BEHAVIORAL ECOLOGY OF WILD TURKEYS

BY

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DISSERTATION

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ABSTRACT

Wild turkey (*Meleagris gallopovo*) hens are solitary and cryptic during the reproductive season, sensitive to observer presence near the nest site, and as a result our understanding of their incubation behavior is limited to a handful of studies. Lacking this important behavioral information, it remains unclear how incubation behavior among turkey hens influences reproductive success. Habitat use among hens during the reproductive season is influenced by forest management strategies such as prescribed fire, however, these inferences are primarily derived from pine (Pinus spp.) forest habitat of the southeastern U.S. and are not likely applicable to hardwood forests of the Midwest. To address these unknowns, I remotely monitored Eastern wild turkeys (*Meleagris gallopovo silvestris*) using micro-GPS and studied their habitat use, incubation behavior, and daily nest survival. Chapter 1 of my dissertation provides a review of animal behavior in the context of wildlife conservation, habitat use in managed landscapes, and wild turkey hen reproductive behavior and success.

In Chapter 2, I sought to examine habitat use among wild turkey hens during the reproductive season as a function of prescribed fire; a forest management strategy that is increasing in use in Illinois to reduce invasive and undesirable vegetation and encourage oak (*Quercus* spp.) regeneration. More specifically, I addressed two questions, (1) Does prescribed fire influence habitat selection among hens? and (2) Does burn regime (time-since-fire and burn frequency) influence hen habitat use among burned forest areas? I found that within their annual and reproductive period ranges, hens generally used burned and non-burned forest in proportion to what was available to them within the flock and annual ranges. During the reproductive season in Illinois, wild turkey hens exhibited habitat selection among burned forest areas as a function of time-since-burn and burn frequency, and non-burned forest represented a large proportion of

their annual and seasonal ranges with most nests occurring in non-burned forests. The effects of time-since-burn and burn frequency on habitat use changed in response to the reproductive period (i.e., egg-laying, incubation, or post-nesting) and spatial scale examined (i.e., annual home range vs. reproductive period home range vs. reproductive period core area). The home ranges and core areas of wild turkey hens in Illinois included a mosaic of fire elements. Habitat use by hens during egg-laying and incubation periods indicated hens selected areas with at least one growing season since burning. The diversity in use of burned and non-burned forest suggests that managing for pyrodiversity in forested landscapes of Illinois may provide a range of habitats that are valuable for nesting and brood-rearing turkeys.

In Chapter 3, I used hidden Markov models to classify activity data collected from hens during each nest attempt to describe individual incubation behavior. I discovered that hens exhibited a partial incubation period which lasted from 1 - 6 days prior to the start of continuous incubation (i.e., the day following the first night spent on the nest). I found that the mean daily recess frequency was 1.3 (SD = 0.7) and ranged between 0 - 5 recesses. Mean recess duration was 45.3 min (SD = 30.7 min) and ranged between 5 – 325 min. Recesses occurred more frequently in the afternoon than in the morning. In addition to growing our understanding of turkey recess behavior, future harvest regulations in Illinois will be informed by improved knowledge of the partial incubation period and the timing of hen recesses.

In Chapter 4, I analyzed 48 nest attempts to evaluate the influence of recess behavior described in Chapter 3, habitat and landscape features, ambient temperature, and temporal variables on daily nest survival. Based on the results from binary-regression models of daily nest survival, I found that daily nest survival rates declined with increasing visual obstruction (51 – 100 cm) of a nest site. Models of incubation recess behavior did a poor job explaining daily

survival rates of nests and ranked below the constant survival model. These results suggest that factors beyond the scope of this study, such as nest predator community composition and abundance, are likely playing a strong role in the survival of wild turkey nests across Illinois.

Taken together, these results suggest that (1) pyrodiversity in a forested landscape may be valuable for Eastern wild turkey hens during the reproductive season, and (2) although recess behavior varied among hens, it did not appear to influence daily nest survival. Managing a forested area with pyrodiversity goals can provide valuable habitat for nesting and brood-rearing wild turkeys, but reproductive success may remain low regardless.

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CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW

Animal behavior in the context of conservation

Studying animal behavior without influencing the behavior of interest is a challenge that must be accounted for to reduce bias in the data (Burghardt et al. 2012). Additional challenges to directly observing animal behavior include the location of the animal, such as underwater or in flight, unpredictable timing of the behavior itself, and sensitivity of the animal to observation (Brown et al. 2013). In addition to potentially influencing behavior, observers may also influence predation risk to the species being observed (Ibáñez-Álamo et al. 2012, Reynolds and Schoech 2012). Among birds, there is some evidence suggesting that observers can influence nest success, and while this differs among orders and guilds, Ibáñez-Álamo et al. (2012) revealed that ground nesting birds were negatively impacted by observer activity at the nest site.

