EFFECTS OF INDIVIDUAL RECESS BEHAVIORS ON NEST AND FEMALE SURVIVAL OF EASTERN WILD TURKEYS

by

ASHLEY K. LOHR

(Under the Direction of MICHAEL J. CHAMBERLAIN)

ABSTRACT

Reproduction is an energetically costly behavior, and nest success is an important parameter influencing avian population dynamics. Galliforms are particularly susceptible to reduced reproductive output due to nest placement, lengthy incubation periods, and substantive reliance on crypsis for survival. Hence, it is plausible that breeding individuals prioritize productivity and survival differently, resulting in a gradient of reproductive strategies. Movement patterns during incubation are not well documented in ground-nesting birds, and their influence on survival is unknown. Using GPS data collected from female eastern wild turkeys (*n* = 278) across the southeastern U.S., we evaluated the influence of incubation recess behaviors on nest and female survival. Modeling revealed females that took longer recess bouts increased individual survival but suffered reduced nest survival. Conversely, females that recessed often suffered greater mortality rates. Our findings suggest behavioral decisions represent trade-offs between predation risk and individual fitness consequences while incubating on an unpredictable landscape.

INDEX WORDS: incubation behavior, recess movements, nest survival, reproduction, wild turkey, *Meleagris gallopavo*

EFFECTS OF INDIVIDUAL RECESS BEHAVIORS ON NEST AND FEMALE SURVIVAL OF EASTERN WILD TURKEYS

by

ASHLEY K. LOHR

BS, Virginia Tech, 2015

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2019

EFFECTS OF INDIVIDUAL RECESS BEHAVIORS ON NEST AND FEMALE SURVIVAL OF EASTERN WILD TURKEYS

by

ASHLEY K. LOHR

Major Professor:	Michael J. Chamberlain
Committee:	James A. Martin
	Mark D. McConnell

Electronic Version Approved:

Suzanne Barbour
Dean of the Graduate School
The University of Georgia
August 2019

DEDICATION

I dedicate this thesis to my parents, Bryan and Suzanne Lohr, for their unwavering love and support as I elected to pursue a nontraditional degree that fostered my passion for wildlife conservation and allowed for the self-discovery of a fascination with entomology.

I also dedicate this thesis to my boyfriend of 6 years, Collin Trepanitis. While a simple “thank you” will never be enough, I deeply appreciate the endless support, encouragement, and respect he’s shown me during the entirety of our relationship, especially over the last 3 years. Thank you for always answering my phone calls, comforting me during times of self-doubt, and accompanying me on my many fieldwork excursions.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my advisor, Dr. Michael Chamberlain, for providing me with the opportunity to pursue my Master's degree at the University of Georgia. I also thank my committee members, Drs. James Martin and Mark McConnell, for their guidance and expertise during this academic endeavor, and Greg Wann for his modeling assistance.

I thank the Georgia Department of Natural Resources-Wildlife Resources Division (GADNR) for providing funding for this project. Specifically, I thank Bobby Bond and Cliff Rushton of GADNR for supporting the project and aiding us with equipment maintenance. I also thank Liz Caldwell of the United States Forest Service for granting us access to much of the study area. Additionally, I thank the Warnell School of Forestry and Natural Resources and the Animal and Dairy Science Department's Eatonton Beef Research Unit at the University of Georgia. I thank Chad Westmoreland and Charles Trumbo of the Eatonton Beef Unit for their support and interest in the project. Special thanks are owed to the Oconee Rivers Audubon Society and the Georgia Chapter of The Wildlife Society for their support and funding.

I thank Brad Cohen and my fellow graduate students, Patrick Wightman, Daniel Sullivan, Kelsey McClearn, and Calvin Wakefield, for their assistance in the office and the field. I also thank Jeremy Wood and Kaylee Pollander for their helpfulness during the early stages of this project and the technicians who assisted with the project, especially Lauren McCullough and Sarah Heimbach. Their hard work and dedication contributed in part to the project's success.

Thank you to my brothers, Kevin, Andrew, and Sean, for providing me company and comic relief over the last 3 years, as well as our late family cats, Misty and Mocha, for the stress-

reducing snuggles. I would be remiss if I didn’t mention my “purrbabies,” Rigatoni and Ravioli. Since adopting Rig and Rav as kittens two years ago, they have showered me with unconditional love and reaffirmed my sense of self.

Lastly, I would like to thank the many friends and acquaintances I’ve made since moving to Athens. Whether we were birding, hosting a movie night, or going to country concerts at the Georgia Theatre, I will forever cherish the memories I’ve made in Athens, GA.

TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS v

LIST OF TABLES ix

LIST OF FIGURES x

CHAPTER

1 INTRODUCTION AND LITERATURE REVIEW 1

  WILD TURKEY ECOLOGY 4

  MOVEMENT AND SPACE USE 6

  LITERATURE CITED 7

2 EFFECTS OF INDIVIDUAL RECESS BEHAVIORS ON NEST AND FEMALE SURVIVAL OF EASTERN WILD TURKEYS 17

  ABSTRACT 18

  INTRODUCTION 19

  STUDY AREAS 22

  METHODS 24

  RESULTS 28

  DISCUSSION 30

  ACKNOWLEDGEMENTS 34

  LITERATURE CITED 35

3 CONCLUSIONS AND MANAGEMENT IMPLICATIONS 59

APPENDICES

A Nesting ecology of female eastern wild turkeys (*Meleagris gallopavo silvestris*) at Cedar Creek (CC) and B. F. Grant (BFG) Wildlife Management Areas and surrounding lands in central Georgia, USA, 2017 and 2018 61

B Incubation chronology of female eastern wild turkeys (*Meleagris gallopavo silvestris*) at Cedar Creek and B. F. Grant Wildlife Management Areas and surrounding lands in central Georgia, USA, 2017 and 2018 63

LIST OF TABLES

Page

Table 2.1: Posterior means and credible intervals for covariates used to model daily survival for eastern wild turkey (*Meleagris gallopavo silvestris*) nests. Means above 0 positively influence daily nest survival whereas means below 0 negatively influence daily nest survival..57

Table 2.2: Posterior means and credible intervals for covariates used to model daily survival for female eastern wild turkeys (*Meleagris gallopavo silvestris*). Means above 0 positively influence daily female survival whereas means below 0 negatively influence daily female survival..58

LIST OF FIGURES

Page

Figure 2.1: Confusion matrix illustrating predicted effects of daily distance traveled (m) and daily recess duration (hr) on survival of nests and individual female eastern wild turkeys (*Meleagris gallopavo silvestris*). Green Φ represents a high survival probability under the specified parameter intensities, red Φ denotes a low survival probability, and yellow Φ corresponds to an intermediate survival probability 48

Figure 2.2: Map of study sites in the southeastern United States where incubation recess behaviors were evaluated for female eastern wild turkeys (*Meleagris gallopavo silvestris*) during 2014-2018. The symbol in South Carolina represents 3 study sites, collectively known as the Webb WMA Complex 49

Figure 2.3: Histograms illustrating the range of observed values for four covariates used to model nest and female eastern wild turkey (*Meleagris gallopavo silvestris*) survival. Solid blue lines represent $\bar{x}$ and dashed red lines indicate $\pm$ 1 standard deviation. Females spent 0-13 hours off the nest each day ($\bar{x}$ = 2.09, SD = 1.80), took 0-7 daily unique recesses ($\bar{x}$ = 1.62, SD = 1.24), and traveled 0-4,103 m in a day ($\bar{x}$ = 357.63 m, SD = 396.58). Values of nest concealment ranged from 8.75-200 cm ($\bar{x}$ = 92.5 cm, SD = 47).50

Figure 2.4: Posterior distributions for covariates used to model daily survival for eastern wild turkey (*Meleagris gallopavo silvestris*) nests. Solid blue lines denote μ, red lines represent 95% credible intervals, and dashed blue lines indicate 0 51

Figure 2.5: Predicted effects of model covariates on daily survival probabilities for eastern wild turkey (*Meleagris gallopavo silvestris*) nests 52

Figure 2.6: Predicted effects of model covariates on period (30 days) survival probabilities for eastern wild turkey (*Meleagris gallopavo silvestris*) nests....................53

Figure 2.7: Posterior distributions for covariates used to model daily survival for female eastern wild turkeys (*Meleagris gallopavo silvestris*). Solid blue lines denote μ, red lines represent 95% credible intervals, and dashed blue lines indicate 0....................54

Figure 2.8: Predicted effects of model covariates on daily survival probabilities for female eastern wild turkeys (*Meleagris gallopavo silvestris*) 55

Figure 2.9: Predicted effects of model covariates on period (30 days) survival probabilities for female eastern wild turkeys (*Meleagris gallopavo silvestris*) 56

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Animals are biologically driven to improve fitness by surviving to reproductive maturity, locating and securing available mates, and producing viable offspring (Clutton-Brock 1988). Increased effort to produce offspring must be balanced with survival strategies, such as predator avoidance and resource acquisition to maximize lifetime reproductive success (Kie 1999). Resource allocation theory posits that resources put towards one life history trait (e.g., survival) cannot simultaneously be put towards another (e.g., reproduction; Boggs 1992). The primary resources animals require to survive include water, food, and escape cover that provides shelter from predation and environmental elements. However, these resources vary spatially and temporally across the landscape. Likewise, environmental variability influences availability of necessary resources and how animals acquire them, and distribution of resources is often patchy and separated by less profitable or inhospitable habitats (Taylor et al. 1993, Tischendorf et al. 2003). To maximize resource acquisition, animals maintain home ranges based on patch quality and availability (Mitchell and Powell 2004), and animals should select patches where potential success is the highest (Fretwell and Lucas 1970). An increase in patch aggregation facilitates animal movement and reduces travel costs (Silver et al. 2000), but as patch aggregation decreases and resources are depleted in one patch, animals must move through less ideal habitat to reach another profitable patch (Henein and Merriam 1990, Silver et al. 2000). These movements are risky because they increase energy expenditures and predation risk.

Animal movement between patches is facilitated not only by physical attributes of the landscape and distance between patches, but also by behavior of the organism (Henein and Merriam 1990). Predation risk largely influences animal behavior (Kie 1999), and animals must balance decisions with energetic tradeoffs to avoid predation and maximize lifetime fitness (Mirza et al. 2006). As a result, animals invest more time in one activity at the expense of another, such as scanning for predators more frequently and foraging less when surrounded by vegetation that restricts visibility (Goldsmith 1990). Other risky behaviors include sleeping, loafing, and moving through the landscape to acquire resources in another patch (Lendrem 1984, Adriaensen et al. 2003). These risky behaviors entail costs as organisms may not fulfill daily energy quotas, or individuals may be pushed into suboptimal foraging habitat due to risk of predation (Goldsmith 1990, Mirza et al. 2006).

To alleviate immediate effects of predation, some avian species raise precocial young, an adaptation prevalent in ground-nesting birds (Starck and Ricklefs 1998, Balasubramaniam and Rotenberry 2016). Common parental behaviors in precocial species include prenatal care, such as incubation and nest concealment, and postnatal care, such as brooding, loafing, female vigilance, and leading or following young (Winkler and Walters 1983, Starck and Ricklefs 1998). Due to time costs associated with raising multiple offspring, optimal brood sizes exist (Winkler and Walters 1983). By producing optimal brood sizes and providing less parental care at the nest site, precocial species can increase survival of offspring while simultaneously lowering their risk of detection by predators (Brockelman 1975). While there is a tradeoff between scanning for predators and acquiring resources, precocial development allows parents to divert energy from feeding offspring to searching for resources to allocate towards their own growth (Walters 1984). Raising offspring often requires a seasonal shift in resource exploitation, which can increase mortality rates as individuals spend more time in unfamiliar habitats at riskier times of the day (Yoder et al. 2004). Therefore, an individual's ability to maximize resource acquisition influences survival.

Resource acquisition presents challenges, particularly to prey species that must remain vigilant for predators. In addition to remaining cognizant of predators, organisms must also perform other tasks in the face of predation, such as locating mates, copulating, raising young, foraging, preening, and sleeping (Lendrem 1984, Endler 1987, Redpath 1988, Wirsing et al. 2007, DeMars and Boutin 2017). Due to individual variation in fitness goals and perceptions of risk, behavioral differences exist within a population, which lead to variations in individual decision-making processes (Wolf et al. 2007). To increase predator avoidance, some individuals may nest, raise offspring, or forage in suboptimal habitat containing lower quality resources, or in areas where perceived predation risk is lower (Caldwell 1986, Lima and Dill 1990, Kotler et al. 1991, Wilson and Cooper 1998, Wirsing et al. 2007). Due to consumption or use of lower quality resources, organisms may suffer from reduced energy intakes, lower reproductive outputs, physiological stress, or increased mortality rates, all of which facilitate reductions in fitness (Caldwell 1986, Lima and Dill 1990, Kotler et al. 1991). Notably, predator avoidance and decision-making are not well studied in gallinaceous birds, and it is unclear how behavioral decisions affect survival and reproductive productivity.

The wild turkey (*Meleagris gallopavo*; hereafter, turkey) is an ideal species for study of behavioral states and life history trade-offs. Female turkeys are reproductively active for approximately one third of the year (Yeldell et al. 2017), which is energetically taxing and makes them vulnerable to predation. Turkeys have an extended laying period followed by a relatively long incubation period (Dickson 1992), and this coupled with the fact that females provide uniparental care to young makes it likely that female turkeys develop strategies to maximize reproductive success while minimizing mortality. Predator avoidance behaviors may displace turkeys into habitat consisting of fewer or lower quality resources, or individuals may interact with unfamiliar areas that amplify risk due to increased exploratory behaviors and a lack of knowledge of the landscape (Yoder et al. 2004). Understanding turkey behaviors and individual survival probabilities during incubation will allow biologists to better define space use during reproduction and manage for nesting habitat that promotes reproductive success.

WILD TURKEY ECOLOGY

Turkey population growth is limited by adult survival and reproductive success (Vangilder 1992, Palmer et al. 1993, Roberts et al. 1995, Thogmartin and Johnson 1999), and factors such as harvest, lack of brood and winter habitat, summer droughts, poor mast production, severe winters, predation, and disease may influence turkey survival and reproduction (Little et al. 1990, Roberts et al. 1995, Wright et al. 1996, McShea et al. 2007, Dreibelbis et al. 2008, Chamberlain et al. 2012). Predation is the primary cause of nest loss and mortality of females (Martin 1995, Dreibelbis et al. 2008; 2011). Predator abundance and richness vary by ecosystem and landscape context, but predators known to prey on adult female turkeys include coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and great horned owls (*Bubo virginianus*; Palmer et al. 1993, Chamberlain and Leopold 1999, Hubbard et al. 1999, Moore et al. 2010). Predator-prey interactions are influenced by biotic and abiotic factors including habitat quality, animal behavior, species presence on the landscape, climate, and stochastic environmental events (Miller and Leopold 1992). Female turkey survival rates vary seasonally, but greatest mortality occurs during spring and summer reproductive seasons, particularly during incubation (Everett et al. 1980, Wilson et al. 2005, Pollentier et al. 2014). Hence, nest site selection is critical for survival.

