, w_i = AIC_c weight.

Table 5.5: Summed model weights of principle components used in logistic regression models differentiating between habitats associated with ARS and extensive straight-line movements of raccoons based on nightly movement paths recorded during February-May 2009-2010, on Sherburne WMA, Louisiana. Model weights are based on the 10 highest ranking models.

Principle Component	Summed model weight
2	1.000
1	0.98
5	0.941
3	0.698
4	0.199
6	0.037

Discussion

Using FPT, I was able to detect the presence of ARS in 94.8% of all nightly movement paths I analyzed, indicating that raccoons do use ARS during foraging bouts. Movement within identified zones of ARS was characterized by a noticeable decrease in speed and increase in turning rate relative to the rest of the movement path; this pattern conforms to the expected characteristics of animals engaging in ARS (Kareiva and Odell 1987, Behnamou 1992). I detected ARS zones occurring across a range of spatial scales, but on average raccoons concentrated their searching activities within the area of a circle with a radius of approximately 40m.

FPT analysis is known to be sensitive to telemetry error (Pinaud 2008), and my findings confirm this. The spatial scale of ARS tended to increase with increasing observer distance from the focal animal, which was likely an artifact of the monitoring protocol used. Because the precision of location estimates obtained via radio telemetry tends to decrease as observer distance increases (Chapter 3), the increase in telemetry error could artificially inflate the distance between 2 successive locations, in turn inflating the perceived spatial scale at which ARS was occurring. Additionally, the

spatial scales of ARS zones associated with raccoons foraging in an artificial food patch were larger than the size of the patch. As such, it appears that FPT had a tendency to slightly overestimate the spatial scale on which ARS occurred, so the average scale at which raccoons concentrated their searching behaviors was in reality probably less than $r = 40\text{m}$. The effect of the monitoring protocol used on the efficiency of the analysis is an important aspect for researchers to consider (Pinaud 2008); conceivably the use of more accurate tracking systems, such as GPS telemetry, would dampen some of these issues when studying terrestrial predators.

I commonly found smaller ARS zones nested within ARS zones of considerably larger scale, an expected result for animals foraging in landscapes in which resources are distributed in a patchy and hierarchal manner (Fauchald and Tveraa 2003, Fauchald and Tveraa 2006). However, in this study some of the larger ARS zones were so large as to make biological interpretation in terms of foraging behavior difficult. These areas encompassed large portions of the total path and masked more obvious biologically relevant behavior at smaller scales nested within them (see fig. 5.3). The presence of some of these large zones ($r \geq 160\text{m}$) was likely related to the spatial ecology of raccoons. Unlike the pelagic sea birds that undergo multi-day foraging trips over vast regions of open-ocean, which have been the subject of most previous studies employing FPT (i.e. Fauchald and Tveraa 2006, Weimerskirch et al. 2007, Hamer et al. 2009, Paiva et al. 2010, and others), raccoons forage within defined home ranges (Gehrt 2003). Based on home range calculations for raccoons during this study (Chapter 3), I found all raccoons could traverse their entire home range during one night, and this would sometimes cause the raccoon to double-back along its path as it moved from one portion

of its home range to another. I believe the presence of these large ARS zones resulted from this doubling back along the path as the raccoon reached the edge of its home range and moved back towards a new area within its home range, rather than a specific behavior related to foraging activity.

As expected, habitat analysis suggested a link existed between movement behavior and habitat features. The particularly strong association between water and ARS zones makes sense in light of known aspects of raccoon ecology. Since crayfish are an important food source for raccoons during spring (Johnson 1970, Gehrt 2003) it stands to reason that raccoons would concentrate their foraging efforts in areas with shallow standing water providing access to crayfish. High concentrations of crayfish (primarily *Procambarus clarkii*) and raccoon sign (i.e., tracks, crayfish carcasses, scat containing crayfish remains) were often observed when visiting ARS zones. Conversely, raccoons tended to move rapidly through forest openings and dry areas with sparse understory vegetation. There are 2 possible, but not mutually exclusive, reasons for this behavior. Raccoons may have used these areas as travel lanes because the lack of dense vegetation made it easy to move through quickly, or they may have moved quickly through these areas because they offered little in the way of foraging opportunities or protective cover.

My findings support the theoretical underpinnings of ARS, namely that in a heterogeneous landscape an animal is expected to move quickly through unprofitable areas where resources are scarce then adopt a more intensive searching strategy (i.e. ARS) characterized by slower movements and increased turning rates once encountering a profitable patch of habitat offering increased resource availability (Kareiva and Odell 1987). The adoption of area-restricted searching should theoretically keep the animal

within the profitable patch until such time that the resource supply is depleted, the animal is satiated, or is required to move off for other reasons (Behnamou 1992). It is reasonable to assume that the wet, lower-lying areas in which raccoons commonly adopted ARS behavior constituted profitable patches due to the high availability of forage resources. Conversely, drier open areas associated with extensive movements offered little in the way of cover or foraging resources and could be considered unprofitable by comparison.