Due to the secretive nature of breeding birds and the concern among researchers regarding observer-effects at nests, studies of nesting behavior have received relatively less focus than other aspects of the reproductive season until the 1990s (Reynolds and Schoech 2012). The suspected reason for this increase is the development of remote monitoring technology (Reynolds and Schoech 2012). Camera technology, *i*Buttons®, perch switches, RFID equipped nest boxes, and VHF/GPS devices permit remote monitoring of nests, attending adults, and nest-related behaviors with minimal disruption to breeding birds (Smith et al. 2015).

The use of remote monitoring technology permits researchers to "observe" many behaviors that would be otherwise unobservable, and data describing these behaviors may prove useful for designing and implementing successful conservation efforts. For example, greater white-fronted geese (*Answer albifrons*) nesting on the Arctic Coastal Plain of Alaska, USA exhibited more frequent recess bouts in industrial-disturbed sites and the effect was slightly

greater among nests closer to industrial activity (Meixell and Flint 2017). Additionally, observer visits led to reductions in nest survival probability ranging from 7 – 35%. Meixell and Flint (2017) concluded that negative effects on avian productivity, particularly in industrial areas where nesting behavior is already affected, can be reduced by limiting direct encounters with nests. In this example, the nesting behavior of the greater white-fronted goose was used as a behavioral indicator, one of three behavioral themes described by Berger-Tal et al. (2011) in which behaviors including movement and spatial use, foraging and vigilance, and social organization and reproductive behavior can provide insight into (a) anthropogenic impacts on animal behavior – behavioral plasticity or rigidity may be problematic for the species; (b) behavior-based management – wherein behavioral modification or behavioral-sensitive management may be required; and (c) behavioral indicators – behavior can be used to reveal threats to conservation and efficiency of management. Using behavioral indicators can provide information on the state of an animal or its environment (Berger-Tal et al. 2016, Goldenberg et al. 2017, Snijders et al. 2017). Some general themes in which behavioral indicators have been used in a conservation framework include responses to human activity (Tadesse and Kotler 2012, Goldenberg et al. 2017, Meixell and Flint 2017), foraging (Stolen 2003, Dietsch et al. 2007, García-Tarrasón et al. 2015), and evaluating habitat use following habitat management (Dees et al. 2001, Houle et al. 2010, Parker et al. 2021).

Wildlife habitat use in a managed landscape

Considering habitat use as a behavioral indicator can support different objectives, such as updating habitat management plans, evaluating the impact of landscape or habitat alteration on wildlife, or informing capture and release programs to ensure animals settle in appropriate habitat (Morris 2003, Stamps and Swaisgood 2007). For example, fishers (*Pekania pennanti*)

reintroduced in the southern Cascade Mountains of Washington state exhibited a preference for a mosaic of old and recently disturbed forest stands (Parsons et al. 2019). Older forest stands provided larger trees and snags for denning and shelter from predators (Zielinski and Gray 2018), whereas the preferred prey, the snowshoe hare (*Lepus americanus*), was associated with younger forest stands (Parsons et al. 2019). Parsons et al. (2019) further revealed that bobcat (*Lynx rufus*) activity also may have contributed to habitat selection by fishers. Fishers avoided areas of high hare activity and appeared to be least active during peak periods of bobcat activity.

Prescribed fire is increasing in use as a forest management strategy to reduce fuel loads, reduce the density of undesirable vegetation in the canopy and understory, and encourage regeneration of desired plant species (Hutchinson et al. 2005, Albrecht and McCarthy 2006, Burton et al. 2011). However, the reintroduction of fire to forests after many decades of fire suppression also is expected to impact wildlife, though the effects are not fully understood (Nowacki and Abrams 2008, Taylor et al. 2012, Pausas 2019). A growing body of research suggests that when prescribed fire is used to manage a landscape, a mosaic application may be the most beneficial approach for wildlife. The mosaic pattern, representing variation in burn regimes across the landscape, is also known as pyrodiversity (Jones and Tingley 2021). Variation in burn regimes within a landscape may include burns of different severity, time-since-burning, burn frequency, or combinations of these characteristics.

Research indicates that pyrodiversity is beneficial for and may promote biodiversity (Martin and Sapsis 1992, Tingley et al. 2016, Kelly et al. 2017, Stillman et al. 2019b, Jones and Tingley 2021). Jones and Tingley (2021) highlighted two examples of habitat use by birds in which pyrodiversity played a key role for different reasons. California spotted owls (*Strix occidentalis occidentalis*) foraged in pyrodiverse areas that were historically fire-depressed and

homogenous, likely because these areas provided habitat for the dusky-footed woodrat (*Neotoma fuscipes*), the preferred prey of spotted owls (Jones et al. 2020, Jones and Tingley 2021, Kramer et al. 2021). Black-backed woodpeckers (*Picoides arcticus*), known for their strong post-fire affinity, exhibited a strong use of pyrodiverse areas for foraging and nesting that were close in proximity to low-severity or non-burned forest (Jones and Tingley 2021). Juvenile woodpeckers that used the low-severity or non-burned areas experienced greater survival relative to those that used high-severity burned areas (Stillman et al. 2019a). These results together indicate that pyrodiversity can be important for wildlife, but the context in which pyrodiversity is considered (e.g., spatial, temporal, or both; burn severity; burn history) will be necessary for making inferences and informing management plans.