Although survival of adult females is an important determinant of stable turkey populations, nest success is a critical component of turkey productivity (Vangilder 1992, Palmer et al. 1993, Roberts and Porter 1996). Nest locations typically have reduced forest canopies with dense understory growth, and are often characterized by increased shrub and ground cover, and increased vegetation height (Lehman et al. 2008, Byrne and Chamberlain 2013, Streich et al. 2015). Some previous authors have noted that vegetative characteristics at nest sites may influence reproductive success (Badyaev et al. 1996, Fuller et al. 2013), however other authors have noted that vegetative conditions at nest sites may not be the main driver of nest success (Lazarus and Porter 1985, Burk et al. 1990, Thogmartin 1999, Byrne and Chamberlain 2013, Conley et al. 2015, Yeldell et al. 2017).

Nest failure is thought to be the primary factor limiting turkey population growth (Vangilder and Kurzejeski 1995, Roberts and Porter 1996). Common nest predators include raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), striped skunks (*Mephitis mephitis*), spotted skunks (*Spilogale putorius*), red fox (*Vulpes vulpes*), grey fox (*Urocyon cinereoargenteus*), feral hogs (*Sus scrofa*), snakes, and American crows (*Corvus brachyrhyncos*; Miller and Leopold 1992, Dreibelbis et al. 2008, Lehman et al. 2008). Due to a wide array of predators that opportunistically locate nests using both olfactory and visual cues, females may initiate nests in denser understories to reduce predation risk (Fuller et al. 2013). However, fire suppression in some areas has allowed understory vegetation to become too dense, resulting in unsuitable nesting habitat that females may avoid (Yeldell et al. 2017). Moreover, habitat fragmentation has increased the amount of edge habitat adjacent to forested areas, resulting in increases in edge effects (Vergara and Hahn 2009). Predators use roads and ecotones as travel corridors, hence fragmentation may increase predator interactions with forest-nesting species, particularly ground-nesting birds such as turkeys (Thogmartin 1999, Hinton et al. 2015).

MOVEMENT AND SPACE USE

Studying animal movements and space use has become more feasible, accurate, and cost-efficient due to Global Positioning System (GPS) technology (Guthrie et al. 2011). Animal movement paths represent decision-making on the landscape, therefore animal behavior can be linked to particular cues such as habitat features and temporal or seasonal changes (Byrne et al. 2014*b*).

While movements are often unrestricted, animals tend to display site fidelity towards certain areas. These areas are typically referred to as an animal's home range. Burt (1943) defined a home range as the area used by an individual to find food, locate a mate, and care for offspring, hence home ranges link animal movements to resource selection and availability (Börger et al. 2008). Methods such as dynamic Brownian Bridge Movement Models (hereafter, dBBMM) create utilization distributions based on movement paths over time (Byrne et al. 2014*a*). Utilization distributions represent where animals spend most of their time, and environmental variables such as habitat metrics can be extracted from these distributions to assess selection for or against various vegetation communities and landscape features throughout the annual cycle (Horne et al. 2008). Utilization distributions are important when manipulating habitat to increase species abundance, and when trying to understand how forest management strategies affect local wildlife populations.

Using GPS technology, we were able to analyze incubation behaviors at an hourly scale to assess their influence on nest and female survival rates within managed landscapes. For the purpose of this study, we collated female turkey reproductive data from 8 study sites occurring in 3 southeastern states: Cedar Creek, B. F. Grant, and Silver Lake WMAs located in Georgia; Kisatchie National Forest and Peason Ridge located in Louisiana; and the Webb WMA Complex located in South Carolina. Habitat and land management activities varied across sites, but all forests were pine-dominated. Chapter 2 discusses recess behaviors and how incubation strategies influence nest and female survival. The final chapter provides conclusions and management implications.

LITERATURE CITED

Adriaensen, F., J. P. Chardon, G. De Blust, E. Swinnen, S. Villalba, H. Gulinck, and E. Matthysen. 2003. The application of ‘least-cost’ modelling as a functional landscape model. Landscape and Urban Planning 64:233-247.

Badyaev, A. V., W. J. Etges, and T. E. Martin. 1996. Habitat sampling and habitat selection by female wild turkeys: ecological correlates and reproductive consequences. The Auk 113:636-646.

Balasubramaniam, P. and J. T. Rotenberry. 2016. Elevation and latitude interact to drive life-history variation in precocial birds: a comparative analysis using galliformes. Journal of Animal Ecology 85:1528-1539.

Boggs, C. L. 1992. Resource allocation: exploring connections between foraging and life history. Functional Ecology 6:508-518.

Börger, L., B. D. Dalziel, and J. M. Fryxell. 2008. Are there general mechanisms of animal home range behavior? A review and prospects for future research. Ecology Letters 11:637-650.

Brockelman, W. Y. 1975. Competition, the fitness of offspring, and optimal clutch size. The American Naturalist 109:677-699.

Burk, J. D., D. R. Smith, G. A. Hurst, B. D. Leopold, and M. A. Melchiors. 1990. Wild turkey use of loblolly pine plantations for nesting and brood rearing. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 44:163-170.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Byrne, M. E., J. C. McCoy, J. W. Hinton, M. J. Chamberlain, and B. A. Collier. 2014*a*. Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. Journal of Animal Ecology 83:1234-1243.

Byrne, M. E., J. D. Guthrie, J. Hardin, B. A. Collier, and M. J. Chamberlain. 2014*b*. Evaluating wild turkey movement ecology: An example using first-passage time analysis. Wildlife Society Bulletin 38:407-413.

Byrne, M. E. and M. J. Chamberlain. 2013. Nesting ecology of wild turkeys in a bottomland hardwood forest. American Midland Naturalist 170:95–110.

Caldwell, G. S. 1986. Predation as a selective force on foraging herons: effects of plumage color and flocking. The Auk 103:494-505.

Chamberlain, M. J., B. A. Grisham, J. L. Norris, N. J. Stafford III, F. G. Kimmel, and M. W. Olinde. 2012. Effects of variable spring harvest regimes on annual survival and recovery rates of male wild turkeys in southeast Louisiana. Journal of Wildlife Management 76:907-910.

Chamberlain, M. J. and B. D. Leopold. 1999. Dietary patterns of sympatric bobcats and coyotes in central Mississippi. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 53:204-219.

Clutton-Brock, T. H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Illinois, USA.

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

Conley, M. D., N. A. Yeldell, M. J. Chamberlain, and B. A. Collier. 2016. Do movement behaviors identify reproductive habitat sampling for wild turkeys? Ecology and Evolution 6:7103-7112.

DeMars, C. A. and S. Boutin. 2017. Nowhere to hide: effects of linear features on predator-prey dynamics in a large mammal system. Journal of Animal Ecology 00:1-11.

Dickson, J. G. 1992. Introduction. Pages 2-5 *in* J. G. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Dreibelbis, J. Z., J. D. Guthrie, R. J. Caveny, J. Hardin, N. J. Silvy, M. J. Peterson, and B. A. Collier. 2011. Predator community and researcher-induced impacts on nest success of Rio Grande wild turkeys in Texas. National Wild Turkey Symposium 10:235-242.

Dreibelbis, J. Z, K. B. Melton, R. Aguirre, B. A. Collier, J. Hardin, N. J. Silvy, and M. J. Peterson. 2008. Predation of Rio Grande wild turkey nests on the Edwards Plateau, Texas. The Wilson Journal of Ornithology 120:906-910.

Endler, J. A. 1987. Predation, light intensity, and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). Animal Behaviour 35:1376-1385.

Everett, D. D., W. K. Maddox, and D. W. Speake. 1980. Natality and mortality of a north Alabama wild turkey population. National Wild Turkey Symposium 4:117–126.

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

Fuller, A. K., S. M. Spohr, D. J. Harrison, and F. A. Servello. 2013. Nest survival of wild turkeys *Meleagris gallopavo silvestris* in a mixed-use landscape: influences at nest site and patch scales. Wildlife Biology 19:138–146.

Godfrey, C. L. and G. W. Norman. 1999. Effect of habitat and movement on wild turkey poult survival. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 53:330-339.

Goldsmith, A. E. 1990. Vigilance behavior of pronghorns in different habitats. Journal of Mammalogy 71:460-462.

Guthrie, J. D., M. E. Byrne, J. B. Hardin, C. O. Kochanny, K. L. Skow, R. T. Snelgrove, M. J. Butler, M. J. Peterson, M. J. Chamberlain, and B. A. Collier. 2011. Evaluation of a global positioning system backpack transmitter for wild turkey research. Journal of Wildlife Management 75:539–547.

Healy, W. M. 1992. Behavior. Pages 46-65 *in* J. G. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Henein, K. and G. Merriam. 1990. The elements of connectivity where corridor quality is variable. Landscape Ecology 4:157-170.

Hinton, J. W., F. T. van Manen, and M. J. Chamberlain. 2015. Space use and habitat selection by resident and transient coyotes (*Canis latrans*). PLoS ONE 10:1–17.

Horne, J. S., E. O. Garton, and J. L. Rachlow. 2008. A synoptic model of animal space use: Simultaneous estimation of home range, habitat selection, and inter/intra-specific relationships. Ecological Modelling 214:338-348.

Hubbard, M. W., D. L. Garner, and E. E. Klass. 1999. Factors influencing wild turkey hen survival in southcentral Iowa. Journal of Wildlife Management 63:731–738.

Kie, J. G. 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. Journal of Mammalogy 80:1114-1129.

Kotler, B. P., J. S. Brown, and O. Hasson. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72:2249-2260.

Lazarus, J. E. and W. F. Porter. 1985. Nest habitat selection by wild turkeys in Minnesota. National Wild Turkey Symposium 5:67-82.

Lehman, C. P., M. A. Rumble, L. D. Flake, and D. J. Thompson. 2008. Merriam's turkey nest survival and factors affecting nest predation by mammals. Journal of Wildlife Management 72:1765-1774.

Lendrem, D. W. 1984. Sleeping and vigilance in birds, II. An experimental study of the Barbary dove (*Streptopelia risoria*). Animal Behaviour 32:243-248.

Lima, S. L. and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Lima, S. L. and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11:131-135.

Little, A. R., N. P. Nibbelink, M. J. Chamberlain, L. M. Conner, and R. J. Warren. 2016. Eastern wild turkey nest site selection in two frequently burned pine savannas. Ecological Processes 5:1-10.

Little, T. W., J. M. Kienzler, and G. A. Hanson. 1990. Effects of fall either-sex hunting on survival in an Iowa wild turkey population. Proceedings of the National Wild Turkey Symposium 6:119-125.

Lowrey, D. K., G. A. Hurst, S. R. Priest, B. S. Weemy. 2000. Influences of selected weather variables on predation of wild turkey females and nest success. National Wild Turkey Symposium 8:173-178.

Martin, J. A., W. E. Palmer, S. M. Juhan Jr., and J. P. Carroll. 2012. Wild turkey habitat use in frequently-burned pine savanna. Forest Ecology and Management 285:179-186.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101-127.

McShea, W. J., W. M. Healy, P. Devers, T. Fearer, F. H. Koch, D. Stauffer, and J. Waldon. 2007. Decline of oaks will impact wildlife in hardwood forests. Journal of Wildlife Management 71:1717-1728.

Melton, K. B., J. Z. Dreibelbis, R. Aguirre, J. Hardin, N. J. Silvy, M. J. Peterson, and B. A. Collier. 2011. Reproductive parameters of Rio Grande wild turkeys on the Edwards Plateau, Texas. National Wild Turkey Symposium 10:227-233.

Miller, J. E. and B. D. Leopold. 1992. Population influences: Predators. Pages 119-128 *in* J. G. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Mirza, R. S., A. Mathis, and D. P. Chivers. 2006. Does temporal variation in predation risk influence the intensity of antipredator responses? A test of the risk allocation hypothesis. Ethology 112:44-51.

Mitchell, M. S. and R. A. Powell. 2004. A mechanistic home range model for optimal use of spatially distributed resources. Ecological Modelling 177:209-232.

Moore, W. F., J. C. Kilgo, W. D. Carlisle, D. C. Guynn, and J. R. Davis. 2010. Nesting success, nest site characteristics, and survival of wild turkey hens in South Carolina. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 64:24–29.

Palmer, W. E., S. R. Priest, R. S. Seiss, P. S. Phalen, and G. A. Hurst. 1993. Reproductive effort and success in a declining wild turkey population. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 47:138–147.

Peoples, J. C., D. C. Sisson, and D. W. Speake. 1995. Mortality of wild turkey poults in coastal plain pine forests. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 49:448-453.

Pollentier, C. D., R. S. Lutz, and S. D. Hull. 2014. Survival and productivity of eastern wild turkey females in contrasting landscapes in Wisconsin. Journal of Wildlife Management 78:985-996.

Redpath, S. 1988. Vigilance levels in preening Dunlin *Calidris alpina*. Ibis 130:555-557.

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

Roberts, S. D. and W. F. Porter. 1996. Importance of demographic parameters to annual changes in wild turkey abundance. National Wild Turkey Symposium 7:15–20.

Silver, P., J. K. Cooper, M. A. Palmer, and E. J. Davis. 2000. The arrangement of resources in patchy landscapes: effects on distribution, survival, and resource acquisition of Chironomids. Oecologia 124:216-224.

Smith, W. P. and R. D. Teitelbaum. 1986. Habitat use by eastern wild turkey hens in southeastern Louisiana. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 40:405-415.

Speake, D. W., R. Metzler, and J. McGlincy. 1985. Mortality of wild turkey poults in northern Alabama. Journal of Wildlife Management 49:472–474.

Starck, J. M. and R. E. Ricklefs. 1998. Avian growth and development: evolution within the altricial-precocial spectrum. Oxford University Press, New York, New York, USA.

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

Syrotuck, W.G. 1972. Scent and the scenting dog. Arner Publishers, Rome, New York, USA.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571-573.

Thogmartin, W. E., and J. E. Johnson. 1999. Reproduction in a declining population of wild turkeys in Arkansas. Journal of Wildlife Management 63:1281–1290.

Thogmartin, W. E. 1999. Landscape attributes and nest-site selection in wild turkeys. Auk 116:912–923.

Tischendorf, L., D. J. Bender, and L. Fahrig. 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. Landscape Ecology 18:41-50.

Vangilder, L. D. 1992. Population Dynamics. Pages 144–164 *in* J. G. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, PA, USA.

Vangilder, L. D. and E. W. Kurzejeski. 1995. Population ecology of the eastern wild turkey in northern Missouri. Wildlife Monographs 130:3-50.

Vergara, P. M. and I. Hahn. 2009. Linking edge effects and patch size effects: importance of matrix nest predators. Ecological Modelling 220:1189-1196.

Walters, J. R. 1984. The evolution of parental behavior and clutch size in shorebirds. Pages 243-287 *in* J. Burger and B. Olla, editors. Shorebirds: Breeding behavior and populations. Plenum Press, New York, NY, USA.

Williams, L. E., Jr., D. H. Austin, T. E. Peoples, and R. W. Phillips. 1971. Laying data and nesting behavior of wild turkeys. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 25:90-106.