FPT correctly identified ARS in all cases in which a focal raccoon was known to be foraging within the artificially created food patch. In the one case in which a focal raccoon encountered the food patch and ARS was not detected, only one radio location fell within the patch and there was no evidence that the raccoon had initiated foraging. Although several marked raccoons would often be recorded within the patch area simultaneously when food was available, raccoons were not observed to remain in the patch on nights when food was not available, indicating raccoon activity was related to foraging, rather than social behaviors. This is important because it lends further support, coupled with results of habitat comparisons, to the validity that FPT analysis can identify real changes in raccoon foraging behavior, and accurately identify ARS zones that represent important foraging patches. While FPT has been used to investigate scale-dependent response to landscape features in ungulates (Frair et al. 2005, Le Corre et al. 2008), mine is the first study to successfully apply FPT analysis to the foraging paths of a terrestrial mammalian predator. By providing a link between behavior and habitat, the application of FPT analysis should prove to be a useful tool in studies concerning the foraging ecology and habitat use of terrestrial predators, as it has proven to be for ungulates and a wide variety of pelagic species.

I focused on the fine-scale movements of raccoons while they were known to be active and foraging, and did not include raccoons that rested or dened during monitoring sessions. The inclusion of periods in which raccoons were resting and stationary would have confounded my analysis by identifying ARS zones centered on resting sites rather than foraging locations, similar to the issue of pelagic sea birds that spend time resting on the water's surface (Weimerskirch et al. 2007). By concentrating solely on times in which an animal is active and foraging, FPT could be applied to terrestrial predators to identify habitats associated with foraging activity. When applied to several movement paths collected for an individual animal on a regular schedule within a given time frame, say daily or weekly, FPT analysis could be useful in identifying the specific locations favored by individual animals for foraging, hunting, or stalking prey. This may be especially insightful in the behavioral study of predators that establish home-ranges, as these animals presumably have knowledge of the profitable patches within their respective home ranges. For example, the data logger placed within the artificial food patch indicated that individual raccoons would visit the site (whether food was available or not) on a regular basis, but stay for only short time periods when no food was available. While tracking a single animal on many consecutive days may be impractical using traditional radio telemetry techniques, the use of GPS tracking devices that collect data independently and on a schedule programmed by the researcher should easily facilitate the type of data collection needed for such a study. FPT could be used in conjunction with other measures of habitat use and selection. The finding that ARS behavior was associated with forested areas offering shallow standing water supports the results of compositional habitat analysis, which indicated that raccoons on Sherburne

selected for water-influenced forest habitats within their home ranges during spring (Chapter 3). In this case FPT not only supports previous analyses, but offers a behavioral link as to *why* raccoons would be preferentially selecting these areas. This is a good example of how FPT could be used in conjunction with other measures of habitat use and selection to provide a richer ecological interpretation.

Any analysis that makes use of movement paths to study habitat use has a clear advantage over use-availability methods (such as compositional analysis) by avoiding the major theoretical pitfall of use-availability methods. In a use-availability analysis, the researcher must define what habitats are available to the animal, and what the researcher defines as available may not necessarily represent availability as the study animal perceives the landscape (Johnson 1980). On the other hand (especially if relocations are collected frequently) movement paths provide a clearer picture of what habitats the animal has actually sampled, greatly minimizing issues related to the arbitrary delineation of available habitat by the researcher. FPT represents an alternative to use-availability methods, and may provide a more accurate, behaviorally-based interpretation of how terrestrial predators respond to the different habitats they encounter. Indeed, Frair et al. (2005) used FPT for data collected over a large temporal scale (locations collected every 2 hrs over the course of several months) to relate elk behavior to environmental conditions such as forage availability and predation risk. Frietas et al. (2008) suggested a method using FPT to quantify habitat selection and use, and while the authors applied their method to marine mammals there is no reason to assume it would not work well if applied to terrestrial predators. Computationally, FPT is a relatively easy method to use,

and researchers should consider incorporating it into their toolbox when designing future studies regarding the foraging ecology and habitat use of terrestrial predators.

Chapter 6: Assessing the Risk of Nest Predation on Wild Turkeys by Raccoons in a Bottomland Hardwood Forest

Introduction

Nest predation has been identified as a primary cause of nest loss for a variety of bird species (Klett et al. 1988, Patterson et al. 1991, Heske et al. 2001, Rollins and Carroll 2001). Logically, the risk of nest predation is a function of how often potential predators encounter nests. Landscape and habitat features may influence encounter rates by concentrating predator activity in nesting areas. For example, landscape fragmentation may increase predator densities in certain habitats that may lead to increased nest predation (Oehler and Litvaitis 1996, Dijak and Thompson 2000, Chalfourn et al. 2002), and studies of real and artificial nests have documented increased nest loss associated with high degrees of forest fragmentation or proximity to forest edge (Paton 1994, Donovan et al. 1997, Heske et al. 2001).

Predators locate nests either through incidental encounters, or through directed searching. Incidental predation occurs when a predator encounters a nest fortuitously while engaged in other activities, and does not subsequently change its foraging behaviors to search for nests (Vickery et al. 1992). In these cases nest predation is essentially a random event. Alternatively, predators may learn to target nests, and may develop micro-habitat search images or exhibit behaviors such as area-restricted search (ARS) in areas likely to contain nests (Tinbergen et al 1967). For example, red squirrels (*Tamiasciurus hudsonicus*) increased predation rates on artificial nests by 150 – 200% following their initial experience destroying a nest (Pelech et al. 2010). Predator activity may influence nest site selection, and evidence exists that some birds choose to place their nests in locations not commonly used by primary nest predators or in areas that limit

predator access. For example, dusky warblers (*Phylloscopus fuscatus*) avoiding predation by Siberian chipmunks (*Tamiasciurus bairdii*) by nesting in isolated shrubs that chipmunks avoid (Forstmeier and Weiss 2004), the ground-nesting veery (*Catharus fuscescens*) avoids nesting in areas of high mouse activity (Schmidt et al. 2006), and northern harriers (*Circus cyaneus*) nest in dense wetlands that are difficult for mammalian nest predators to access (Byrne 2007). Nest predation is a complex phenomenon, and accurately assessing the risk of nest predation requires knowledge of the nesting ecology of avian species, as well as the behavior of nest predators, in relation to the local landscape.