Vegetation response to prescribed fire

Burn regimes (i.e., burn frequency, severity, time-since-burn) play an important role in the success of prescribed fire as a habitat management tool (Albrecht and McCarthy 2006, Jones and Tingley 2021). Burton et al. (2011) demonstrated that increasing burn frequency in upland oak (*Quercus* spp.) forests led to increased species richness and cover by understory forbes and C3 graminoids, and woody plant cover and canopy closure did not change in response to burn frequency. Albrecht and McCarthy (2006) found that in the years immediately following a dormant-season burn oak recruitment was low and suggested that altering fire severity or the timing of fires could reduce resprouting rates of competing hardwood species (e.g., red maple (*Acer rubrum*)). Knapp et al. (2015) examined the effects of burning in an oak-hickory (*Carya* spp.) forest that indicated oak-regeneration can be achieved through a long-term burning program that includes a "fire-free" period to permit sapling recruitment into the canopy. Altogether, areas that vary in fire frequency, severity, and time-since-burn can provide a

heterogenous mosaic (i.e., pyrodiverse) of habitat structure and composition that may be important for wildlife (Kelly and Brotons 2017, Kelly et al. 2017, Jones and Tingley 2021).

Habitat use by wild turkeys

During the reproductive season, the habitat requirements of nesting wild turkey hens change as the hen shifts from one reproductive period to the next (i.e., egg-laying to incubation, incubation to brood-rearing; Miller and Conner 2007, Wood et al. 2018, Wood et al. 2019). Turkey hens nest on the ground and during the nesting period they generally select sites with greater nest concealment and ground cover, and nests are often located near roads (Thogmartin 1999, Yeldell et al. 2017, Wood et al. 2019). During the brood-rearing period, hens tend to select sites with greater amounts of ground and understory cover (Wood et al. 2019). As the habitat requirements of nesting hens change throughout the year, it is not surprising that habitat changes following forest management would influence where hens spend time during the reproductive season (Spears et al. 2007, Byrne et al. 2011). For example, Martin et al. (2012) reported that hens used pine (*Pinus* spp.) savannahs less than expected, preferred areas burned within < 2 years, and used burned pine savannah stands almost immediately post-fire. More recently, Wood et al. (2018) described the variation in hen use of managed pine forests as a function of seral stage and time-since-burn, and hens exhibited a preference for mature and young pine stands that had been burned in the previous 1-2 years. A potentially important factor that is not explicitly examined in studies of turkey habitat use in fire-managed landscapes is the use of non-burned forest. Non-burned forest may provide valuable refuge for turkeys and other wildlife during active burns, as well as nesting locations during the reproductive period.

Wild turkey incubation behavior

Incubation behavior may be an important behavioral indicator of the state of incubating individuals as well as the environment in which the nest is located. For many bird species, including wild turkeys, studies of incubation behavior are few (Williams Jr et al. 1971, Green 1982, Bakner et al. 2019, Lohr et al. 2020). Wild turkey hens are notoriously cryptic during the nesting period and are known to abandon nests when flushed by an observer (Williams Jr et al. 1971, Williams 1991). Most bird studies that involve monitoring a nest often report incidents of observer influence, for example: the nest becomes abandoned; the behavior of the involved parent(s) changes in response to observer presence; or the observer presence attracts attention of potential nest predators (Livezey 1980, Major 1990). Due to these potential impacts and challenges with direct observation of nests, the development of technology to monitor nests remotely has led to an increase in studies of incubation behavior in birds (Smith et al. 2015, Croston et al. 2018).

Prior to using GPS telemetry to study wild turkey reproduction, documentation of incubation behavior among hens was rare. Green (1982) reported that the frequency with which hens engaged in incubation recesses varied considerably among individuals (n = 4) that were directly monitored in Michigan. Williams Jr et al. (1971) also directly monitored nesting turkey hens, in Florida, and among 7 nests observed determined that the mean recess duration was 1 hr 50 min. The authors also described evidence of partial incubation among hens and surmised that this behavior usually began in the middle of the egg-laying period (Williams Jr et al. 1971). Spohr (2001) monitored incubating turkey hens (n = 15) in Connecticut using VHF telemetry and a Rustrak chart recorder to detect movements away from the nest. Incubating hens in Connecticut took 0.94 daily recesses which lasted 77.2 min, on average. Mean total daily recess

time was 76.5 min (Spohr 2001). Spohr (2001) also reported that nocturnal recesses tended to be longer than daytime recesses, by an average difference of 81.8 min.