Wilson, R. R. and R. J. Cooper. 1998. Acadian flycatcher nest placement: does placement influence reproductive success? The Condor 100:673-679.

Wilson, W. B., M. J. Chamberlain, and F. G. Kimmel. 2005. Seasonal space use and habitat selection of female wild turkeys in a Louisiana bottomland hardwood forest. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 59:114-125.

Winkler, D. and J. Walters. 1983. The determination of clutch size in precocial birds. Pages 33-68 *in* R. Johnston, editor. Current Ornithology. Springer, Boston, MA, USA.

Wirsing, A. J., M. R. Heithaus, and L. M. Dill. 2007. Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. Animal Behaviour 74:93-101.

Wolf, M., G. Sander van Doorn, O. Leimar, and F. J. Weissing. 2007. Life-history trade-offs favour the evolution of animal personalities. Nature 447:581-584.

Wood, J. D., B. S. Cohen, T. J. Prebyl, L. M. Connor, B. A. Collier, and M. J. Chamberlain. 2018. Time-since-fire and stand seral stage affect habitat selection of eastern wild turkeys in a managed longleaf pine ecosystem. Forest Ecology and Management 411:203-212.

Wright, R. G., R. N. Paisley, and J. F. Kubisiak. 1996. Survival of wild turkey hens in southwestern Wisconsin. Journal of Wildlife Management 60:313–320.

Yeldell, N. A., B. S. Cohen, A. R. Little, B. A. Collier, and M. J. Chamberlain. 2017. Nest site selection and nest survival of eastern wild turkeys in a pyric landscape. Journal of Wildlife Management 81:1073-1083.

Yoder, J. M., E. A. Marschall, D. A. Swanson. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. Behavioral Ecology 15:469-476.

CHAPTER 2

EFFECTS OF INDIVIDUAL RECESS BEHAVIORS ON NEST AND FEMALE SURVIVAL OF EASTERN WILD TURKEYS[1]

---

[1] Lohr, A. K., J. A. Martin, G. T. Wann, B. S. Cohen, B. A. Collier, and M. J. Chamberlain. To be submitted to *The Auk: Ornithological Advances*.

ABSTRACT

Reproduction is an energetically costly behavior, and nest success is an important parameter influencing avian population dynamics. Galliforms are particularly susceptible to reduced reproductive output due to exposure of ground nests to multiple predator guilds, lengthy incubation periods, and substantive reliance on crypsis for survival. Hence, it is plausible that breeding individuals prioritize productivity and survival differently, resulting in a gradient of reproductive strategies. Fine-scale movement patterns during incubation are not well documented in ground-nesting birds, and their influence on survival is largely unknown. Using GPS data collected from female eastern wild turkeys (*n* = 278) across the southeastern United States, we evaluated the influence of incubation recess behaviors on nest and female survival rates. We quantified daily recess behaviors including recess duration, recess frequency, total distance traveled, and range size for each nest attempt, and also included nest concealment, nest attempt, and nest age as covariates in our models. Of 374 nests, 91 (24%) hatched and 39 (14%) females were depredated during incubation. The average period nest survival rate was 0.19, whereas the average period female survival rate was 0.78. On average, females took 1.62 daily unique recesses (SD = 1.24), spent 2.09 hours off the nest each day (SD = 1.80), and traveled 357.63 m in a day (SD = 396.58). Average nest concealment was 92.5 cm (SD = 47). We found that females who took longer recess bouts increased individual survival, but suffered increased nest failure. Conversely, females who recessed more often suffered greater mortality rates. Our findings suggest behavioral decisions made during incubation represent life history trade-offs between predation risk and reproductive success on an unpredictable landscape.

INTRODUCTION

Reproduction is an energetically costly behavior necessary for population viability and genetic exchange (Avise 1996). Individual fitness, the ability to survive to reproductive maturity, mate, and produce viable offspring (Clutton-Brock 1988), is largely influenced by annual fecundity, the number of offspring a female produces each year (Nagy and Holmes 2004). Female investment in producing offspring versus individual growth and self-maintenance is governed by the resource allocation theory, which states resources put towards one life history trait (i.e., survival) cannot simultaneously be put towards another (i.e., reproduction; Boggs 1992, Audzijonyte and Richards 2018). Hence, females must balance energetic demands of producing offspring with associated energy expenditures, such as resource acquisition and predator avoidance (Boggs 1992, Kie 1999). Species evolved under various degrees of predation pressure (Martin 1995, Lamanna and Martin 2016), and predator-rich environments have driven evolution of diverse life-history strategies, such as bet-hedging to reduce temporal variance in individual fitness (Simovich and Hathaway 1997, Einum and Fleming 2004, Fontaine and Martin 2006, Fontaine et al. 2007). In unpredictable environments, bet-hedging may involve prioritizing individual survival over producing offspring to ensure future reproductive opportunities (Cohen 1966, Cohen 1967, Simovich and Hathaway 1997, Danforth 1999). Within avian taxa, nesting mortality shapes reproductive strategies (Ricklefs 1969, Bergerud and Gratson 1988, Fontaine and Martin 2006), and failure to respond to predation risk produces negative fitness consequences. Hence, individuals within a population likely prioritize productivity and survival differently, resulting in a gradient of reproductive strategies (Drent 1975, Afton 1980, Jones 1989).

Nest success is an important parameter influencing avian population dynamics (Ricklefs 1969, Sæther and Bakke 2000). Gallinaceous birds are particularly susceptible to reduced reproductive output due to exposure of ground nests to multiple predator guilds, lengthy incubation periods, and substantive reliance on crypsis for survival (Blomberg et al. 2015). Furthermore, female only incubation is common within many galliform species, which is energetically taxing and makes females especially vulnerable to predation (Johnsgard 1983, Cockburn 2006). For these reasons, wild turkeys (*Meleagris gallopavo*) are an ideal gallinaceous bird in which to examine reproductive behaviors and life history trade-offs. Female turkeys have particularly lengthy incubation periods, ranging from 25-30 days (Healy 1992, Conley et al. 2015). In the southeastern United States, numerous predator species depredate nests (Miller and Leopold 1992, Dreibelbis et al. 2008, Lehman et al. 2008, Martin et al. 2015) and adults during incubation periods (Palmer et al. 1993, Chamberlain and Leopold 1999, Hubbard et al. 1999, Moore et al. 2010). Extensive research has characterized vegetation at nest sites and described nest site selection by female turkeys (Porter 1992, Lehman et al. 2008, Fuller et al. 2013, Streich et al. 2015, Little et al. 2016), but vegetation at nest sites may not be the main driver of nest success (Lazarus and Porter 1985, Burk et al. 1990, Thogmartin 1999, Byrne and Chamberlain 2013, Yeldell et al. 2017).

While nest placement may influence nest and female survival, incubating females must also balance embryonic development and resource acquisition via recess movements (Williams et al. 1971). Extensive literature on a suite of avian species suggests nest attentiveness is influenced by predation risk, egg-cooling, and female body condition (Haftorn 1988, Weathers and Sullivan 1989, Wiebe and Martin 1997, Wiebe and Martin 2000, MacDonald et al. 2013). For wild turkeys, recess bouts are thought to enable incubating females to defecate and forage away from the nest, but recess behaviors in wild turkeys are poorly understood and based on sporadic observations of birds during the incubation period (Williams et al. 1971, Green 1982, Conley et al. 2015). Notably, contemporary works using fine-scale movements to detail recess behaviors have either been hampered by modest samples sizes (Conley et al. 2015), or detailed average recess behaviors for each nest attempt (Bakner 2018), rather than seeking to identify consequences of daily recess behaviors on individual fitness metrics.

To expand upon earlier (Williams et al. 1971, Green 1982) and more contemporary works describing incubation recess behaviors of wild turkeys (Conley et al. 2015, Bakner 2018), our objectives were to: 1) examine daily recess behaviors of incubating female eastern wild turkeys and 2) relate incubation behaviors and nest concealment to nest and female survival, so that we could determine whether individual females used strategies to maximize nest success and survival during incubation. We hypothesized incubating females prioritize productivity and survival differently, which would influence daily movements and space use.

We generated a confusion matrix illustrating the predicted effects of daily distance traveled and daily recess duration on nest and female survival since these covariates best reflected nest attentiveness and movements proximal to a nest (Fig. 2.1). We assumed vegetation mediated the effects of daily movements on survival and therefore did not include nest concealment in the matrix. Green Φ represented a high survival probability under the specified parameter intensities, red Φ denoted a low survival probability, and yellow Φ corresponded to an intermediate survival probability. Under average conditions, we predicted a female would either reduce daily movements while spending more time off the nest at the expense of the nest (Q3), or spend more time incubating but increase daily movements at the expense of the female (Q1). Both scenarios allowed a female to balance resource acquisition, embryonic development, and predator avoidance (Jones 1989, Boggs 1992, Kie 1999). Considering turkeys are a long-lived species capable of renesting multiple times each reproductive season (Yeldell et al. 2017, Wood et al. 2018), we predicted a female would spend more time off the nest and increase daily movements (Q4) if she perceived direct (i.e. predator) or indirect (i.e. environmental) threats to survival (Ghalambor and Martin 2001). This may demonstrate a bet-hedging strategy used by species with long incubation periods and high adult survival outside the nesting season (Ghalambor and Martin 2001, Martin 2002). Bet-hedging behaviors have obvious negative repercussions for the nest, but increase the likelihood a female will survive to renest later that season or in a successive breeding season (Wiebe and Martin 2000, Matysioková and Remeš 2018). Lastly, if a female prioritized nest survival over self-maintenance or perceived low predation risk, she would spend more time incubating and reduce her daily movements (Q2; Fontaine and Martin 2006).

STUDY AREAS

We conducted research on 8 study sites and surrounding privately-owned land in 3 southeastern states (Fig. 2.2). The study sites consisted predominantly of mixed pine-hardwood forests managed with dormant and growing-season prescribed fire. Specifically, we conducted research on 2 sites in west-central Louisiana, Kisatchie National Forest (KNF) and Peason Ridge Wildlife Management Area (WMA). The KNF was owned and managed by the United States Forest Service (USFS), whereas Peason Ridge WMA was owned and managed by the United States Army. These sites consisted of pine-dominated forests, hardwood riparian zones, and forested wetlands, with forest openings, utility right-of-ways, and forest roads distributed throughout. Dominant overstory species included longleaf pine (*Pinus palustris*), loblolly pine (*P. taeda*), oaks (*Quercus* spp.), hickories (*Carya* spp.), red maple (*Acer rubrum*), and sweetgum

(*Liquidambar styraciflua*). Prescribed fire was applied on a 3-5 year return interval. For a detailed description of site conditions on KNF and Peason Ridge WMA, see Yeldell et al. (2017).

We also conducted research on 3 sites in Georgia; Cedar Creek, B. F. Grant, and Silver Lake WMAs. Silver Lake WMA, located in southwest Georgia, was owned and managed by the Georgia Department of Natural Resources-Wildlife Resources Division (GADNR). Silver Lake WMA was comprised of mature pine forests and forested wetlands. Overstory species were predominantly longleaf pine, loblolly pine, slash pine (*P. elliottii*), oaks, and sweetgum. Prescribed fire was applied on a 2-3 year return interval. For a detailed description of site conditions on Silver Lake WMA, see Wood et al. (2018).

Cedar Creek and B. F. Grant WMAs were both located in the Piedmont region of Georgia. Cedar Creek WMA was owned by the U. S. Forest Service and managed in partnership with GADNR. Cedar Creek WMA was composed primarily of upland loblolly pine stands, mixed pine-hardwood forests, and hardwood lowlands dominated by oaks, sweetgum, and hickories. B. F. Grant WMA was owned by the Daniel B. Warnell School of Forestry and Natural Resources at the University of Georgia, and was managed cooperatively by the GADNR and the Warnell School. B. F. Grant WMA consisted primarily of loblolly pine stands, agricultural fields, mixed pine-hardwood forests, and hardwood bottoms similar in composition to Cedar Creek. Agricultural fields were mainly grazed mixed fescue (*Festuca* spp.) and hay fields planted for rye grass (*Lolium* spp.). Utility right-of-ways and forest roads were found throughout both study sites, and prescribed fire was applied on both sites on a 3-5 year return interval. Much of the private land surrounding these WMAs was subject to intensive timber harvest regimes.

Lastly, we conducted research on 3 contiguous WMAs (Webb, Hamilton Ridge, and Palachucola; hereafter, Webb WMA Complex) in southwestern South Carolina, all managed by the South Carolina Department of Natural Resources (SCDNR). The Webb WMA Complex consisted of longleaf, loblolly, and slash pine forests as well as hardwood stands along riparian corridors and bottomland hardwood wetlands. Prescribed fire was applied on a 3-5 year return interval. For a detailed description of site conditions on the Webb WMA Complex, see Wightman et al. (2018*b*).

METHODS

Turkey Capture and Processing

We captured female turkeys using rocket nets from January-March 2014-2018. Captured individuals were aged using the presence (adult) or absence (juvenile) of barring on the ninth and tenth primary feathers (Pelham and Dickson 1992). We banded each bird with a serially-numbered aluminum leg band (National Band and Tag Company, Newport, Kentucky) and radio-tagged each female with a backpack-style, mortality-sensitive GPS transmitter with VHF capabilities (Lotek Wireless Inc., United Kingdom; Guthrie et al. 2011). We programmed transmitters to record hourly locations from 0500-2000 and one nightly location at 23:59 for the life of the unit or until the unit was recovered (Cohen et al. 2018). All birds were released at the capture location immediately following processing. Turkey capture, handling, and marking procedures were approved by the Institutional Animal Care and Use Committee at the University of Georgia (Protocol #A2014 06008Y1A0, A343701, and A2016 04-001-R1) and the Louisiana State University Agricultural Center (Protocol #A2014-013 and A2015-07).

Nest Monitoring

We used a hand-held, 3-element Yagi antenna and R2000 receiver (Advanced Telemetry Systems, Inc., Isanti, MN) to monitor survival and reproductive activity of all radio-tagged females. We downloaded GPS locations from each female ≥ 1 time per week. We assumed onset of incubation when GPS locations were fixed around a central point for at least 24 hours (Yeldell et al. 2017). We monitored incubating females daily using radio telemetry. Once incubation was terminated, we located the nest using GPS coordinates to determine nest fate and recorded the precise nest location for future analyses. We considered nests successful if ≥ 1 egg hatched (Conley et al. 2016). We continued to monitor females for additional nest attempts until reproductive activity ceased.

Vegetation Sampling at Nest Sites

Because nest concealment may influence nest and female survival (Nguyen et al. 2004, Lehman et al. 2008, Fuller et al. 2013), we conducted vegetation surveys at each nest site at expected time of hatch regardless of nest fate (McConnell et al. 2017). We estimated lateral visual obstruction (cm) by placing a 2-m tall Robel pole (Robel et al. 1970) at the nest bowl and recording minimum vegetation height readings from 15 m away in each cardinal direction, as this encompassed the vegetative conditions immediately surrounding the nest (Yeldell et al. 2017, Wood et al. 2018). We then averaged the visual obstruction readings to generate one value at each nest site.