Raccoons are often implicated as important nest predators of a variety of ground nesting birds, including passerines (Heskeet et al. 2001, Schmidt 2003), colonial water-birds (Ellis et al. 2007), and game species such as wild turkey (Miller and Leopold 1992), quail (Rollins and Carroll 2001), and waterfowl (Urban 1970). Nest predation has been identified as the leading cause of wild turkey nest failure on Sherburne (Chapter 4). Reproductive success is an important factor influencing wild turkey population dynamics (Vangilder 1992, Roberts and Porter 1996) and, as a documented nest predator (Miller and Leopold 1992), raccoons may act as a considerable source of reproductive failure in this system.

Core areas represent the portion of an animal's home range that receives the most concentrated use (Samuel et al. 1985) and it seems a fair assumption that a raccoon is more likely to discover and destroy nests located in this area. As such, the risk to turkey reproduction is likely high if raccoons are establishing core areas comprised of the same habitats selected by turkeys for nesting. Similarly, if large portions of raccoon nightly

movement paths are within likely turkey nesting areas, then raccoons would be expected to have a better chance of encountering a turkey nest than if they spend little time in such areas.

Resources are not evenly distributed across the landscape and foraging theory predicts that a predator should work to maximize its time spent foraging in patches that offer high prey availability (Stephens and Krebs 1986). As discussed in Chapter 5, a predator may accomplish this by engaging in ARS, characterized by reduced speed and increased path tortuosity, when encountering a high quality patch. Methods of analyzing animal movement paths such as first-passage time analysis (FPT, Fauchald and Tveraa 2003) can help identify areas along a trajectory where a foraging predator is using ARS. Since predators are expected to use an intensive search strategy when encountering profitable patches, identifying the areas along a movement path where ARS is occurring simultaneously identifies important foraging areas. For example, Scheffer et al. (2010) used FPT to show that king penguins (*Aptenodytes patagonicus*) concentrate their foraging activities within warm-core eddies and oceanic areas with high thermal gradients. The ability to identify foraging areas and the landscape and habitat characteristics associated with concentrated foraging has application to the study of nest predation. I compared the habitat associated with concentrated foraging of raccoons to habitats selected by wild turkeys for nesting. My objective in this chapter was to evaluate the relationships between habitat, wild turkey nest site selection, and raccoon foraging behavior to determine if raccoons select habitats that are structurally similar to those used by nesting turkeys and to assess raccoon movements through various habitats.

The ultimate goal is to assess whether raccoon predation on turkey nests is a chance event or if raccoons are actively targeting the habitats used by nesting turkeys.

Methods

Female wild turkeys were captured and fitted with mortality-sensitive VHF radio transmitters as described in Chapter 1. Turkey nests were located, monitored, and associated with micro-habitat and landscape level attributes as described in Chapter 4. I quantified the observed level of nest loss potentially inflicted by raccoons based on observations of nests whose fates were known. Since it was difficult to assign nest predation losses to specific predators, I considered raccoons responsible for nest predation events where evidence was consistent with mammalian predation, such as eggs consumed away from the nest site, trampled vegetation at the nest site, and/or the presence of crushed eggs at the nest. Because other potential mammalian nest predators are found on Sherburne and may have been responsible for some of the observed nest losses, these estimates represent the maximum levels of potential raccoon-caused nest destruction.

I used nest site data to create a GIS layer of likely turkey nesting areas (TNA) on Sherburne in ArcGIS 9 (ESRI, Redlands, California). Since all turkey nests were located in upland forests or openings (35 and 6 nests respectively, Chapter 4), I first considered only these habitats as potential nesting locations. A detailed description of how I delineated habitat types is presented in Chapter 1. Turkeys did not nest in openings associated with high levels of human disturbance, such as hunting camps or shooting ranges, so these areas were excluded as potential nesting areas. Since no nests were located in areas that had undergone forest management within the last 10 years (see

Chapter 4), I excluded these areas as potential nesting habitat. Of nests located in upland forests, 33 of 35 (94.3%) were placed within 150m of a forest edge, thus within upland forests only areas within 150m of such edges were considered as likely nesting habitat. Finally, since the smallest contiguous patch of forest in which a nest was located was 11.7ha, I considered only upland forest patches ≥ 11.7 ha (29 acre) as likely nesting areas. Thus, likely wild turkey nesting areas on Sherburne were defined as forest openings not associated with human activity, in areas within 150m of forest edges, and within mature upland forest patches ≥ 11.7 ha.

Raccoons were captured and fitted with mortality-sensitive VHF transmitters as described in Chapter 2. Home range and core use areas of raccoons were calculated seasonally as described in Chapter 2. For this analysis, I used raccoon space-use data calculated for the raccoon breeding season (1 Feb – 31 May), which coincided with wild turkey egg laying and incubation. I intersected raccoon home ranges and core areas with the TNA coverage in ArcGIS 9. I categorized all remaining portions of the study area not considered as likely turkey nesting areas as other and performed a compositional analysis (Aebischer et al. 1993) to test whether raccoons preferentially selected TNA within core areas relative to availability within home ranges using the package “adehabitat” (Calenge 2006) for R software.