With the increased use of VHF-GPS to monitor wild turkey movements, studies of reproductive behavior among turkeys are increasing in number and sample size. Conley et al. (2015) remotely monitored 25 nest attempts among 18 Rio Grande hens in Texas using VHF/GPS units on hens. Incubating hens exhibited variation in recess schedules and travel distances to/from the nest during recess (Conley et al. 2015). Bakner et al. (2019) monitored 269 nest attempts by 206 turkey hens in South Carolina, Georgia, and Louisiana using VHF/GPS and estimated that hens, on average, took 1.7 recesses per day and most recesses occurred between 10:00 and 15:00 each day. With an additional year of data among the same study areas as Bakner et al. (2019), Lohr et al. (2020) monitored 374 nest attempts by 278 turkey hens and estimated that hens, on average, took 1.62 recesses and spent 2.09 hr off the nest daily. Despite the increases in sample size among recent studies of wild turkey incubation behavior, the inferences made are based on the unlikely assumption that behavior occurring between hourly location data is static (Conley et al. 2015, Bakner et al. 2019, Lohr et al. 2020).

More refined estimates of time spent in recess, when they occur, and the frequency with which they occur are needed to better understand wild turkey nesting ecology. These measures can be produced by increasing the sampling rate for VHF-GPS units, which may result in shorter unit life, or by analyzing activity data recorded by accelerometers that are often built into VHF-GPS units (Foley and Sillero-Zubiri 2020). Accelerometers recording activity data at short intervals (e.g., 5 min or less) require minimal battery power to operate and can provide researchers with the ability to detect changes in activity levels among individual animals (Foley and Sillero-Zubiri 2020). With large increases in data from GPS and accelerometer units,

advances in statistical modeling techniques permit researchers to detect unobserved behavior patterns using machine learning (Nathan et al. 2012). The use of hidden Markov models (hereafter 'HMMs'), a type of machine learning, is increasing in popularity in the field of ecology (Leos-Barajas et al. 2017, McClintock et al. 2020). HMMs can be used for behavioral state prediction and to evaluate drivers of behavior (Leos-Barajas et al. 2017). Challenges associated with the analysis include selecting appropriate software, determining the number of states, parameter estimation, and state interpretation (McClintock et al. 2020). Computational challenges notwithstanding, HMMs are a boon for researchers interested in studying animal behavior, particularly among cryptic or geographically remote species (Campbell et al. 2013, Patterson et al. 2019, Wang 2019). For example, Patterson et al. (2019) collected accelerometer data from thick-billed murres (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*) to classify standing, swimming, and flying behavior using HMM's, and reported > 90% accuracy for both species. This example demonstrates the value of HMM's to classify behaviors for two seabird species that cannot be observed for any length of time to provide quantifiable behavior data. For similar reasons, I expect HMMs will be particularly useful in future research of cryptic behaviors such as incubation in birds and as datasets continue to grow (McClintock et al. 2020).

Wild turkey nest survival

Although not a behavior, nest survival can also serve as an important indicator of the state of the involved parent(s), and the environment in which the nest is located (Badyaev et al. 1996, Benson et al. 2010, Gibson et al. 2016, Fogarty et al. 2017). In a gyneparental incubation strategy (as seen in wild turkeys) the female of the species relies primarily on internal reserves of energy and nutrients to form and incubate a clutch of eggs without male assistance (Steven and Raveling 1987, Deeming 2002). Energy reserves of incubating females can influence how much

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time is spent on the nest incubating or away from the nest to forage (Aldrich and Raveling 1983, Steven and Raveling 1987, Bueno-Enciso et al. 2017). Individuals that invest more time incubating generally have shorter incubation periods, and often have greater nest success, relative to less attentive individuals (Aldrich and Raveling 1983, Deeming 2002, Bueno-Enciso et al. 2017). Lohr et al. (2020) revealed that wild turkey hens that took longer recess bouts had higher individual survival but experienced increased loss of nests, whereas hens that recessed more frequently experienced lower individual survival. Bakner et al. (2019) reported an increase in nest survival with increasing cumulative distance traveled during recess bouts. However, the relationship between incubation behavior and nest survival remains unclear for wild turkeys. With so few studies and methods describing incubation behavior and its relationship to nest survival among wild turkeys, it is apparent that more research is needed to: (a) develop a standardized method for monitoring and describing the behavior, (b) provide basic information about the behavior; (c) examine factors that may influence the behavior, and (d) evaluate the relative influence of incubation behavior on nest survival.

In addition to behavior of the incubating adult(s), many factors are suspected to influence nest survival among birds including exposure to extreme temperatures (Brown and Downs 2003, Deeming and Reynolds 2015), habitat characteristics (e.g., visual obstruction of the nest; Byrne and Chamberlain 2013), landscape characteristics (e.g., distance to water source; Kauffman et al. 2021)), and characteristics of the incubating parent(s), such as body condition or age (Wilson et al. 2007). Ground nesting species, such as wild turkeys, are exposed to multiple predator species that rely on different cues to detect prey (e.g., visual, scent, heat), and as a result experience high amounts of nest predation. Predation risk may influence where birds place nests (Porter 1992), and within a selected habitat, birds should select a nest location that provides concealment of the