Incubation Analysis

To isolate incubation behaviors from pre- and post-nesting movements, we censored the first and last days of incubation (Conley et al. 2015). To account for potential GPS error and short movements away from the nest that did not constitute recess movements, we placed a 27.5

m buffer around each nest (Collier et al. 2019). Following Bakner (2018), we defined recess movements as any GPS location > 27.5 m from the nest coordinates, whereas GPS locations ≤ 27.5 m from the nest coordinates were considered as nest (incubation) locations. Previous studies have noted that space use may influence survival and reproductive success (Badyaev et al. 1996, Yoder et al. 2004, Patrick and Weimerskirch 2017), and movements to and from nests may increase predation risk to parents and offspring (Wiebe and Martin 1997, Martin 2002, Bakner 2018). Hence, we sought to quantify incubation recess behaviors such as daily range size and daily movements. We defined a unique recess as ≥ 1 GPS location > 27.5 m from the nest coordinates prior to a female returning to the nest. We determined recess duration as the total number of GPS locations that fell outside of the nest buffer each day. Using R version 3.4.1 (R Core Team 2017), we measured total daily distance traveled, number of daily unique recesses, daily recess duration, and daily range size for each nest attempt. We used dynamic Brownian Bridge Movement Models (hereafter, dBBMM) to quantify 99% daily utilization distributions, using a window size of 7, margin of 3, and location error of 20 m (Kranstauber et al. 2012, Cohen et al. 2018). We performed all utilization distribution calculations using R package move (Kranstauber et al. 2017).

Nest Survival Model

We constructed a Bayesian hierarchical model using the R2jags package in R (R Core Team 2017) to estimate nest survival. We parameterized models using covariates likely to influence survival of ground nests (Wiebe and Martin 1997, Lehman et al. 2008, Bakner 2018), which included daily distance traveled, unique recesses taken daily, recess duration, daily range size, and nest concealment. For most precocial avian species, older nests are more likely to survive because nests in riskier locations are depredated early (Klett and Johnson 1982). Hence, we also included nest attempt and nest age to assess effects of time-dependent variables on nest survival (Wilson et al. 2007). We estimated period survival as the daily survival rate expanded for the entire 30-day incubation cycle (Shaffer and Thompson 2007). To avoid introducing bias into our predicted survival rates, we included censored nests and females in our period survival estimates. To examine collinearity, we calculated Pearson correlations (*r*) for all pairs of predictor variables. We ultimately removed daily range size from our models due to a positive correlation with daily distance traveled ($r = 0.737$; Dormann et al. 2013). We assumed covariates that had < 5% influence on period survival rates were not biologically significant.

As per Royle and Dorazio (2008), we treated nest fate between successive days as the sampling unit. We designated nest attempt *i* on a given day of incubation *j* as 1 for an active nest and 0 for a nest that had been depredated or otherwise failed. We treated the probability of nest survival from day *j* to day *j+1* as a Bernoulli distribution. We specified site (KNF, Peason Ridge, Cedar Creek, B. F. Grant, Silver Lake, Webb WMA Complex) and year (2014-2018) as random effects with site nested within year. We assumed normal distributions for both fixed and random effects with a mean of 0 and small precision terms (0.001). We then built the following model using nest survival covariates on the logit scale:

$$logit(\Phi_{i,j}) = \beta_0 + \beta_1 * attempt_i + \beta_2 * conceal_i + \beta_3 * distance_{i,j} + \beta_4 * duration_{i,j} \\ + \beta_5 * recess_{i,j} + \beta_6 * nage_{i,j} + Year_i + Site_i$$

Where $attempt_i$ and $nage_{i,j}$ represented the effects of nest attempt and nest age on nest survival, respectively. $Conceal_i$ characterized the effect of nest concealment on survival, $distance_{i,j}$ symbolized the effect of daily distance traveled on nest survival, $duration_{i,j}$ denoted the effect of daily recess duration on nest survival, and $recess_{i,j}$ represented the effect of daily recess frequency on nest survival. Temporal and spatial random effects were denoted by $Year_i$ and $Site_i$.

Female Survival Model

We used the R2jags package in R (R Core Team 2017) to generate an additional Bayesian hierarchical model to estimate female survival. With the exception of nest age, we used the same parameters as the nest survival model because those covariates likely influence female survival during incubation (Lehman et al. 2008, Martin 2002, Dudko et al. 2019). Following Royle and Dorazio (2008), we treated female fate between successive days as the sampling unit. We designated individual female *i* on a given day of incubation *j* as 1 for alive and 0 for a female that had been depredated. We treated the probability of female survival from day *j* to day *j+1* as a Bernoulli distribution. We then built the following model using female survival covariates on the logit scale:

$$logit(\Phi_{i,j}) = \beta_0 + \beta_1 * attempt_{i,j} + \beta_2 * conceal_{i,j} + \beta_3 * distance_{i,j} + \beta_4 * duration_{i,j} \\ + \beta_5 * recess_{i,j} + Year_i + Site_i$$

The scope of covariates represented in the female survival model was the same as those in the nest survival model.

For both the nest and female survival models, we used Markov Chain Monte Carlo (MCMC) to estimate posterior distributions of the model parameters. We conducted simulations using 3 chains, 4,000 iterations, a burn-in value of 800, and a thinning rate of 3 for the nest survival model, whereas we used 7,000 iterations and a burn-in value of 2,000 for the female survival model (Gelman and Rubin 1992). All estimated parameters had R-hat values < 1.1, meaning all chains converged (Gelman et al. 2004).

RESULTS

We used 374 nests (262 initial attempts, 90 second attempts, 20 third attempts, 2 fourth attempts) incubated by 278 female wild turkeys (248 adults, 30 juveniles) during 2014-2018 for nest and female survival analyses. Prior to analysis, we removed 32 nests that were incubated < 3 days since we were unable to isolate incubation behaviors from nests of such short duration. We observed earliest onset of incubation on day 77 (March 18) and last date of termination on day 201 (July 20), resulting in an incubation season spanning 124 days. Of 374 nests, 91 (24%) hatched and 39 (14%) females were depredated during incubation. Based on GPS data and anecdotal evidence detailing the presence of feathers or a carcass proximal to the nest bowl, we inferred that 13 (99%) females were killed at the nest site. Average daily and period nest survival rates were 0.95 and 0.19, respectively, whereas average daily and period female survival rates were 0.99 and 0.78, respectively. On average, females took 1.62 daily unique recesses (SD = 1.24), spent 2.09 hours off the nest each day (SD = 1.80), and traveled 357.63 m in a day (SD = 396.58; Fig. 2.3). Average nest concealment was 92.5 cm (SD = 47; Fig. 2.3).

The prediction that females would prioritize nest survival over individual survival was not supported. For nest survival, posterior response to daily recess duration was stronger than all other parameter responses (μ of posterior distribution with 95% credible intervals = -0.17, -0.40 to 0.08; Table 2.1, Fig. 2.4). Nests were 1.19 times less likely to survive with every 1.8 hour increase in daily recess duration (Figs. 2.5 and 2.6). There were no biologically significant effects of nest attempt, nest age, nest concealment, daily distance traveled, or daily unique recesses on nest survival rates (Figs. 2.4-2.6).

In general, the prediction that females would prioritize individual survival over nest survival was supported. For female survival, posterior responses were strongest for daily recess duration (μ of posterior distribution with 95% credible intervals = 0.76, -0.14 to 1.96; Table 2.2, Fig. 2.7) and number of daily recesses (μ of posterior distribution with 95% credible intervals = -0.55, -1.50 to 0.22; Table 2.2, Fig. 2.7). Incubating females were 2.14 times more likely to survive with every 1.8 hour increase in daily recess duration (Figs. 2.8 and 2.9). Conversely, odds of survival for incubating females were 1.74 times less likely as number of daily recesses increased by 1.24 (Figs. 2.8 and 2.9). There were no apparent effects of nest attempt, nest concealment, or daily distance traveled on female survival (Figs. 2.7-2.9).

DISCUSSION

Recess movements enable incubating birds to balance embryonic development with resource acquisition and predator avoidance (Williams et al. 1971, Wiebe and Martin 2000). Hence, recess behaviors may bear important implications to fitness. Extant literature on wild turkey incubation behaviors is based on observations of females leaving or returning to nests (Williams et al. 1971, Green 1982), and only recently have we gained the ability to thoroughly describe recess behaviors (Conley et al. 2015, Bakner 2018, Dudko et al. 2019). Our findings support the hypothesis that female wild turkeys use multiple strategies during incubation, presumably driven by life history trade-offs between predation risk and reproductive success on a dynamic landscape. We found that recess duration and recess frequency had the strongest effects on nest and female survival. Poor period nest survival combined with high female mortality at the nest site suggests that females may be altering their incubation behaviors to prioritize individual survival and ensure future reproductive opportunities.

We observed daily recess duration influenced daily survival of both nests and females. Shorter daily recess bouts correspond to increased daily nest attentiveness which may make incubating females more susceptible to predation, particularly by predators that rely on olfactory cues to locate prey (Hubbard et al. 1999, Isaksson et al. 2007, Martin et al. 2015). Alternatively, longer daily recess bouts result in unattended nests while females undergo other activities, such as resource acquisition or predator avoidance (Conway and Martin 2000, MacDonald et al.

2013). Smith et al. (2012) observed a positive relationship between nest predation and proportion of time shorebirds left nests unattended. Prolonged recess bouts may also slow embryonic development, increase incubation periods, and lengthen nest exposure times (Lyon and Montgomerie 1985, Haftorn 1988, MacDonald et al. 2013). Incubation strategies featuring longer daily recess durations may indicate females perceive heightened individual predation risk, and therefore prioritize individual survival to ensure future reproductive opportunities, either by renesting later in the season or postponing reproduction until the subsequent nesting season (Milonoff 1989, Philippi and Seger 1989, Fontaine and Martin 2006, Lima 2009). While this type of strategy likely has a negative population-level effect on within-year productivity, it may benefit longer-term productivity if females increase reproductive effort in subsequent years.

Considering the majority of females were killed at their nests, movements away from a nest may enable incubating females to obtain resources while avoiding predation (Eggers et al. 2005). This behavior supports the positive relationship we observed between daily distance traveled and female survival. However, such movements negatively influenced nest survival, most likely due to decreased nest attendance (Lecomte et al. 2009, Smith et al. 2012), although the predicted effects of daily distance moved were less relevant than daily recess duration. Increased daily movements could reflect females traveling to distant foraging sites or prolonged movements proximal to a nest. Movements close to a nest may be indicative of poor female body condition or nest guarding tactics in the event of a threat, such as a snake or mammalian mesopredator that a female turkey could effectively ward off (Martindale 1982, Marzluff 1985, Hakkarainen et al. 2002). Conversely, distant recesses may reflect a lack of resources near the nest (Criscuolo et al. 2000, Lecomte et al. 2009) or heightened perceived predation risk, although the latter is not understood. More research is needed assessing the relationship between distance traveled while recessing and nest and female survival.

Instances of egg depredation and nest loss may be associated with female movements to and from nests (Wiebe and Martin 1997, Spaans et al. 2007). We noted that number of daily unique recesses had a limited effect on nest survival but had a noticeable negative effect on female survival. Frequent, direct movements to and from nest sites likely attract predators observing parental activity or increase numbers of scent trails that guide predators to a nest (Erikstad 1986, Weathers and Sullivan 1989, Storaas and Wegge 1997). Hence, females taking numerous recesses per day may hamper population productivity over time due to decreases in female survival (Collier et al. 2009).

Previous authors have found that nests attempted later in the season may have a higher probability of hatching due to a lower density of nests on the landscape, improved vegetative cover when compared to the onset of the nesting season, and increased availability of alternative food sources (Lockwood and Sutcliffe 1985, Myrberget 1988, Rumble and Hodorff 1993, Norman et al. 2001, Lehman et al. 2008). Munkebye et al. (2003) observed greatest rates of nest predation in willow ptarmigan immediately before the first nest hatched, and nest predation rate increased with increasing numbers of available clutches. However, we found that nest age and nest attempt were not significant predictors of nest or female survival. While recent findings suggest the majority of turkey nests fail within 14 days of incubation (Bakner 2018), we observed low nest success regardless of nest age. Increased nest failure regardless of nest initiation date may be due to increased predator densities (Keith 1961, Johnson et al. 1989, Coates and Delehanty 2010), possibly paired with a lack of suitable nesting habitat on the landscape (Jokimäki and Huhta 2000, Evans 2004). The overall low nest success we observed may suggest turkeys are nesting on a predator-rich landscape.

Nest concealment, described as a measure of vegetation obstruction on the projected hatch date of each nest attempt, had no apparent effect on nest or female survival. Previous research has detailed the significance of understory conditions, such as vegetation height and stem density, to nest placement and nest success (Lehman et al. 2008, Fuller et al. 2013, Conley et al. 2015, Streich et al. 2015, Little et al. 2016), although there are notable inconsistencies among studies in regards to which vegetative characteristics, if any, most influence nest success or survival (Byrne and Chamberlain 2013, Yeldell et al. 2017). Regardless, trade-offs between nest and female survival may exist as nest concealment increases. For example, white-tailed ptarmigan nests placed in areas with increased cover were less likely to be depredated, but incubating adults were more vulnerable to mammalian predators (Wiebe and Martin 1998). Likewise, vegetation obstruction, as we measure it, may not be an important metric influencing nest or female survival (Lazarus and Porter 1985, Burk et al. 1990, Storaas and Wegge 1997, Thogmartin 1999).

Our findings suggest that female wild turkeys exhibit a gradient of incubation strategies geared towards prioritization of productivity or individual survival. Landscapes featuring an abundance of nest predators may favor longer incubation bouts (via reduced daily recess duration) and few daily unique recesses to reduce activity around the nest and increase nest attendance (Wiebe and Martin 1997, Coates and Delehanty 2008, Smith et al. 2012). Alternatively, if larger predators capable of taking females are abundant, incubating females likely benefit from taking few but significantly longer daily unique recesses (Conway and Martin 2000). In North America, predator richness increases at southern latitudes (Wilson 1974, Sandom et al. 2013), and predator guilds within the southeastern United States have changed over the course of the last half-century (Hill et al. 1987, Lovell et al. 1998). Given this increase in predator diversity, it may be challenging for turkeys to balance such opposing incubation strategies. Additionally, turkeys live in a stochastic environment and many predation events, particularly nest depredations, may be a result of opportunistic foraging (Storaas and Wegge 1997, Byrne and Chamberlain 2015). Therefore, it is plausible that turkeys have not yet developed an adequate ability to perceive predation risk. As predators continue to influence evolution of life-history traits by placing constraints on recess behaviors (Fontaine et al. 2007, Conway and Martin 2000), natural selection will begin to favor optimal incubation strategies that ensure future reproductive success. Future studies examining temporal variance in female incubation rhythms, spatial and temporal predation patterns during the nesting season, and plasticity of phenotypic traits (such as clutch and egg size) are necessary to further explore reproductive strategies within wild turkey populations.