I used focal runs to track nightly movements of individual raccoons during the turkey nesting seasons 2008-2010 as described in Chapter 5. I intersected individual movement paths with TNA and calculated the percentage of each movement path that fell within TNA. Additionally, I calculated the percentage of individual telemetry locations gathered during each focal run that were located within TNA. If the focal raccoon

temporarily denned during the tracking session, I considered relocations associated with the den as a single location.

I used FPT analysis (Fauchald and Tveraa 2003) to identify the scale and location of ARS behavior along movement paths as detailed in Chapter 5. To characterize the habitat associated with intensive searching by raccoons, I collected information on habitat characteristics within ARS zones, such as the amount of standing water and vegetation density (Chapter 5), and qualitatively compared the habitat of raccoon ARS zones to micro-habitat characteristics associated with wild turkey nests (Chapter 4). I created a shape theme in ArcGIS by buffering the central point of each ARS zone by its respective spatial scale r , as determined by a peak in the variance in log FPT (see Chapter 5). ARS zones were then intersected with the coverage of TNA to calculate the percentage of each ARS zone in TNA.

Results

Of 32 wild turkey nests in which fates were known (excluding nests which may have been abandoned due to observer disturbance), 11 (34%) were destroyed by predators. Assigning nest predation events to specific predators is tenuous, however I am confident in assigning 3 nest predations during the 2010 season to rat snakes (*Elaphe obsoleta*) based on the disappearance of the clutch without any signs of trampling at the nest site and the visual observation of snakes close to each nest (within 15m) soon after nest loss. The remaining 8 nests showed signs of trampled vegetation, crushed eggs, and/or eggs that were taken away from the nest and consumed, which is consistent with mammal predation, and may be attributed to raccoons. Thus, the percentage of all nests of known fate that may have been destroyed by raccoons was $\leq 25\%$, and raccoon

predation may have accounted for up to 40% of known predation related nest losses.

Areas identified as TNA encompassed 19% of the total study area, and mapping of known nest locations ($n = 39$) showed that 92% of nests were located within these areas.

I estimated 48 home ranges and core areas from 37 raccoons (33 male, 4 female) during the 2008 and 2009 breeding seasons. The median percentage of TNA within raccoon home ranges was 31% (Range 0 – 70%, Figure 6.1A). The median percentage of raccoon core areas made up of TNA was 28% (range 0 – 88%), and the frequency distribution was skewed to the right, meaning most raccoon core areas were concentrated at lower percentage values (Figure 6.1B). Core areas generally contained less TNA than home ranges; 45.8% of raccoon core areas consisted of < 25% TNA, and 29% were comprised of $\leq 10\%$ TNA. Compositional analysis showed that raccoons showed significant selection for areas that did not constitute likely turkey nesting areas within core areas relative to availability across home ranges ($\lambda = 0.91$, $df = 1$, $P = 0.038$) during the breeding season.

I collected 42 movement trajectories from 16 raccoons (12 male, 4 female), including 9 paths from 9 March – 5 May 2008, 33 paths from 28 February – 4 May 2009, and 1 path on 22 April 2010. The median percentage of raccoon paths that were in TNA was 8% (range 0 – 90%). The frequency distribution was skewed to the right, meaning most raccoon paths were concentrated at lower percentage values (Figure 6.2A); 30 % of raccoon paths did not pass through any TNA, and the number of paths in which < 10% of the total length passed through TNA was more than half (53%). An average of 32 telemetry locations were collected for 42 movement paths (range 19-37), and the median

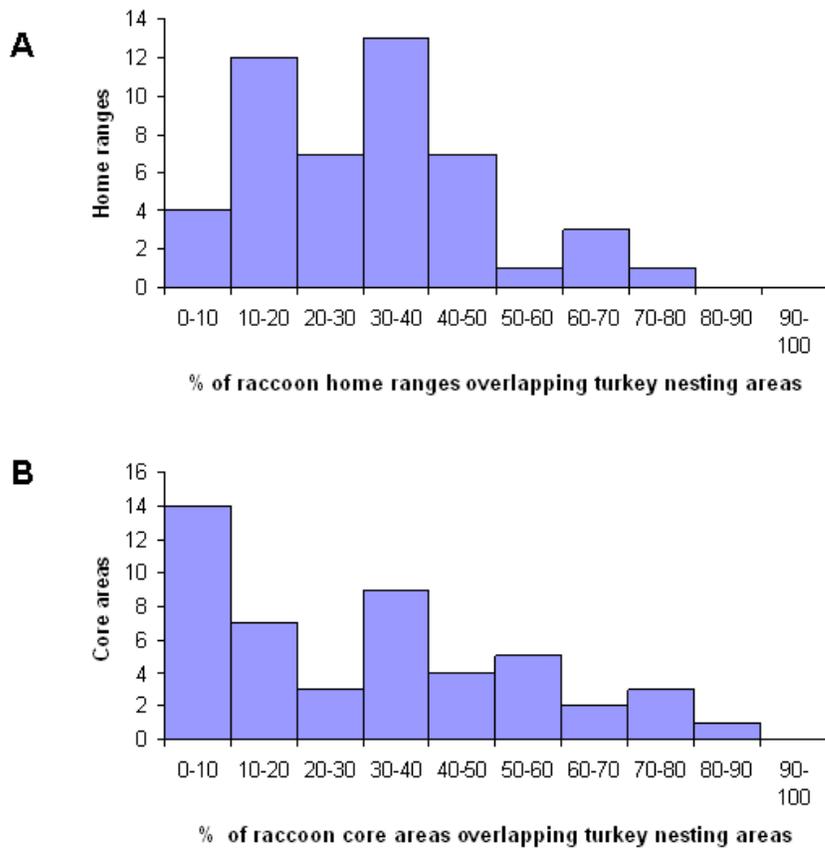


Figure 6.1: Frequency histograms of the percentage of wild turkey nesting areas found within raccoon home ranges (A) and core areas (B) on Sherburne Wildlife Management Area, Louisiana, during the 2008 – 2009 raccoon breeding seasons (1 Feb – 31 May).