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nest and incubating adult, while providing open views for the incubating adult to be able to detect and react to approaching predators (Götmark et al. 1995, Howlett and Stutchbury 1996, Wiebe and Martin 1998). Presumably, habitats with greater diversity in vegetation cover and structure can provide more potential nest sites and can increase the time spent by predators searching for prey (Martin 1993b). The habitat and nest site can also determine the predator community birds will be exposed to (Martin 1993a, Rangen et al. 1999). For example, among ground-nesting species, selecting nest sites based on nest concealment is most beneficial during the egg stage and is largely motivated by predators using visual cues (Latif et al. 2012). Among bird species that may face predators using different cues to detect prey, nest concealment may be less important to in nest survival (Rangen et al. 1999). The relationship between nest concealment and wild turkey nest survival remains unclear (Fuller et al. 2013, Lohr et al. 2020), yet nest concealment continues to be considered an important habitat feature for nesting hens.

Strutting into the future

Extensive research on wild turkeys, including population dynamics, nest site selection, and general habitat use has been conducted to improve the management and conservation of wild turkeys (Collier and Chamberlain 2011). With the development and use of VHF-GPS transmitters on turkeys, researchers can explore a much more diverse set of questions that will further develop our understanding of wild turkey ecology and inform management practices. Currently, we know that hens use a variety of habitats throughout the annual cycle and forest management may influence this habitat use, but most of this knowledge is based on research in the pine ecosystems of the southeast and these inferences may not be applicable in upland hardwood forests. Regarding the reproductive season, our knowledge of incubation behavior is limited to just a handful of studies from which inferences are relatively limited due to sample

size or methodological design. Finally, researchers have just begun to investigate the role that incubating hen behavior plays in nest survival. The importance of nest survival to the population dynamics of wild turkeys creates urgency to pursue novel (within turkey research) investigations of things such as incubation behavior, that may improve our understanding of nest survival within a species that experiences high rates of nest failure.

Dissertation organization

Investigations of animal behavior that do not influence the behavior itself are becoming more common as technology allows for remote monitoring techniques. To address the questions and objectives described herein, I monitored Eastern wild turkey hens across Illinois using micro-GPS units to describe habitat selection, incubation behavior, and nest survival.

The use of prescribed fire as a forest management tool is increasing across North America and the influence of this management on wild turkeys in upland hardwood forests remains unclear. Most research studying the influence of prescribed fire on wild turkeys has been conducted in the pine forests of the southeast. Therefore, in Chapter 2 I examine habitat use of wild turkey hens at multiple spatial scales, with a specific focus on different periods of time during the reproductive season.

Studies of wild turkey incubation behavior are few, yet the behavior may prove to be an important component in predicting nest survival. In Chapter 3 I classify accelerometer data from incubating turkey hens using hidden Markov models to detect and describe incubation recess behavior. Then in Chapter 4, I evaluate the relative fit of models predicting daily nest survival among wild turkey hens. Models include relevant habitat and landscape characteristics, temporal variables, intrinsic hen and nest variables, and characteristics of recess behavior.

REFERENCES

Albrecht, M. A., and B. C. McCarthy. 2006. Effects of prescribed fire and thinning on tree
recruitment patterns in central hardwood forests. Forest Ecology and Management
226:88-103.

Aldrich, T. W., and D. G. Raveling. 1983. Effects of experience and body-weight on incubation
behavior of Canada geese. Auk **100**:670-679.

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

Bakner, N. W., L. R. Schofield, C. Cedotal, M. J. Chamberlain, and B. A. Collier. 2019.
Incubation recess behaviors influence nest survival of wild turkeys. Ecology and
Evolution **9**:14053-14065.

Benson, T. J., N. M. Anich, J. D. Brown, and J. C. Bednarz. 2010. Habitat and landscape effects
on brood parasitism, nest survival, and fledgling production in Swainson's warblers. The
Journal of Wildlife Management **74**:81-93.

Berger-Tal, O., D. T. Blumstein, S. Carroll, R. N. Fisher, S. L. Mesnick, M. A. Owen, D. Saltz,
C. C. St. Claire, and R. R. Swaisgood. 2016. A systematic survey of the integration of
animal behavior into conservation. Conservation Biology **30**:744-753.

Berger-Tal, O., T. Polak, A. Oron, Y. Lubin, B. P. Kotler, and D. Saltz. 2011. Integrating animal
behavior and conservation biology: a conceptual framework. Behavioral Ecology **22**:236-
239.

Brown, D. D., R. Kays, M. Wikelski, R. Wilson, and A. P. Klimley. 2013. Observing the
unwatchable through acceleration logging of animal behavior. Animal Biotelemetry **1**:20.

Brown, M., and C. T. Downs. 2003. The role of shading behaviour in the thermoregulation of breeding crowned plovers (*Vanellus coronatus*). Journal of Thermal Biology **28**:51-58.

Bueno-Enciso, J., R. Barrientos, E. S. Ferrer, and J. J. Sanz. 2017. Do extended incubation recesses carry fitness costs in two cavity-nesting birds? Journal of Field Ornithology **88**:146-155.