ACKNOWLEDGEMENTS

We appreciate funding and logistical support provided by the Georgia Department of Natural Resources-Wildlife Resources Division, United States Forest Service, Oconee Rivers Audubon Society, Georgia Chapter of The Wildlife Society, and the Eatonton Beef Research Unit. We thank N. Bakner, A. Gerritts, K. McClearn, N. Yeldell, C. Wakefield, P. Wightman, and J. Wood for assistance with data collection, along with various field technicians. We are especially grateful for the many private landowners who graciously granted access to their property.

LITERATURE CITED

Afton, A. D. 1980. Factors affecting incubation rhythms of northern shovelers. Condor 82:132-137.

Audzijonyte, A. and S. A. Richards. 2018. The energetic cost of reproduction and its effect on optimal life-history strategies. The American Naturalist 192:1-24.

Avise, J. C. 1996. Three fundamental contributions of molecular genetics to avian ecology and evolution. Ibis 138:16-25.

Badyaev, A. V., W. J. Etges, and T. E. Martin. 1996. Ecological and behavioral correlates of variation in seasonal home ranges of wild turkeys. Journal of Wildlife Management 60:154-164.

Bakner, N. W. 2018. Does incubation recess behavior influence nest success of upland ground-nesting birds? Thesis, Louisiana State University, Baton Rouge, Louisiana, USA.

Bergerud, A. T. and M. W. Gratson. 1988. Survival and breeding strategies of grouse. Pages 473-577 *in* A. T. Bergerud and M. W. Gratson, editors. University of Minnesota Press, Minneapolis, Minnesota, USA.

Blomberg, E. J., D. Gibson, and J. S. Sedinger. 2015. Biases in nest survival associated with choice of exposure period: a case study in North American upland game birds. The Condor 117:577-588.

Boggs, C. L. 1992. Resource allocation: exploring connections between foraging and life history. Functional Ecology 6:508-518.

Burk, J. D., D. R. Smith, G. A. Hurst, B. D. Leopold, and M. A. Melchiors. 1990. Wild turkey use of loblolly pine plantations for nesting and brood rearing. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 44:163-170.

Byrne, M. E. and M. J. Chamberlain. 2013. Nesting ecology of wild turkeys in a bottomland hardwood forest. American Midland Naturalist 170:95–110.

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

Chamberlain, M. J. and B. D. Leopold. 1999. Dietary patterns of sympatric bobcats and coyotes in central Mississippi. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 53:204-219.

Clutton-Brock, T. H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Illinois, USA.

Coates, P. S. and D. J. Delehanty. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. The Condor 110:627-638.

Coates, P. S. and D. J. Delehanty. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management 74:240-248.

Cockburn, A. 2006. Prevalence of different modes of parental care in birds. Proceedings of the Royal Society B 273:1375-1383.

Cohen, B. S., T. J. Prebyl, B. A. Collier, and M. J. Chamberlain. 2018. Home range estimator method and GPS fix schedule affect selection inferences for wild turkeys. Wildlife Society Bulletin 42:150−159.

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. Journal of Theoretical Biology 12:119-129.

Cohen, D. 1967. Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. Journal of Theoretical Biology 16:1-14.

Collier, B. A., K. B. Melton, J. B. Hardin, N. J. Silvy, and M. J. Peterson. 2009. Impact of reproductive effort on survival of Rio Grande wild turkey *Meleagris gallopavo intermedia* hens in Texas. Wildlife Biology 15:370-379.

Collier, B. A., N. Fyffe, A. Smallwood, B. Oleson, N. W. Bakner, J. R. Heffelfinger, and M. J. Chamberlain. 2019. Reproductive ecology of Goulds wild turkeys in Arizona. Wilson Journal of Ornithology, In Press.

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

Conley, M. D., N. A. Yeldell, M. J. Chamberlain, and B. A. Collier. 2016. Do movement behaviors identify reproductive habitat sampling for wild turkeys? Ecology and Evolution 6:7103-7112.

Conway, C. J. and T. E. Martin. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. Evolution 54:670-685.

Criscuolo, F., M. Gauthier-Clerc, G. W. Gabrielsen, and Y. L. Maho. 2000. Recess behaviour of the incubating common eider *Somateria mollissima*. Polar Biology 23:571-574.

Danforth, B. N. 1999. Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*. Proceedings of the Royal Society of London 266:1985-1994.

Dickson, J. G. 1992. Introduction. Pages 2-5 *in* J. G. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27-46.

Dreibelbis, J. Z, K. B. Melton, R. Aguirre, B. A. Collier, J. Hardin, N. J. Silvy, and M. J. Peterson. 2008. Predation of Rio Grande wild turkey nests on the Edwards Plateau, Texas. The Wilson Journal of Ornithology 120:906-910.

Drent, R. H. 1975. Incubation. Pages 333-420 *in* D. S. Farner and J. R. King, editors. Avian biology, volume 5. Academic Press, New York, New York, USA.

Dudko, J. E., P. S. Coates, and D. J. Delehanty. 2019. Movements of female sage grouse *Centrocercus urophasianus* during incubation recess. Ibis 161:222-229.

Eggers, S., M. Griesser, and J. Ekman. 2005. Predator-induced plasticity in nest visitation rates in the Siberian jay (*Perisoreus infaustus*). Behavioral Ecology 16:309-315.

Einum, S. and I. A. Fleming. 2004. Environmental unpredictability and offspring size: conservative versus diversified bet-hedging. Evolutionary Ecology Research 6:443-455.

Evans, K. L. 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1-13.

Fontaine, J. J., M. Martel, H. M. Markland, A. M. Niklison, K. L. Decker, and T. E. Martin. Testing ecological and behavioral correlates of nest predation. Oikos 116:1887-1894.

Fontaine, J. J. and T. E. Martin. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. Ecology Letters 9:428-434.

Fuller, A. K., S. M. Spohr, D. J. Harrison, and F. A. Servello. 2013. Nest survival of wild turkeys *Meleagris gallopavo silvestris* in a mixed-use landscape: influences at nest site and patch scales. Wildlife Biology 19:138–146.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis (2nd ed.). Chapman & Hall, Boca Raton, Florida, USA.

Gelman, A. and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457-511.

Ghalambor, C. K. and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292:494-497.

Green, H. E. 1982. Reproductive behavior of female wild turkeys in northern Lower Michigan. Journal of Wildlife Management 46:1065-1071.

Guthrie, J. D., M. E. Byrne, J. B. Hardin, C. O. Kochanny, K. L. Skow, R. T. Snelgrove, M. J. Butler, M. J. Peterson, M. J. Chamberlain, and B. A. Collier. 2011. Evaluation of a global positioning system backpack transmitter for wild turkey research. Journal of Wildlife Management 75:539–547.

Haftorn, S. 1988. Incubating female passerines do not let the egg temperature fall below the ‘physiological zero temperature’ during their absences from the nest. Ornis Scandinavica (Scandinavian Journal of Ornithology) 19:97-110.

Hakkarainen, H., I. Yli-Tuomi, E. Korpimäki, and R. Ydenberg. 2002. Provisioning response to manipulation of apparent predation danger by parental pied flycatchers. Ornis Fennica 79:139-144.

Healy, W. M. 1992. Behavior. Pages 46-65 *in* J. G. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Hill, E. P., P. W. Sumner, and J. B. Wooding. 1987. Human influences on range expansion of coyotes in the southeast. Wildlife Society Bulletin 15:521-524.

Hubbard, M. W., D. L. Garner, and E. E. Klass. 1999. Factors influencing wild turkey hen survival in southcentral Iowa. Journal of Wildlife Management 63:731–738.

Isaksson, D., J. Wallander, and M. Larsson. 2007. Managing predation on ground-nesting birds: the effectiveness of nest exclosures. Biological Conservation 136:136-142.

Johnsgard, P. A. 1983. The grouse of the world. University of Nebraska Press, Lincoln, Nebraska, USA.

Johnson, D. H., A. B. Sargeant, and R. J. Greenwood. 1989. Importance of individual species of predators on nesting success of ducks in the Canadian Prairie Pothole Region. Canadian Journal of Zoology 67:291-297.

Jokimäki, J. and E. Huhta. 2000. Artificial nest predation and abundance of birds along an urban gradient. The Condor 102:838-847.

Jones, G. 1989. Optimizing time off the nest during incubation in female swallows (*Hirundo rustica* [L.]). Functional Ecology 3:303-309.

Keith, L. B. 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. Wildlife Monographs 6:1-88.

Kie, J. G. 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. Journal of Mammalogy 80:1114-1129.

Klett, A. T. and D. H. Johnson. 1982. Variability in nest survival rates and implications to nesting studies. The Auk 99:77-87.

Kranstauber, B., M. Smolla, and A. K. Scharf. 2017. Package 'move': visualizing and analyzing animal track data. <http://computational-ecology.com/main-move.html> Accessed 15 January 2019.

Kranstauber, B., R. Kays, S. D. LaPoint, M. Wikelski, and K. Safi. 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. Journal of Animal Ecology 81:738-746.

LaManna, J. A. and T. E. Martin. 2016. Costs of fear: behavioural and life-history responses to risk and their demographic consequences vary across species. Ecology Letters 19:403-413.

Lazarus, J. E. and W. F. Porter. 1985. Nest habitat selection by wild turkeys in Minnesota. National Wild Turkey Symposium 5:67-82.

Lecomte, N., G. Gauthier, and J. Giroux. 2009. A link between water availability and nesting success mediated by predator-prey interactions in the Arctic. Ecology 90:465-475.

Lehman, C. P., M. A. Rumble, L. D. Flake, and D. J. Thompson. 2008. Merriam’s turkey nest survival and factors affecting nest predation by mammals. Journal of Wildlife Management 72:1765-1774.

Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485-513.

Little, A. R., N. P. Nibbelink, M. J. Chamberlain, L. M. Conner, and R. J. Warren. 2016. Eastern wild turkey nest site selection in two frequently burned pine savannas. Ecological Processes 5:1-10.

Lockwood, D. R. and D. H. Sutcliffe. 1985. Distribution, mortality, and reproduction of Merriam’s turkey in New Mexico. National Wild Turkey Symposium 5:309-316.

Lovell, C. D., B. D. Leopold, C. C. Shropshire. 1998. Trends in Mississippi predator populations, 1980-1995. Wildlife Society Bulletin 26:552-556.

Lyon, B. E. and R. D. Montgomerie. 1985. Incubation feeding in snow buntings: female manipulation or indirect male parental care? Behavioral Ecology and Sociobiology 17:279-284.

MacDonald, E. C., A. F. Camfield, J. E. Jankowski, and K. Martin. 2013. Extended incubation recesses by alpine-breeding Horned Larks: a strategy for dealing with inclement weather? Journal of Field Ornithology 84:58-68.

Martin, J. A., S. M. Juhan, Jr., W. E. Palmer, and J. P. Carroll. 2015. Incubation and predation ecology of wild turkey nests: a cautionary case study regarding video camera surveillance. National Wild Turkey Symposium 11:295-301.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101-127.

Martin, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. Proceedings of the Royal Society of London. Series B: Biological Sciences 269:309-316.

Martindale, S. 1982. Nest defense and central place foraging: a model and experiment. Behavioral Ecology and Sociobiology 10:85-89.

Marzluff, J. M. 1985. Behavior at a pinyon jay nest in response to predation. The Condor 87:559-561.

Matysioková, B. and V. Remeš. 2018. Evolution of parental activity at the nest is shaped by the risk of nest predation and ambient temperature across bird species. Evolution 72:2214-2224.

McConnell, M. D., A. P. Monroe, L. W. Burger, Jr., and J. A. Martin. 2017. Timing of nest vegetation measurement may obscure adaptive significance of nest-site characteristics: A simulation study. Ecology and Evolution 7:1259-1270.

Miller, J. E. and B. D. Leopold. 1992. Population influences: Predators. Pages 119-128 *in* J. G. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Milonoff, M. 1989. Can nest predation limit clutch size in precocial birds? Oikos 55:424-427.

Moore, W. F., J. C. Kilgo, W. D. Carlisle, D. C. Guynn, and J. R. Davis. 2010. Nesting success, nest site characteristics, and survival of wild turkey hens in South Carolina. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 64:24–29.

Munkebye, E., H. C. Pedersen, J. B. Steen, and H. Brøseth. 2003. Predation of eggs and incubating females in willow ptarmigan *Lagopus l. lagopus*. Fauna Norvegica 23:1-8.

Myrberget, S. 1988. Demography of an island population of willow ptarmigan in northern Norway. Pages 379-419 *in* A. T. Bergerud and M. W. Gratson, editors. University of Minnesota Press, Minneapolis, Minnesota, USA.

Nagy, L. R. and R. T. Holmes. 2004. Factors influencing fecundity in migratory songbirds: is nest predation the most important? Journal of Avian Biology 35:487-491.

Nguyen, L. P., J. Hamr, and G. H. Parker. 2004. Nest site characteristics of eastern wild turkeys in central Ontario. Northeastern Naturalist 11:255-260.

Norman, G. W., J. C. Pack, C. I. Taylor, D. E. Steffen, and K. H. Pollock. 2001. Reproduction of eastern wild turkeys in Virginia and West Virginia. Journal of Wildlife Management 65:1-9.

Palmer, W. E., S. R. Priest, R. S. Seiss, P. S. Phalen, and G. A. Hurst. 1993. Reproductive effort and success in a declining wild turkey population. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 47:138–147.

Patrick, S. C. and H. Weimerskirch. 2017. Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference. Journal of Animal Ecology 86:674-682.

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

Philippi, T. and J. Seger. 1989. Hedging one’s evolutionary bets, revisited. Trends in Ecology and Evolution 4:41-44.

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

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295-297.

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

Royle, J. A. and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, New York, New York, USA.

Rumble, M. A. and R. A. Hodorff. 1993. Nesting ecology of Merriam's turkeys in the Black Hills, South Dakota. Journal of Wildlife Management 57:789-801.

Sandom, C., L. Dalby, C. Fløjgaard, W. D. Kissling, J. Lenoir, B. Sandel, K. Trøjelsgaard, R. Ejrnæs, and J. Svenning. 2013. Mammal predator and prey species richness are strongly linked at macroscales. Ecology 94:1112-1122.

Sæther, B. E. and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 82:642-653.

Shaffer, T. L. and F. R. Thompson III. 2007. Making meaningful estimates of nest survival with model-based methods. Studies in Avian Biology 34:84-95.

Simovich, M. A. and S. A. Hathaway. 1997. Diversified bet-hedging as a reproductive strategy of some ephemeral pool anostracans (Branchiopoda). Journal of Crustacean Biology 17:38-44.

Smith, P. A., I. Tulp, H. Schekkerman, H. G. Gilchrist, and M. R. Forbes. 2012. Shorebird incubation behaviour and its influence on the risk of nest predation. Animal Behaviour 84:835-842.

Spaans, B., K. van't Hoff, W. van der Veer, and B. S. Ebbinge. 2007. The significance of female body stores for egg laying and incubation in dark-bellied brent geese *Branta bernicla bernicla*. Ardea 95:3-15.

Storaas, T. and P. Wagge. 1997. Relationships between patterns of incubation and predation in sympatric capercaillie *Tetrao urogallus* and black grouse *T. tetrix*. Wildlife Biology 3:163-167.