percentage of locations per path that fell within TNA was 14%. The frequency distribution was again skewed to the right, meaning that most of the telemetry locations were concentrated at lower percentage values (Figure 6.2B); 18 paths had no locations within TNA.

Micro-habitat characteristics associated with wild turkey nests were detailed in Chapter 4, and habitats associated with raccoon ARS zones were discussed in Chapter 5. Briefly, turkeys nested in drier, upland areas and nests were often placed in relatively dense cover while avoiding areas with sparse understory vegetation. Raccoons did not

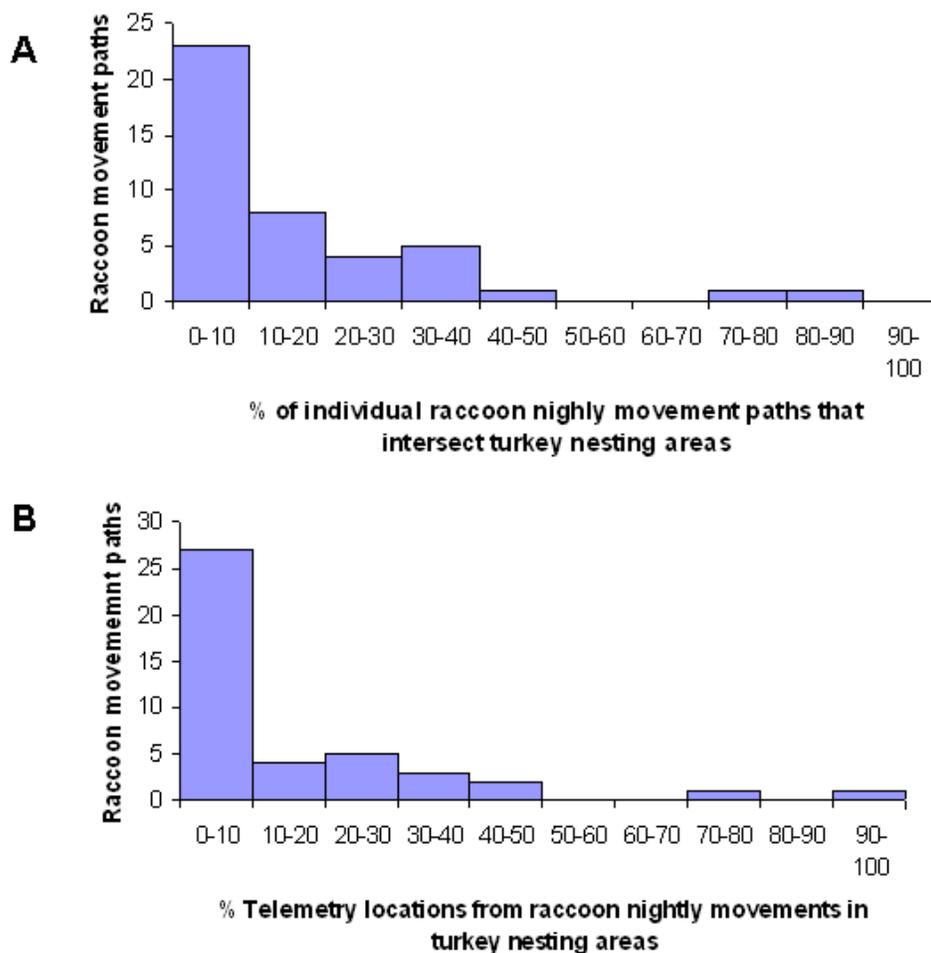


Figure 6.2: Frequency histograms of the percentage of wild turkey nesting areas intersected by raccoon movement paths (A) and the percentage of telemetry relocations from movement paths within turkey nesting areas (B) on Sherburne Wildlife Management Area, Louisiana, Feb – May, 2008 – 2010.

concentrate their intensive foraging in the types of habitats that turkeys used for nesting. Instead, raccoons concentrated their searching behavior in lower lying areas that contained considerable amounts of shallow standing water, often associated with a high abundance of crayfish.

I identified 47 ARS zones with spatial scales (r) ranging from 20 – 100m. Twenty-nine ARS zones (61.7%) contained no TNA, and raccoons did not seem to target TNA for intensive searching-related activity (Figure 6.3). In most cases in which TNA

comprised a substantial portion of an ARS zone, it was when a narrow ditch or section of flooded forest bisected a patch of upland forest.