Burghardt, G. M., J. N. Bartmess-LeVasseur, S. A. Browning, K. E. Morrison, C. L. Stec, C. E. Zachau, and T. M. Freeberg. 2012. Perspectives - minimizing observer bias in behavioral studies: A review and recommendations. Ethology **118**:511-517.

Burton, J. A., S. W. Hallgren, S. D. Fuhlendorf, and D. M. Leslie. 2011. Understory response to varying fire frequencies after 20 years of prescribed burning in an upland oak forest. Plant Ecology **212**:1513-1525.

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

Byrne, M. E., M. J. Chamberlain, and F. G. Kimmel. 2011. Seasonal space use and habitat selection of female wild turkeys in a Louisiana bottomland forest. Pages 8-14 *in* Proceedings of the Southeastern Association of Fish and Wildlife Agencies.

Campbell, H. A., L. Gao, O. R. Bidder, J. Hunter, and C. E. Franklin. 2013. Creating a behavioural classification module for acceleration data: using a captive surrogate for difficult to observe species. The Journal of Experimental Biology. **216**:4501-4506.

Collier, B., and M. Chamberlain. 2011. Redirecting research for wild turkeys using global positioning system transmitters. Pages 81-92 *in* Proceedings of the National Wild Turkey Symposium.

Conley, M., J. Oetgen, J. Barrow, M. Chamberlain, K. Skow, and B. Collier. 2015. Habitat
selection, incubation, and incubation recess ranges of nesting female Rio Grande wild
turkeys in Texas. Pages 117-126 *in* Proceedings of the National Wild Turkey
Symposium.

Croston, R., C. A. Hartman, M. P. Herzog, M. L. Casazza, and J. T. Ackerman. 2018. A new
approach to automated incubation recess detection using temperature loggers. The
Condor **120**:739-750.

Deeming, C. 2002. Avian incubation: behaviour, environment and evolution. Oxford University
Press, Oxford.

Deeming, D. C., and S. J. Reynolds. 2015. Nests, eggs, and incubation: new ideas about avian
reproduction. Oxford University Press, USA.

Dees, C. S., J. D. Clark, and F. T. Van Manen. 2001. Florida panther habitat use in response to
prescribed fire. The Journal of Wildlife Management **65**:141-147.

Dietsch, T. V., I. Perfecto, and R. Greenberg. 2007. Avian foraging behavior in two different
types of coffee agroecosystem in Chiapas, Mexico. Biotropica **39**:232-240.

Fogarty, D. T., R. D. Elmore, S. D. Fuhlendorf, and S. R. Loss. 2017. Influence of olfactory and
visual cover on nest site selection and nest success for grassland-nesting birds. Ecology
and Evolution **7**:6247-6258.

Foley, C. J., and C. Sillero-Zubiri. 2020. Open-source, low-cost modular GPS collars for
monitoring and tracking wildlife. Methods in Ecology and Evolution **11**:553-558.

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.

García-Tarrasón, M., J. Bécares, S. Bateman, J. M. Arcos, L. Jover, and C. Sanpera. 2015. Sex-specific foraging behavior in response to fishing activities in a threatened seabird. Ecology and Evolution **5**:2348-2358.

Gibson, D., E. J. Blomberg, M. T. Atamian, and J. S. Sedinger. 2016. Nesting habitat selection influences nest and early offspring survival in greater sage-grouse. Condor **118**:689-702.

Goldenberg, S. Z., I. Douglas-Hamilton, D. Daballen, and G. Wittemyer. 2017. Challenges of using behavior to monitor anthropogenic impacts on wildlife: a case study on illegal killing of African elephants. Animal Conservation **20**:215-224.

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

Götmark, F., D. Blomqvist, O. C. Johansson, and J. Bergkvist. 1995. Nest site selection: A trade-off between concealment and view of the surroundings? Journal of Avian Biology **26**:305-312.

Houle, M., D. Fortin, C. Dussault, R. Courtois, and J.-P. Ouellet. 2010. Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest. Landscape Ecology **25**:419-433.

Howlett, J. S., and B. J. Stutchbury. 1996. Nest concealment and predation in hooded warblers: Experimental removal of nest cover. The Auk **113**:1-9.

Hutchinson, T. F., R. E. J. Boerner, S. Sutherland, E. K. Sutherland, M. Ortt, and L. R. Iverson. 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. Canadian Journal of Forest Research **35**:877-890.

Ibáñez-Álamo, J. D., O. Sanllorente, and M. Soler. 2012. The impact of researcher disturbance on nest predation rates: a meta-analysis. Ibis **154**:5-14.

Jones, G. M., H. A. Kramer, S. A. Whitmore, W. J. Berigan, D. J. Tempel, C. M. Wood, B. K. Hobart, T. Erker, F. A. Atuo, N. F. Pietrunti, R. Kelsey, R. J. Gutiérrez, and M. Z. Peery. 2020. Habitat selection by spotted owls after a megafire reflects their adaptation to historical frequent-fire regimes. Landscape Ecology **35**:1199-1213.