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

Thogmartin, W. E. 1999. Landscape attributes and nest-site selection in wild turkeys. Auk 116:912–923.

Vangilder, L. D. and E. W. Kurzejeski. 1995. Population ecology of the eastern wild turkey in northern Missouri. Wildlife Monographs 130:3-50.

Weathers, W. W. and K. A. Sullivan. 1989. Nest attentiveness and egg temperature in the yellow-eyed junco. The Condor 91:628-633.

Wiebe, K. L. and K. Martin. 1997. Effects of predation, body condition and temperature on incubation rhythms of white-tailed ptarmigan *Lagopus leucurus*. Wildlife Biology 3:219-227.

Wiebe, K. L. and K. Martin. 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. Animal Behaviour 56:1137-1144.

Wiebe, K. L. and K. Martin. 2000. The use of incubation behavior to adjust avian reproductive costs after egg laying. Behavioral Ecology and Sociobiology 48:463-470.

Wightman, P. H., J. Cantrell, C. Ruth, M. E. Byrne, M. J. Chamberlain, and B. A. Collier. 2018*a*. Impact of supplemental feeding for northern bobwhite on movement ecology of

Eastern wild turkeys in South Carolina. Journal of the Southeastern Association of Fish and Wildlife Agencies. 5:114-124.

Wightman, P. H., J. C. Kilgo, M. Vukovich, J. R. Cantrell, C. R. Ruth, B. S. Cohen, M. J. Chamberlain, and B. A. Collier. 2018*b*. Gobbling chronology of Eastern wild turkeys in South Carolina. Journal of Wildlife Management 83:325-333.

Williams, L. E., Jr., D. H. Austin, T. E. Peoples, and R. W. Phillips. 1971. Laying data and nesting behavior of wild turkeys. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 25:90-106.

Wilson, J. W. III. 1974. Analytical zoogeography of North American mammals. Evolution 28:124-140.

Wilson, S., K. Martin, and S. J. Hannon. 2007. Nest survival patterns in willow ptarmigan: influence of time, nesting stage, and female characteristics. The Condor 109:377-388.

Wood, J. D., B. S. Cohen, T. J. Prebyl, L. M. Connor, B. A. Collier, and M. J. Chamberlain. 2018. Time-since-fire and stand seral stage affect habitat selection of eastern wild turkeys in a managed longleaf pine ecosystem. Forest Ecology and Management 411:203-212.

Yeldell, N. A., B. S. Cohen, A. R. Little, B. A. Collier, and M. J. Chamberlain. 2017. Nest site selection and nest survival of eastern wild turkeys in a pyric landscape. Journal of Wildlife Management 81:1073-1083.

Yoder, J. M., E. A. Marschall, D. A. Swanson. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. Behavioral Ecology 15:469-476.

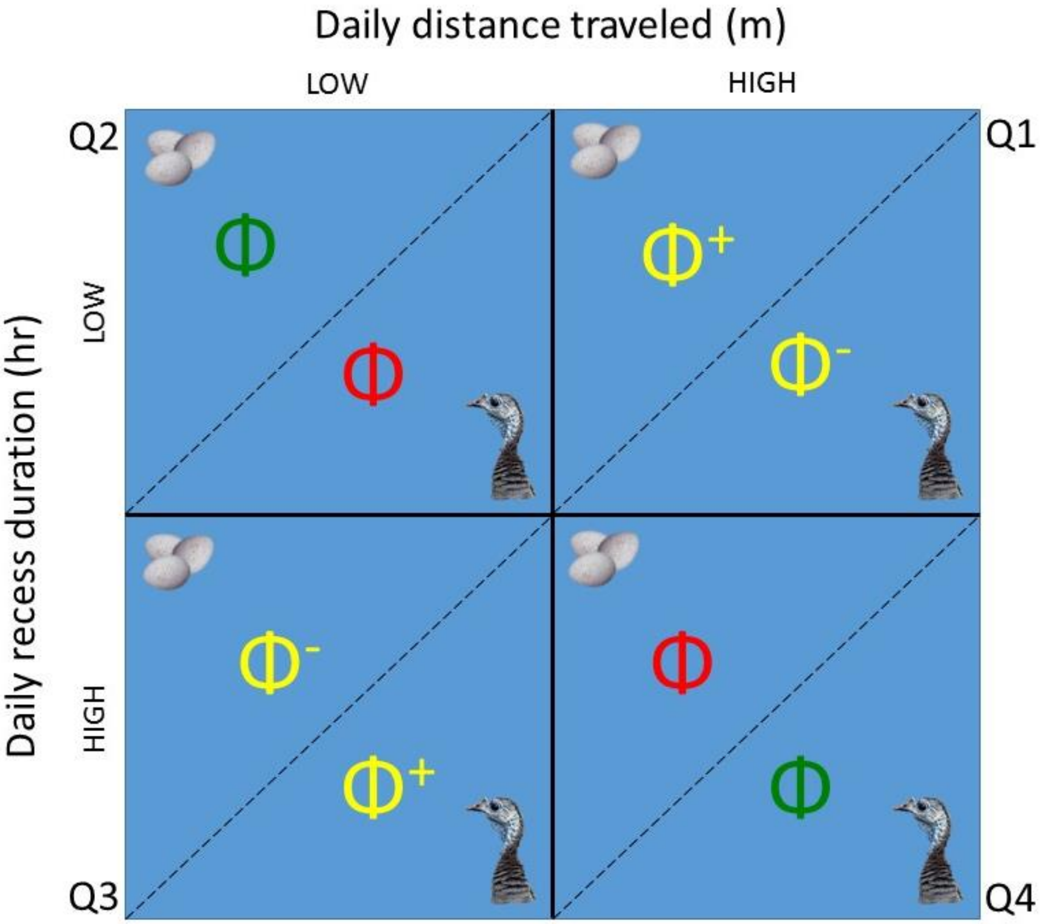

Figure 2.1. Confusion matrix illustrating predicted effects of daily distance traveled (m) and daily recess duration (hr) on survival of nests and individual female eastern wild turkeys (*Meleagris gallopavo silvestris*). Green Φ represents a high survival probability under the specified parameter intensities, red Φ denotes a low survival probability, and yellow Φ corresponds to an intermediate survival probability.

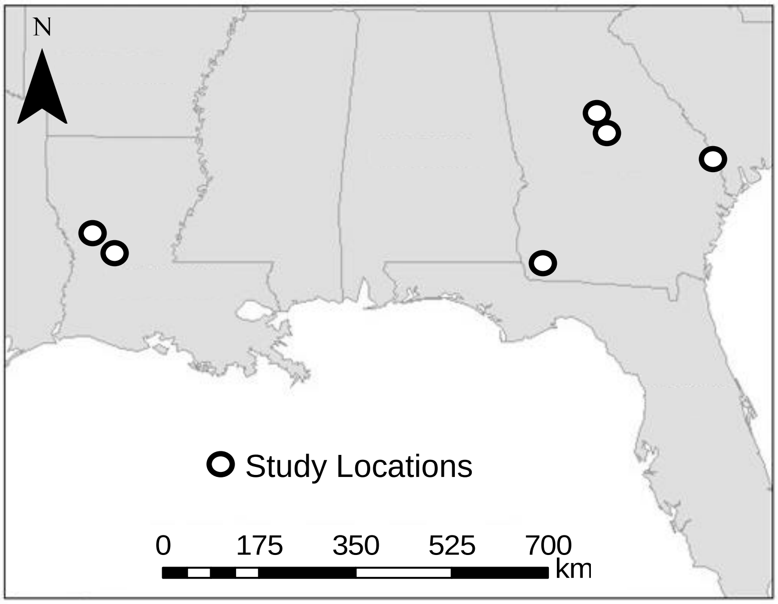

Figure 2.2. Map of study sites in the southeastern United States where incubation recess behaviors were evaluated for female eastern wild turkeys (*Meleagris gallopavo silvestris*) during 2014-2018. The symbol in South Carolina represents 3 study sites, collectively known as the Webb WMA Complex.

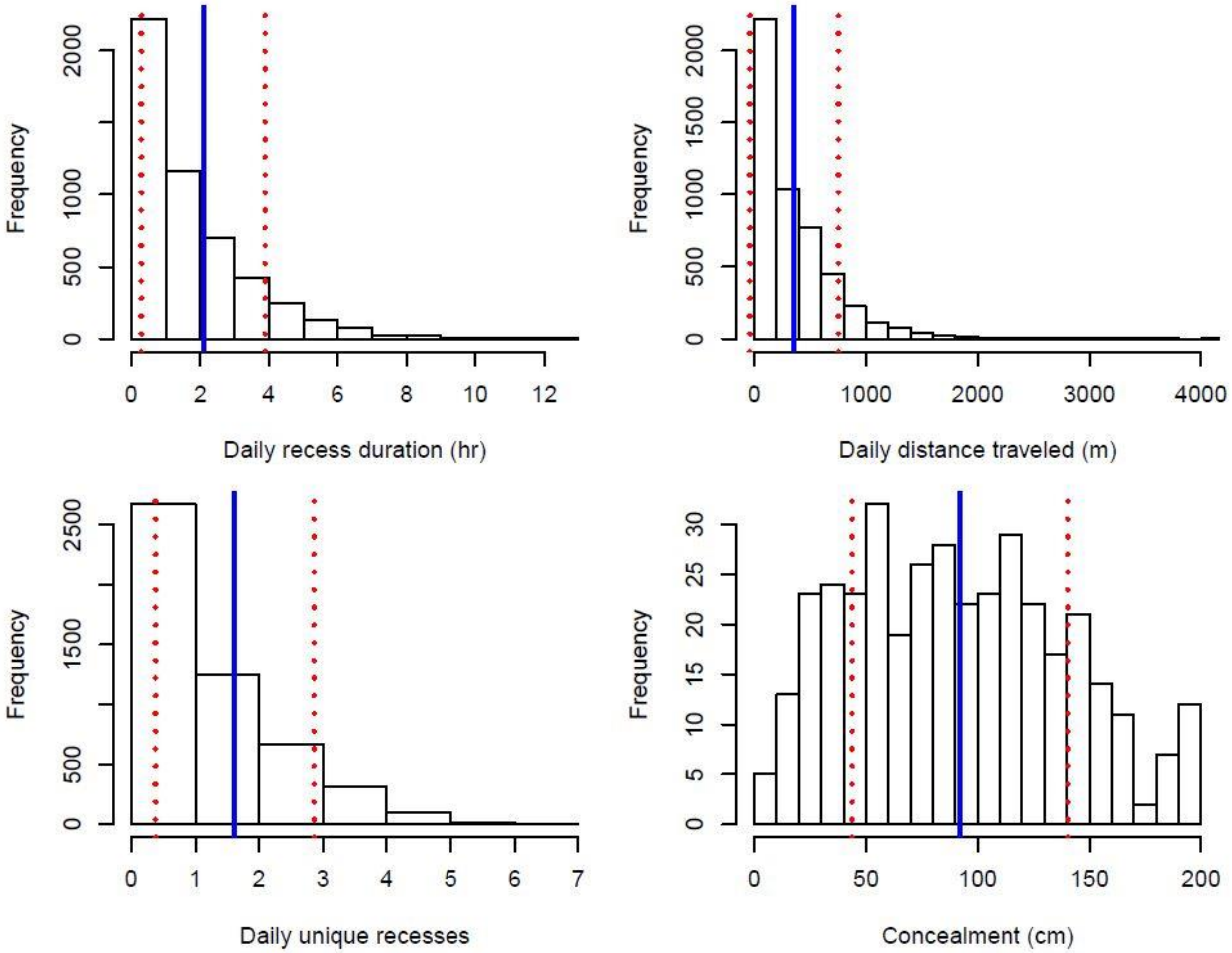

Figure 2.3. Histograms illustrating the range of observed values for four covariates used to model nest and female eastern wild turkey (*Meleagris gallopavo silvestris*) survival. Solid blue lines represent $\bar{x}$ and dashed red lines indicate $\pm$ 1 standard deviation. Females spent 0-13 hours off the nest each day ($\bar{x}$ = 2.09, SD = 1.80), took 0-7 daily unique recesses ($\bar{x}$ = 1.62, SD = 1.24), and traveled 0-4,103 m in a day ($\bar{x}$ = 357.63 m, SD = 396.58). Values of nest concealment ranged from 8.75-200 cm ($\bar{x}$ = 92.5 cm, SD = 47).

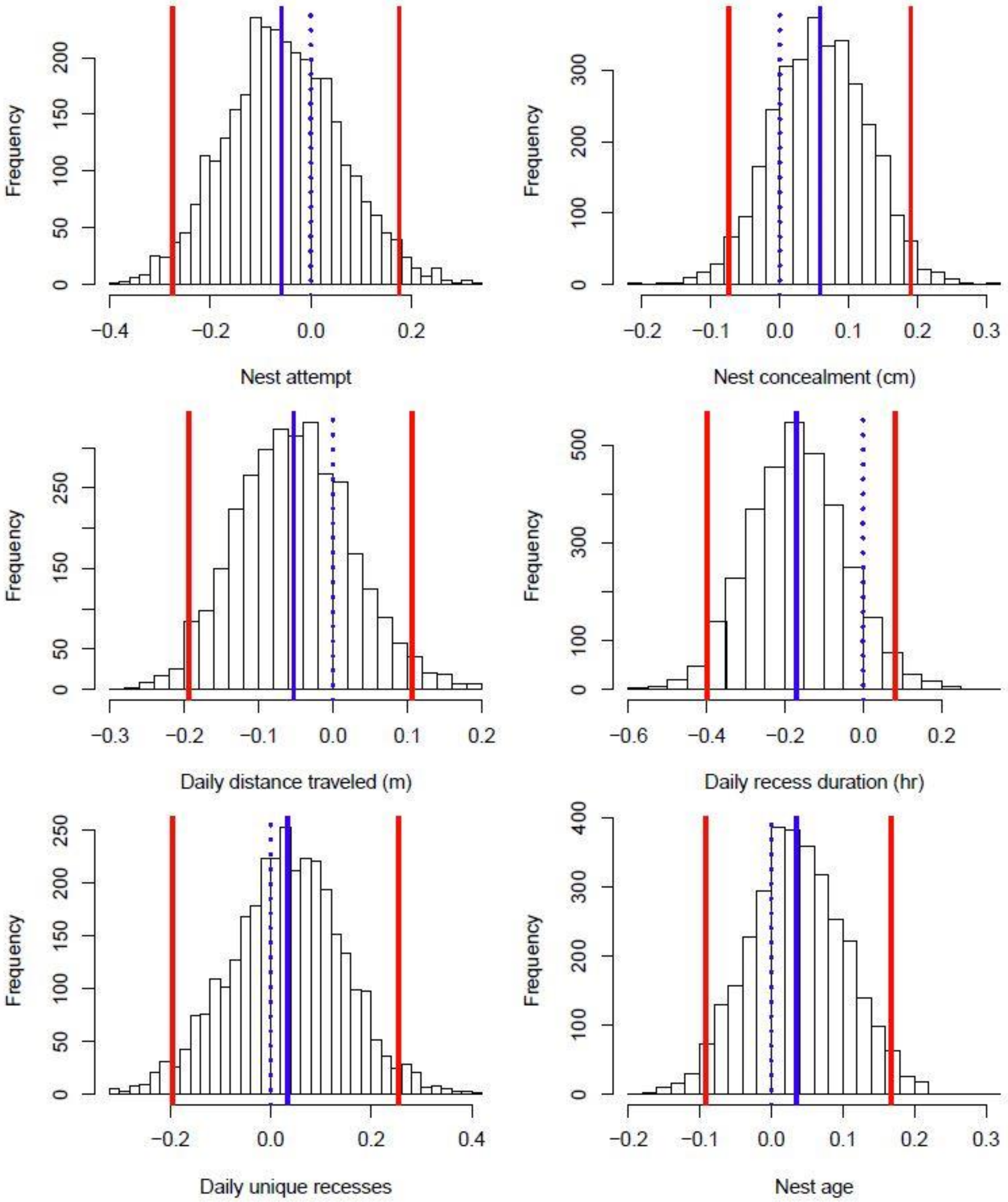

Figure 2.4. Posterior distributions for covariates used to model daily survival for eastern wild turkey (*Meleagris gallopavo silvestris*) nests. Solid blue lines denote μ, red lines represent 95% credible intervals, and dashed blue lines indicate 0.