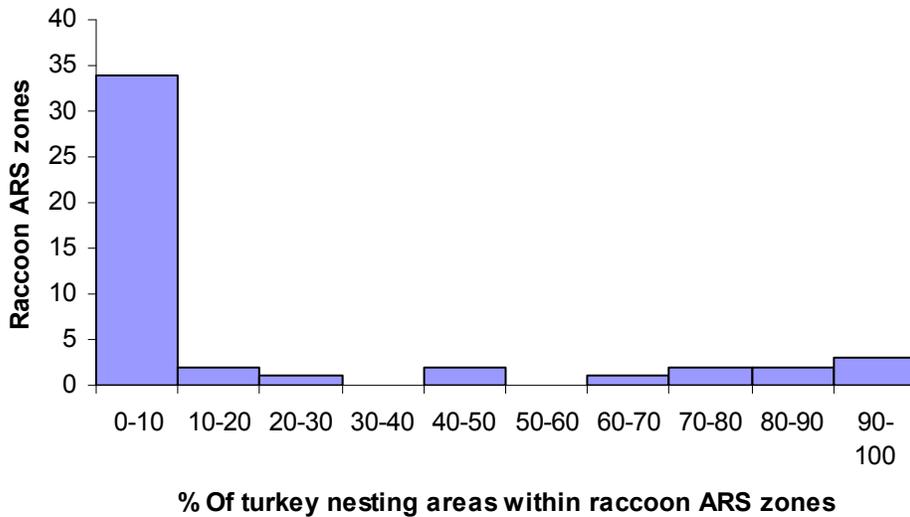


Figure 6.3: Frequency histogram of the percentage of likely turkey nesting areas within raccoon ARS zones detected along nightly movement paths collected on Sherburne Wildlife Management Area, Louisiana, Feb – May 2008-2010.

Discussion

Raccoons are known to favor heterogeneous landscapes (Oehler and Litvaitis 1996) and on Sherburne raccoons tended to establish home ranges in areas that provided access to a variety of habitat types and forest patches (Chapter 2). This led to raccoon home ranges that necessarily contained the forest openings and forest edges that turkeys selected for nesting (Chapter 4). However, my findings suggest that at smaller spatial scales, raccoons are not directing their foraging efforts towards locating turkey nests, or otherwise concentrating their activities in the areas and habitats that wild turkeys use for nesting. Areas likely to harbor turkey nests were not selected by raccoons when establishing core areas within their home ranges, and analysis of movement paths shows that raccoons generally did not spend much time in these areas.

Analysis of habitat use (Chapter 2) and movements (Chapter 5) indicates that raccoons appear to center their activities on water-influenced forests during the turkey nesting period, rather than in upland forests turkeys use for nesting. Crayfish and other invertebrates are known to comprise a large portion of raccoon diets during winter and spring (Baker et al. 1945, Johnson 1970, Gehrt 2003), and crayfish are abundant in the shallow flooded forests on Sherburne at this time of year. Concentrated use of areas with standing water and high crayfish availability was evident when examining movement behaviors and the areas in which raccoons engage in ARS. As discussed in Chapter 5, raccoons commonly used ARS in low-lying areas associated with shallow water and the presence of crayfish, and evidence of raccoons foraging on crayfish was commonly encountered when investigating ARS zones.

The fact that raccoons are not targeting turkey nesting areas for foraging suggests that raccoon predation on turkey nests on Sherburne is incidental; raccoons may occasionally encounter and destroy turkey nests while traversing between more profitable patches within their home ranges, but they are not actively foraging in areas where turkeys typically nest. It is unclear whether predation on nests is strictly incidental, as the definition of incidental predation implies that the predator does not change its behavior after feeding on a nest (Vickery et al. 1992). To say predation was entirely incidental would require documenting a nest predation event by a raccoon, then showing that the raccoon did not subsequently change its behavior, which was not possible given the nature of data collection. Nevertheless, my findings indicate that raccoons are not targeting turkey nests and that any raccoon predation on turkey nests is a chance event.

The threat of nest predation by any individual raccoon is likely low. At low to moderate population densities, the preference for water-influenced forests likely results in areas relatively free of raccoon use, even within individual raccoon home ranges. Other species of birds are known to exploit predator free zones for nesting (e.g. Schmidt et al. 2006), and wild turkeys may do the same. In addition to not foraging in wild turkey nesting habitats, raccoons spent relatively little time traversing such areas during nightly foraging bouts (Figure 6.2), which should theoretically further reduce the chance of a raccoon encountering a nest. Raccoons have been observed using forest edges and other linear habitat features as travel lanes (Pedlar et al. 1997, Dijack and Thompson 2000, Barding and Nelson 2008). Because wild turkeys often nest close to forest edges in a variety of landscapes (Speake et al. 1975, Everett et al. 1985, Campo et al. 1989, Seiss et al. 1990, Still and Baumann 1990) including Sherburne (Chapter 4), this behavior would be expected to increase the probability of raccoons encountering nests. However, on Sherburne raccoons were not observed to travel along forest edges with any regularity, and raccoons avoided forest openings. Forested areas of Sherburne are relatively contiguous, whereas raccoon use of edge areas seems more pronounced in more fragmented landscapes, such as agricultural landscapes of the mid-west (Barding and Nelson 2008).

The specific geomorphology of Sherburne likely aids in the creation of spaces free of raccoon use. The construction of levees and the ridge and swale topography at Sherburne allow for the ponding of shallow water in lower lying areas. This allows raccoons to concentrate their foraging in the wet, lower elevation areas that provide abundant food availability, and spend less time in the non-flooded forest areas used for

nesting by turkeys. A similar scenario may not occur in an unaltered flood plain where flooding is a more direct result of river-level rise, and where the relatively smooth topography may not provide an abundance of areas of impounded shallow water offering raccoons access to crayfish.