Jones, G. M., and M. W. Tingley. 2021. Pyrodiversity and biodiversity: A history, synthesis, and outlook. Diversity and Distributions **00**:1-18.

Kauffman, K. L., R. D. Elmore, C. A. Davis, S. D. Fuhlendorf, L. E. Goodman, C. A. Hagen, and E. P. Tanner. 2021. Role of the thermal environment in scaled quail (*Callipepla squamata*) nest site selection and survival. Journal of Thermal Biology **95**:102791.

Kelly, L. T., and L. Brotons. 2017. Using fire to promote biodiversity. Science **355**:1264-1265.

Kelly, L. T., L. Brotons, and M. A. McCarthy. 2017. Putting pyrodiversity to work for animal conservation. Conservation Biology **31**:952-955.

Knapp, B. O., K. Stephan, and J. A. Hubbart. 2015. Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, U.S.A. Forest Ecology and Management **344**:95-109.

Kramer, A., G. M. Jones, S. A. Whitmore, J. J. Keane, F. A. Atuo, B. P. Dotters, S. C. Sawyer, S. L. Stock, R. J. Gutiérrez, and M. Z. Peery. 2021. California spotted owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes. Forest Ecology and Management **479**:118576.

Latif, Q. S., S. K. Heath, and J. T. Rotenberry. 2012. How avian nest site selection responds to predation risk: testing an 'adaptive peak hypothesis'. Journal of Animal Ecology **81**:127-138.

Leos-Barajas, V., T. Photopoulou, R. Langrock, T. A. Patterson, Y. Y. Watanabe, M.
Murgatroyd, and Y. P. Papastamatiou. 2017. Analysis of animal accelerometer data using
hidden Markov models. Methods in Ecology and Evolution **8**:161-173.

Livezey, B. C. 1980. Effects of selected observer-related factors on fates of duck nests. Wildlife
Society Bulletin **8**:123-128.

Lohr, A. K., J. A. Martin, G. T. Wann, B. S. Cohen, B. A. Collier, and M. J. Chamberlain. 2020.
Behavioral strategies during incubation influence nest and female survival of wild
turkeys. Ecology and Evolution **10**:11752-11765.

Major, R. E. 1990. The effect of human observers on the intensity of nest predation. Ibis
132:608-612.

Martin, R. E., and D. B. Sapsis. 1992. Fires as agents of biodiversity: pyrodiversity promotes
biodiversity. Pages 150-157 *in* Proceedings of the conference on biodiversity of
northwest California ecosystems. Cooperative Extension, University of California,
Berkeley.

Martin, T. E. 1993a. Nest predation among vegetation layers and habitat types: Revising the
dogmas. The American Naturalist **141**:897-913.

Martin, T. E. 1993b. Nest predation and nest sites. Bioscience **43**:523.

McClintock, B. T., R. Langrock, O. Gimenez, E. Cam, D. L. Borchers, R. Glennie, and T. A.
Patterson. 2020. Uncovering ecological state dynamics with hidden Markov models.
Ecology Letters **23**:1878-1903.

Meixell, B. W., and P. L. Flint. 2017. Effects of industrial and investigator disturbance on
Arctic-nesting geese. The Journal of Wildlife Management **81**:1372-1385.

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

Morris, D. W. 2003. How can we apply theories of habitat selection to wildlife conservation and management? Wildlife Research **30**:303-319.

Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience **58**:16.

Parker, C., W. M. Schelsky, L. Garver, and J. P. Hoover. 2021. Pyrodiversity matters: Wild turkey habitat selection in a fire managed landscape. Forest Ecology and Management **493**:119227.

Parsons, M. A., J. C. Lewis, B. Gardner, T. Chestnut, J. I. Ransom, D. O. Werntz, and L. R. Prugh. 2019. Habitat selection and spatiotemporal interactions of a reintroduced mesocarnivore. The Journal of Wildlife Management **83**:1172-1184.

Patterson, A., H. G. Gilchrist, L. Chivers, S. Hatch, and K. Elliott. 2019. A comparison of techniques for classifying behavior from accelerometers for two species of seabird. Ecology and Evolution **9**:3030-3045.

Pausas, J. G. 2019. Generalized fire response strategies in plants and animals. Oikos **128**:147-153.

Porter, W. 1992. Habitat requirements. Pages 202-213 The wild turkey: biology and management. Stackpole, Harrisburg, Pennsylvania, USA.

Rangen, S. A., R. G. Clark, and K. A. Hobson. 1999. Influence of nest-site vegetation and predator community on the success of artificial songbird nests. Canadian Journal of Zoology **77**:1676-1681.

Reynolds, S. J., and S. J. Schoech. 2012. A known unknown: elaboration of the 'observer effect' on nest success? Ibis **154**:1-4.

Smith, J., C. Cooper, S. Reynolds, D. Deeming, and S. Reynolds. 2015. Advances in techniques to study incubation. Pages 179-195. Nests, eggs, and incubation: new ideas about avian reproduction. Oxford University Press, USA.