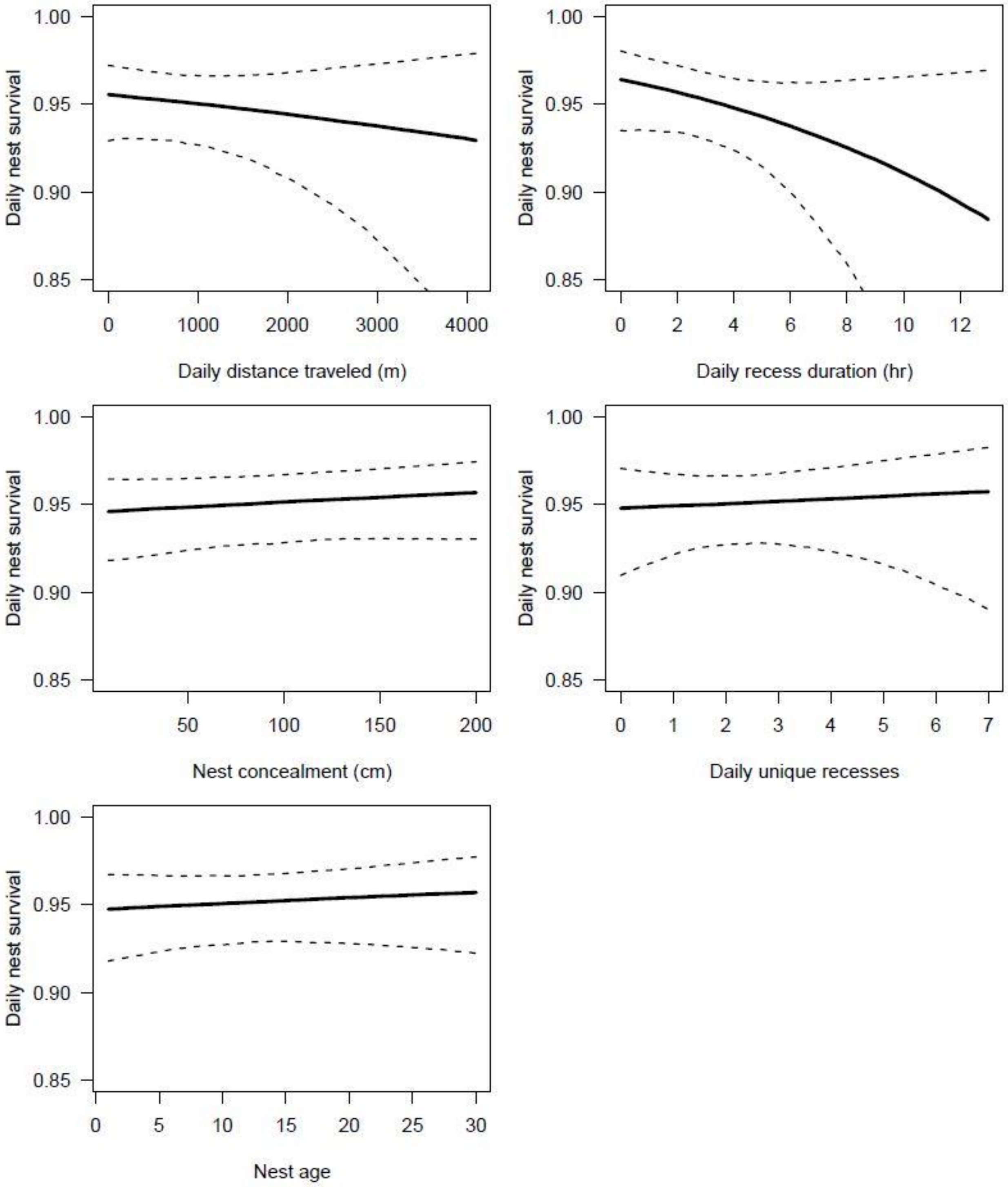

Figure 2.5. Predicted effects of model covariates on daily survival probabilities for eastern wild turkey (*Meleagris gallopavo silvestris*) nests.

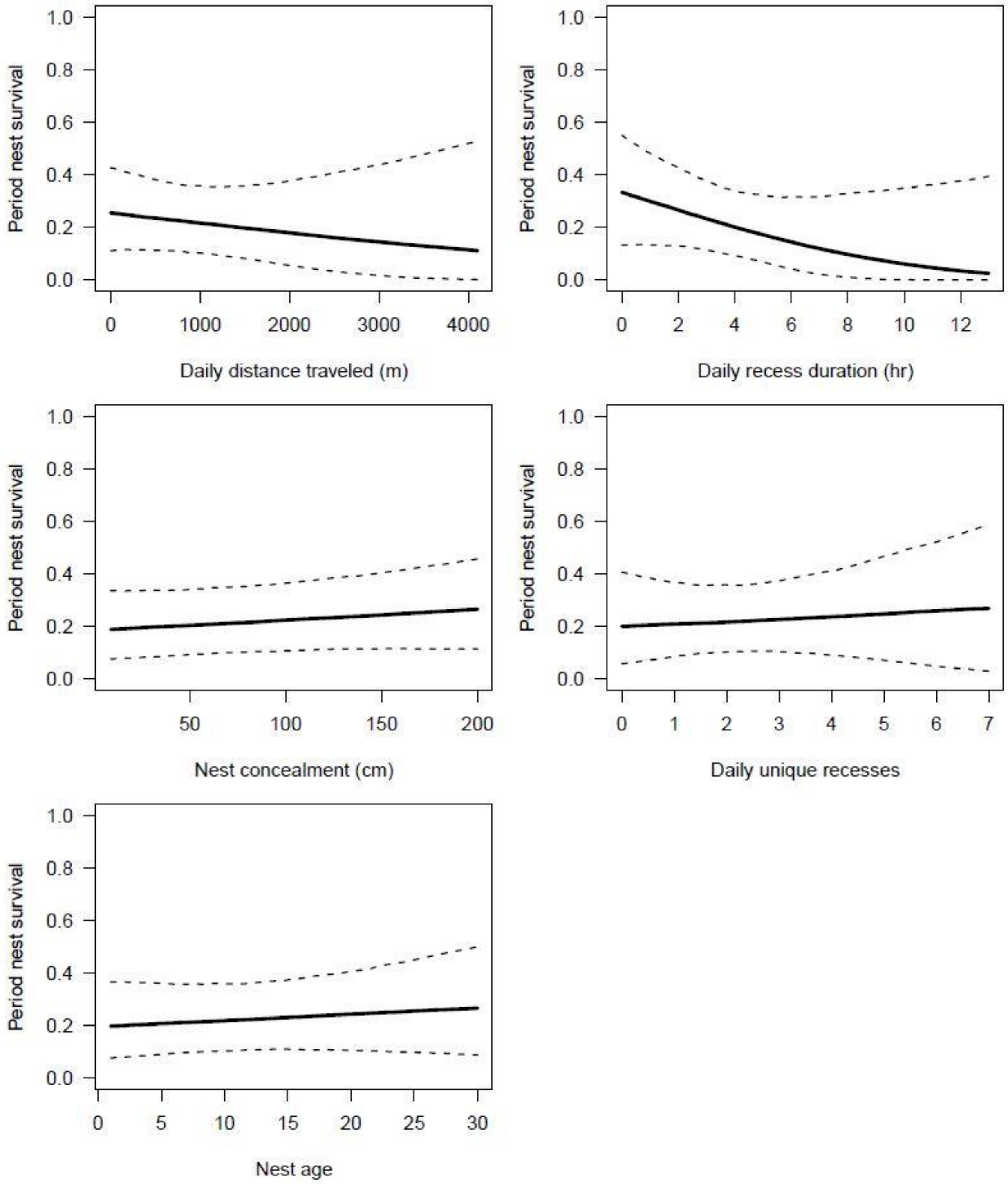

Figure 2.6. Predicted effects of model covariates on period (30 days) survival probabilities for eastern wild turkey (*Meleagris gallopavo silvestris*) nests.

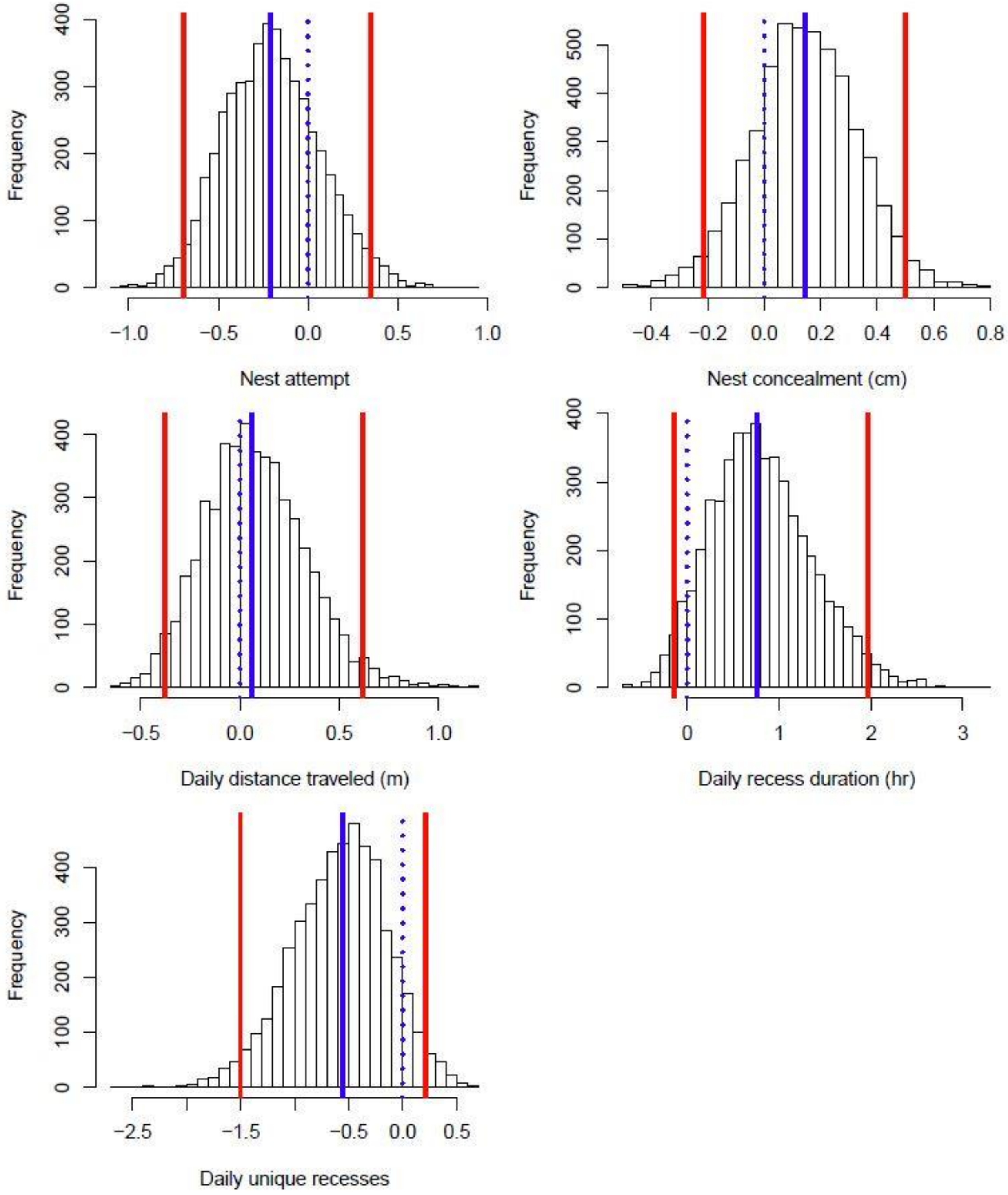

Figure 2.7. Posterior distributions for covariates used to model daily survival for female eastern wild turkeys (*Meleagris gallopavo silvestris*). Solid blue lines denote μ, red lines represent 95% credible intervals, and dashed blue lines indicate 0.