Increasing raccoon population densities and dense concentrations of turkey nests could increase the risk of raccoon predation on turkey nests. High predator densities have been linked to increased nest loss in a number of bird species (Angelstam 1986, Schmidt et al. 2006, Fontaine et al. 2007). High population densities of raccoons may force individuals to exploit sub-optimal habitats, which may lead to increased use of the openings and upland forest areas that turkeys nest in, thus reducing the availability of raccoon-free areas for turkeys to nest in. Schmidt and Whelan (1999) showed raccoons to exhibit a density-dependent response to artificial ground nests, with raccoons preying heavily on nests when they occurred at high densities. Raccoons in that study targeted ground nests at very high densities, much higher than would be expected to occur naturally. Foraging theory predicts that raccoons should try to maximize their energy gains while minimizing their energy losses (Stephens and Krebs 1986), and it seems unlikely that turkeys would nest in such densities that it would be profitable for raccoons to specifically target them when other abundant food sources (such as crayfish) are readily available.

Based on their behavior and habitat selection, raccoon predation on turkey nests is likely a chance event and I feel that raccoons are not a major threat to wild turkey nests in this bottomland system. Several courses of future research may be applied to further assess the specific risk of raccoons as well as other potential nest predators. Using

methods to positively identify predators responsible for nest loss would help quantify the portion of nests that are actually destroyed by raccoons and other predators. While studies employing artificial nests have recognized pitfalls (Moore and Robinson 2004), I feel that carefully designed studies may be useful to further understand the nature of raccoon nest predation on turkey nests in these systems. For instance, the hypothesis that the predation risk is greater for turkey nests in high use portions of raccoon home ranges (such as core areas) could be tested as has been done for Steller's jays (*Cyanocitta stellari*) in the Pacific northwest (Vigallon and Marzluff 2005). One could test whether raccoon predation is truly incidental by offering artificial nests to radio-marked raccoons and observing if raccoon foraging behavior changes following predation of an artificial nest (Pelech et al. 2010). Additionally, one could test whether raccoon predation of nests increases in portions of the study area with higher raccoon density. Likewise, using artificial nests in a designed experiment may be helpful to augment observations of real turkey nests, which are difficult to locate in large numbers.

Conclusions

First-passage time analysis (FPT) identified area-restricted searching (ARS) in nearly all (95%) of the nightly raccoon paths I analyzed. ARS activity in raccoons was related to habitat as would be expected based on the theoretical underpinnings of ARS; namely that organisms should adopt ARS behavior when in profitable habitat patches. This conclusion is further strengthened by my ability to induce ARS behavior with artificial feeding. Areas in which raccoons engaged in ARS were lower-elevation forests with shallow standing water that commonly provided access to crayfish, which are the primary prey item of raccoons at this time of year. These forest patches offered raccoons abundant foraging opportunities and could be considered quality habitat patches. Conversely, raccoons moved quickly through drier upland forests with sparse understory vegetation and through forest openings, areas that offer little in the way of foraging opportunities or cover but facilitate easy movement across the landscape.

My work represents the first time FPT has been applied to a terrestrial mammalian predator. By providing a link between behavior and habitat, the application of FPT analysis should prove to be a useful tool in studies evaluating foraging ecology and habitat use of terrestrial predators, as it has proven to be for ungulates and a variety of pelagic species. Researchers working with predators in terrestrial environment should consider incorporating FPT into their study designs.

Raccoon habitat use varied seasonally and since there was no indication that den sites or water resources were a limiting factor on Sherburne, the observed variation in habitat selection likely represents a response to spatio-temporal variation in food availability. During the spring breeding season raccoons selected water-influenced

forests that offered high crayfish availability, during summer raccoons selected thinned forests and upland areas with high availability of elderberries and other soft-mast, whereas during the fall/winter period raccoons selected mature upland forests that offered abundant hard-mast.

During wild turkey nesting periods, raccoons selected habitat types and concentrated their searching activities in areas that wild turkeys did not use for nesting. While raccoons primarily concentrated on water-influenced forests, turkeys nested in forest openings or in upland forests, close (mean distance = 55.8m) to forest edges. There is no evidence that raccoons on Sherburne purposefully target turkey nests or the areas that turkeys use for nesting, and any nest loss that does occur is likely the result of raccoons incidentally encountering turkey nests while traversing between more profitable areas within their home ranges. While nest predation was the most common cause of nest failure, a number of potential nest predators are present on Sherburne and it is unclear exactly what portion of nest failures raccoons are responsible for.

Lack of quality nesting habitat appears to be a major factor limiting turkey reproduction on Sherburne. The large pre-incubation home ranges observed relative to other times of the year suggests that turkeys are required to greatly expand their space-use while searching for a suitable nesting location. Turkeys on Sherburne are forced to nest in higher elevation areas to avoid flooding and in many upland areas ground cover, is sparse due to canopy shading. Nests placed in sub-optimal habitat may experience high mortality during the laying stage and nest initiation rates on Sherburne are among the lowest reported in the literature. A number of individuals which were never found to incubate a nest exhibited behaviors consistent with egg-laying, indicating nests may have

been lost prior to incubation. Additionally, individuals unable to locate suitable nesting cover may not have attempted to nest.