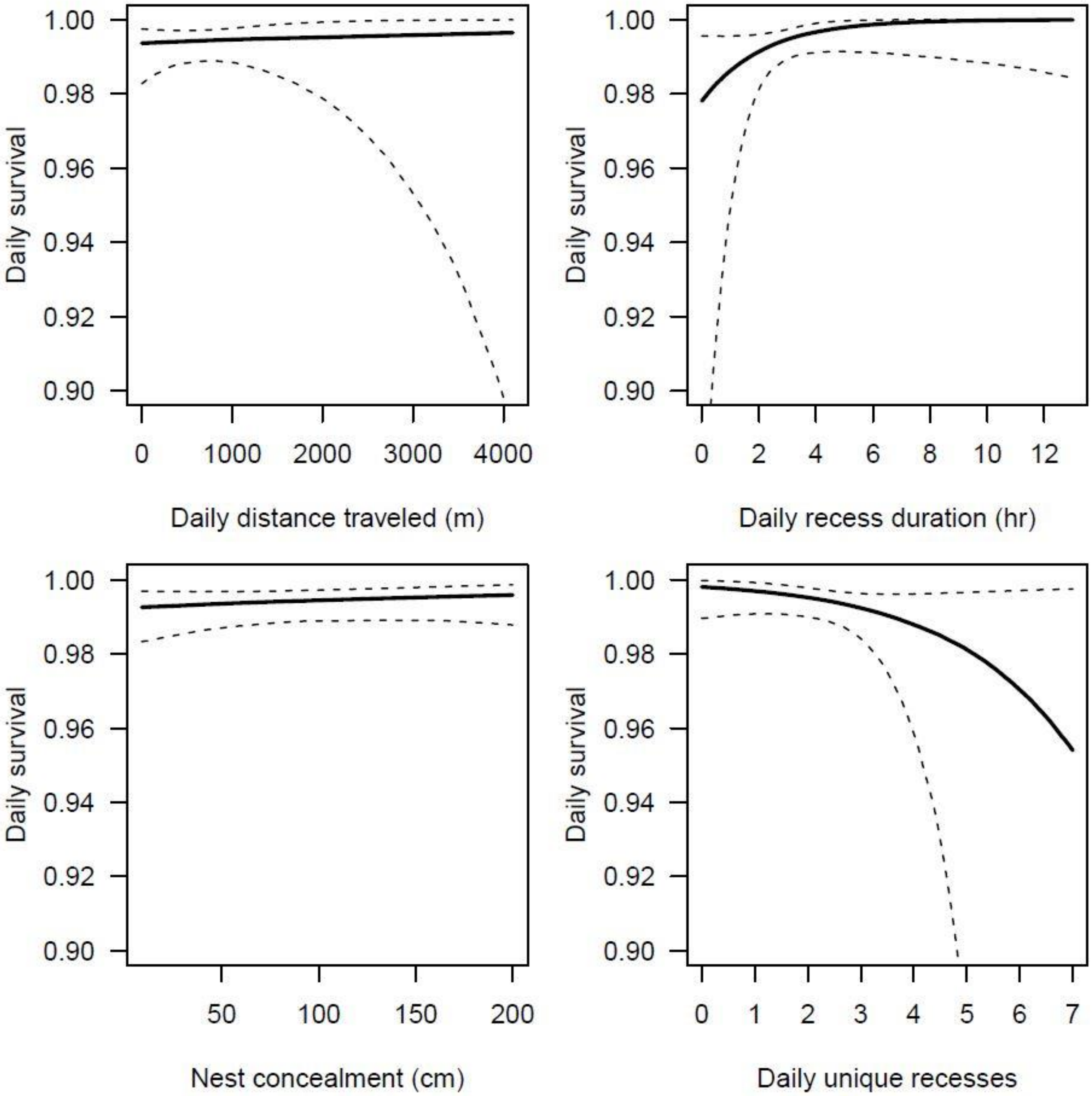

Figure 2.8. Predicted effects of model covariates on daily survival probabilities for female eastern wild turkeys (*Meleagris gallopavo silvestris*).

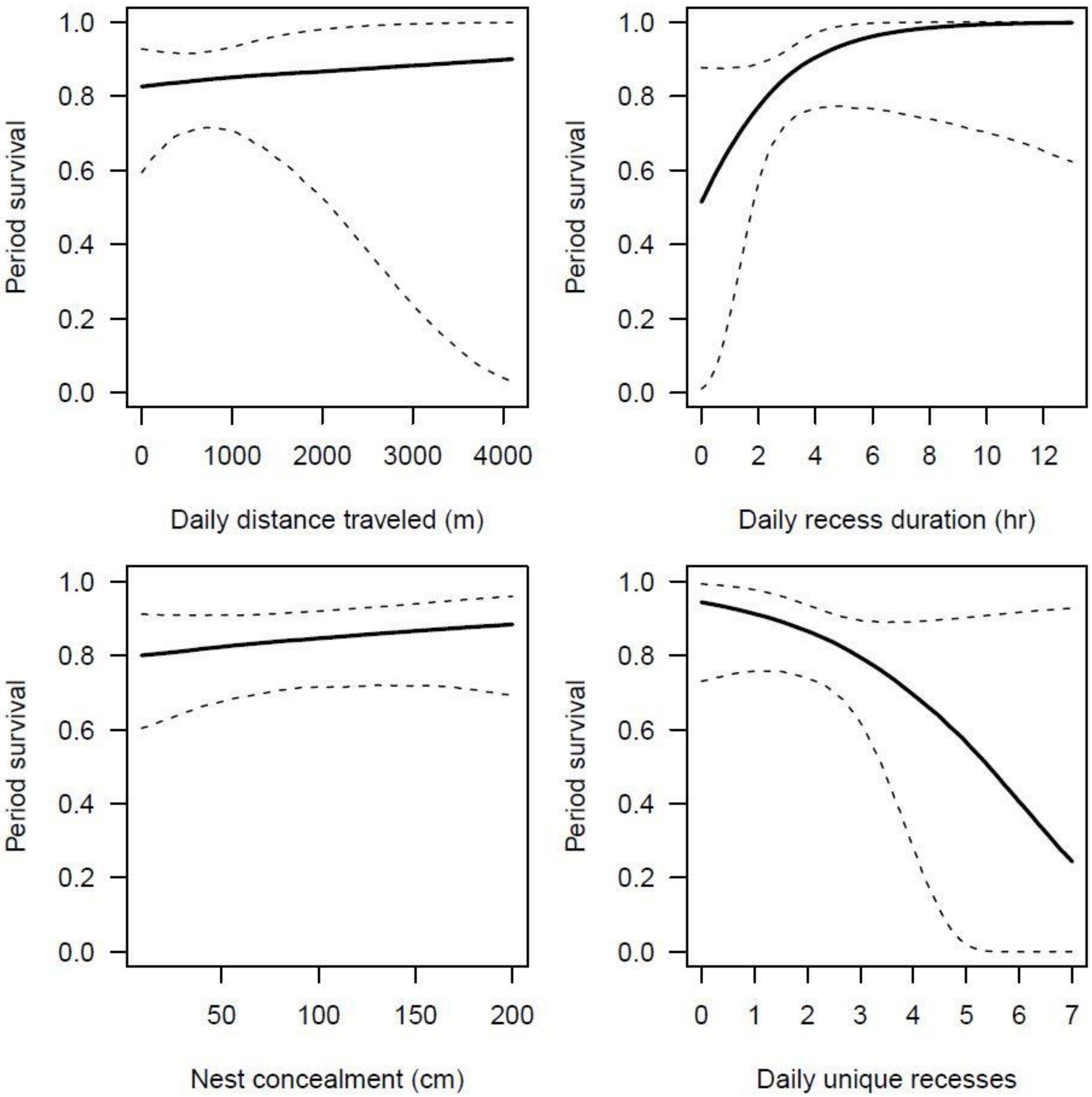

Figure 2.9. Predicted effects of model covariates on period (30 days) survival probabilities for female eastern wild turkeys (*Meleagris gallopavo silvestris*).

Table 2.1. Posterior means and 95% credible intervals for covariates used to model daily survival for eastern wild turkey (*Meleagris gallopavo silvestris*) nests. Means above 0 positively influence daily nest survival whereas means below 0 negatively influence daily nest survival.

Survival covariates	Credible Intervals				
	0.025	0.250	0.500	0.750	0.975
Intercept (β_0)	2.501	2.863	3.027	3.182	3.514
Nest attempt (β_1)	-0.275	-0.130	-0.059	0.022	0.176
Concealment (β_2)	-0.075	0.011	0.059	0.107	0.190
Distance traveled (β_3)	-0.193	-0.105	-0.053	-0.001	0.106
Recess duration (β_4)	-0.397	-0.251	-0.171	-0.087	0.082
Unique recesses (β_5)	-0.196	-0.040	0.033	0.108	0.255
Nest age (β_6)	-0.092	-0.008	0.035	0.081	0.167

Table 2.2. Posterior means and 95% credible intervals for covariates used to model daily survival for female eastern wild turkeys (*Meleagris gallopavo silvestris*). Means above 0 positively influence daily female survival whereas means below 0 negatively influence daily female survival.

Survival covariates	Credible Intervals				
	0.025	0.250	0.500	0.750	0.975
Intercept (β_0)	4.398	5.037	5.372	5.696	6.339
Nest attempt (β_1)	-0.692	-0.390	-0.208	-0.024	0.350
Concealment (β_2)	-0.215	0.025	0.144	0.269	0.498
Distance traveled (β_3)	-0.380	-0.098	0.061	0.238	0.618
Recess duration (β_4)	-0.142	0.421	0.762	1.157	1.962
Unique recesses (β_5)	-1.499	-0.872	-0.554	-0.283	0.215

CHAPTER 3

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

My findings suggest that of the incubation covariates I modeled, daily recess duration was the most important factor influencing daily and period nest survival rates of female wild turkeys (hereafter, turkeys). Recess duration negatively influenced nest survival. Daily distance traveled may also negatively impact nest survival, although the predicted effects of this parameter were less pronounced than those of recess duration. There were no biologically significant effects of nest attempt, nest age, nest concealment, or number of recesses on daily or period nest survival.

My findings also suggest that of the incubation covariates I modeled, recess duration and number of recesses were the most important factors influencing female turkey survival. Recess duration positively influenced female survival, whereas number of recesses negatively influenced female survival. There were no biologically significant effects of nest attempt, nest concealment, or daily distance traveled on daily or period female survival rates.

My findings suggest that understanding incubation recess behaviors can aid wildlife professionals and landowners in making informed management decisions for gamebirds and species of conservation concern. Fine-scale movement data obtained from incubating females convey important information regarding space use during reproduction and the effects of environmental variables on daily incubation rhythms. I recommend the continued use of GPS transmitters to collect recess data from nesting birds in order to better inform management decisions relating to habitat manipulation or predator control. Future studies should examine temporal variance in female incubation rhythms, spatial and temporal predation patterns during the nesting season, and plasticity of phenotypic traits (such as clutch and egg size) to further explore reproductive strategies within wild turkey populations.

APPENDIX A

Table 1. Nesting ecology of female eastern wild turkeys (*Meleagris gallopavo silvestris*) at Cedar Creek (CC) and B. F. Grant (BFG) Wildlife Management Areas and surrounding lands in central Georgia, USA, 2017 and 2018.

Year	Site	*n*[a]	% 1st nest attempt (*n*)[b]	% 1st attempt success (*n*)[c]	% 2nd nest attempt (*n*)[d]	% 2nd attempt success (*n*)[e]	% 3rd nest attempt (*n*)[f]	% 3rd attempt success (*n*)[g]	% 4th nest attempt (*n*)[h]	% 4th attempt success (*n*)[i]
2017	CC	31	90 (28)	14 (4)	67 (10)	10 (1)	33 (3)	33 (1)	100 (1)	0
	BFG	11	91 (10)	10 (1)	50 (4)	0 (0)	67 (2)	0	0	0
2018	CC	13	100 (13)	15 (2)	75 (6)	17 (1)	50 (2)	0	0	0
	BFG	27	100 (27)	37 (10)	46 (6)	33 (2)	0	0	0	0
Pooled sites and years		82	95 (78)	22 (17)	59 (26)	15 (4)	35 (7)	14 (1)	50 (1)	0

[a] Number of radio-tagged females monitored from the earliest known nesting attempt (2017: 20 March; 2018: 15 March).

[b] Number of females successfully laying a clutch and establishing continuous incubation of ≥1 nest.

[c] Number of first nest attempts hatching ≥1 live poult.

[d] Number of females initiating and incubating a second nest following the loss of a first nest or brood within 28 days post-hatch.

[e] Number of second nest attempts hatching ≥1 live poult.

[f] Number of females initiating and incubating a third nest following the loss of a second nest or brood within 28 days post-hatch.

[g] Number of third nest attempts hatching ≥1 live poult.

[h] Number of females initiating and incubating a fourth nest following the loss of a third nest or brood within 28 days post-hatch.

[i] Number of fourth nest attempts hatching ≥1 live poult.

APPENDIX B

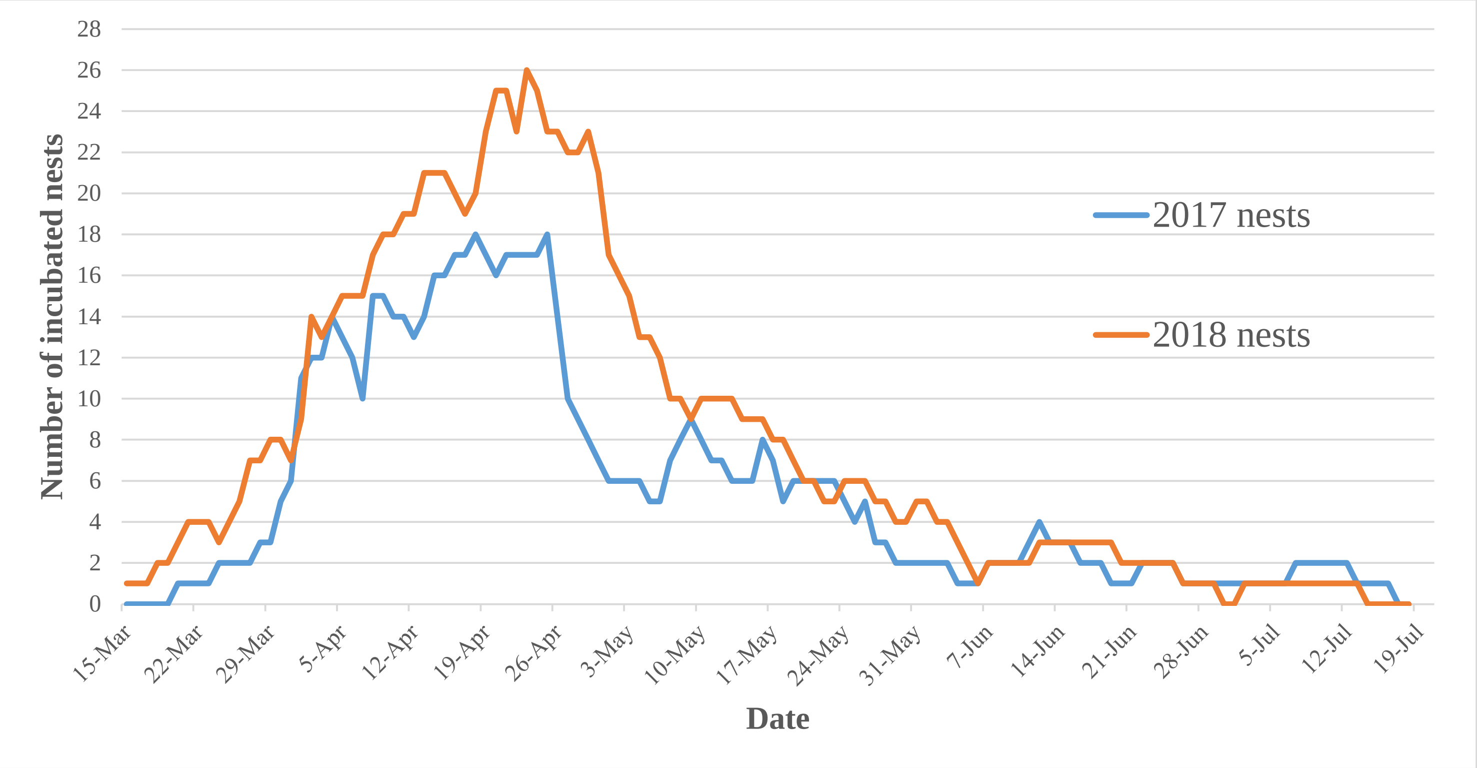

Figure 1. Incubation chronology of female eastern wild turkeys (*Meleagris gallopavo silvestris*) at Cedar Creek and B. F. Grant Wildlife Management Areas and surrounding lands in central Georgia, USA, 2017 and 2018.