Nesting success on Sherburne was near the range-wide average reported for eastern wild turkeys. This means that individuals that reached incubation fared no worse at successfully hatching a brood than turkeys in other areas. There is no evidence of population declines over time, indicating recruitment must occur despite the low nest initiation rates. Thus, turkey reproduction on Sherburne seems to be characterized by low nest initiation rates, likely due to low availability of nesting habitat, counter-balanced by adequate nesting success and brood survival. Information on brood survival is needed to fully understand nest ecology and should be a goal of future research on Sherburne.

Mature upland forests were important to female wild turkeys throughout the year. These forests do not flood and tend to have more understory cover than lower elevation forests. Upland forests were important nesting areas and the vegetative structure and high food availability found in upland forests provide good brood-rearing habitat. Forest stands undergoing management aimed at reducing canopy cover and encouraging understory growth, such as group selection and shelterwood cuttings, were not used by female turkeys within 2 – 10 years of treatment. While these types of forest treatments have been beneficial to turkeys in other landscapes, and have been shown to be beneficial to other wildlife on Sherburne, the rapid understory growth associated with these areas seems to make them unsuitable for turkeys within 2 growing seasons of treatment. Interestingly, while nesting turkeys avoided managed areas, nests were often associated with small natural breaks in the forest canopy. These isolated openings allowed understory vegetation to flourish, and also provided cover in the form of debris from the

fallen trees. Hurricane Gustav impacted Sherburne in the fall of 2008, causing an estimated 30% reduction in canopy cover across the area and the following nesting season (2009) was characterized by high nesting rates, and the highest observed female success rate for the study. Periodic natural disturbances, such as hurricanes, that cause spot reductions in canopy over a wide area appear to create quality nesting habitat, and may be an important element maintaining turkey populations in bottomland systems. Management for wild turkeys in bottomland hardwood systems should concentrate on maintaining mature forest stands in higher elevation areas that are not prone to flooding, particularly those adjacent to forest openings. Additionally, regular disturbance of openings during the brood-rearing period may offer wild turkeys additional brood-rearing habitat.

Avenues of Future Research

This study has identified several avenues of future research. As previously mentioned FPT analysis has wide applications to studies of the habitat use and foraging ecology of terrestrial predators. For example, as in this study, by concentrating solely on times in which an animal is active and foraging, FPT could be applied to terrestrial predators to identify habitats associated with foraging activity. When applied to several movement paths collected for an individual animal on a regular schedule within a given time frame, FPT analysis could be useful in identifying the specific locations favored by individual animals for foraging, hunting, or stalking prey. This may be especially insightful in the behavioral study of predators that establish home-ranges, as these animals presumably have knowledge of the profitable patches within their respective home ranges. FPT could be used in conjunction with other measures of habitat use and

selection to provide a behavioral link as to *why* an animal may select for particular habitat types, leading to richer ecological interpretations. Alternatively, FPT may represent an alternative to use-availability methods of quantifying habitat selection, providing a more accurate, behaviorally-based interpretation of how terrestrial predators respond to the different habitats they encounter.

Sherburne supports a diverse community of potential nest predators, and research aimed at identifying and quantifying the effect of specific predators on turkey nests would be useful and help to guide future studies. In regards to the specific influences raccoons have on turkey reproduction, I offer that carefully designed artificial nest experiments may help answer some questions raised by my work, as well as solidify some of the assumptions I made. For instance, the assumption that the predation risk is greater for turkey nests in high use portions of raccoon home ranges (such as core areas) could be tested, one could test whether raccoon predation is truly incidental by offering artificial nests to radio-marked raccoons and observing if raccoon foraging behavior changes following predation of an artificial nest, or one could test whether raccoon predation increases in portions of the study area with higher raccoon density.

In the present study it was not possible to determine a female turkey's reproductive status until incubation started, making it impossible to accurately determine if an individual had a nesting attempt destroyed prior to incubation, or if an individual had not attempted to nest at all. Given the low nest initiation rates observed on Sherburne, this information would be useful to have. While nearly impossible to obtain with standard radio-telemetry methods, recently developed GPS telemetry (Guthrie et al.

2011) should be able to provide enough fine scale data on an individual bird's movements to determine reproductive status prior to incubation.

Despite low nest initiation, there is no evidence of a population decline on Sherburne, suggesting that brood survival may be high, and future studies concentrating on poult survival would be especially fruitful in regard to understanding turkey reproduction in bottomland hardwood forests. An interesting hypothesis I raise in this study is that natural disturbances such as hurricanes may be important in maintaining turkey populations in the region's bottomland hardwood forests. These disturbances may provide an ephemerally high availability of quality nesting habitat that results in a spike in turkey reproductive output in the nesting season immediately following the disturbance event. This could be tested by developing a long term dataset of turkey reproduction that could be correlated with disturbance events, or by a carefully designed experiment involving the manipulation of forest parcels in an effort to reproduce the effects of a natural disturbance such as a hurricane.

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AMERICAN MIDLAND NATURALIST

By Yvonne Hillebrand / gm

Date 10/20/11

Vita

Michael Byrne was born and raised on Long Island, New York. After finishing high school, he moved with his family to Massachusetts and obtained a bachelor's degree in biology from Worcester State College in 2003. He attended the University of Rhode Island in pursuit of a master's degree in the biological sciences, which he earned in 2007 on the subject of the nesting ecology and behavior of Northern Harriers in coastal New England. A few short weeks after handing in his thesis, he moved to Baton Rouge, Louisiana, to begin work on his dissertation in wildlife and fisheries science at Louisiana State University. He is expected to obtain the degree of Doctor of Philosophy from Louisiana State University in December 2011.