Snijders, L., D. T. Blumstein, C. R. Stanley, and D. W. Franks. 2017. Animal social network theory can help wildlife conservation. Trends in Ecology & Evolution **32**:567-577.

Spears, B. L., M. C. Wallace, W. B. Ballard, R. S. Phillips, D. P. Holdstock, J. H. Brunjes, R. Applegate, M. S. Miller, and P. S. Gipson. 2007. Habitat use and survival of preflight wild turkey broods. The Journal of Wildlife Management **71**:69-81.

Spohr, S. M. 2001. Variables influencing nest success of eastern wild turkeys in Connecticut: nesting habitat, home range-scale fragmentation, and nest attentiveness. University of Maine, Electronic Theses and Dissertations.

Stamps, J. A., and R. R. Swaisgood. 2007. Someplace like home: Experience, habitat selection and conservation biology. Applied Animal Behaviour Science **102**:392-409.

Steven, C. T., and D. G. Raveling. 1987. Incubation behavior of emperor geese compared with other geese: Interactions of predation, body size, and energetics. The Auk **104**:707-716.

Stillman, A. N., R. B. Siegel, R. L. Wilkerson, M. Johnson, C. A. Howell, and M. W. Tingley. 2019a. Nest site selection and nest survival of black-backed woodpeckers after wildfire. The Condor **121**:1-13.

Stillman, A. N., R. B. Siegel, R. L. Wilkerson, M. Johnson, M. W. Tingley, and L. Brudvig. 2019b. Age-dependent habitat relationships of a burned forest specialist emphasise the role of pyrodiversity in fire management. Journal of Applied Ecology **56**:880-890.

Stolen, E. D. 2003. The effects of vehicle passage on foraging behavior of wading birds. Waterbirds **26**:429-436.

Tadesse, S. A., and B. P. Kotler. 2012. Impact of tourism on Nubian Ibex (*Capra nubiana*) revealed through assessment of behavioral indicators. Behavioral Ecology **23**:1257-1262.

Taylor, R. S., S. J. Watson, D. G. Nimmo, L. T. Kelly, A. F. Bennett, and M. F. Clarke. 2012. Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? Diversity and Distributions **18**:519-529.

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

Tingley, M. W., V. Ruiz-Gutiérrez, R. L. Wilkerson, C. A. Howell, and R. B. Siegel. 2016. Pyrodiversity promotes avian diversity over the decade following forest fire. Proceedings of the Royal Society B: Biological Sciences **283**:20161703.

Wang, G. 2019. Machine learning for inferring animal behavior from location and movement data. Ecological Informatics **49**:69-76.

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.

Williams Jr, L. E., D. H. Austin, T. E. Peoples, and R. W. Phillips. 1971. Laying data and nesting behavior of wild turkeys. Pages 90-106 *in* Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners.

Williams, L. E. 1991. Wild Turkey Country. NorthWord Press, Minnetonka, Minnesota.

Wilson, S., K. Martin, and S. J. Hannon. 2007. Nest survival patterns in Willow Ptarmigan: Influence of time, nesting stage, and female characteristics. Condor **109**:377-388.

Wood, J. D., B. S. Cohen, L. M. Conner, B. A. Collier, and M. J. Chamberlain. 2019. Nest and brood site selection of eastern wild turkeys. The Journal of Wildlife Management **83**:192-204.

Wood, J. D., B. S. Cohen, T. J. Prebyl, L. M. Conner, 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. The Journal of Wildlife Management **81**:1073-1083.

Zielinski, W. J., and A. N. Gray. 2018. Using routinely collected regional forest inventory data to conclude that resting habitat for the fisher (Pekania pennanti) in California is stable over ~20 years. Forest Ecology and Management **409**:899-908.

CHAPTER 2: PYRODIVERSITY MATTERS: WILD TURKEY HABITAT SELECTION IN A

FIRE MANAGED LANDSCAPE[1]

ABSTRACT

Throughout North America, prescribed fire is becoming a common technique to manage

natural landscapes. How this management tool affects wildlife remains poorly understood by

land managers and biologists. Wild turkeys (*Meleagris gallopavo*) are an economically important

upland game bird that thrive in forests with a diverse understory structure. Diversity in forest

understory structure and composition can be achieved using prescribed fire. However, the

influence of prescribed fire on turkey habitat selection during the reproductive period is not

clear. We sought to answer two questions: 1) Does prescribed fire influence habitat selection

among wild turkey hens? and 2) How does hen habitat selection respond to differing burn

regimes? During 2015 – 2017 we monitored the habitat use of 47 hens in south-central Illinois,

USA using micro-GPS tags. We first compared hen use of burned and non-burned forest to

determine if prescribed fire, in general, influenced hen habitat selection. We then evaluated hen

use of burned forest areas to determine if time-since-burn (number of years) and burn frequency

(number of burns within four years) influenced hen habitat selection. Both questions were

examined at multiple scales of inference including individual-annual range, individual-

reproductive period range, and individual-reproductive period core area. When compared to

burned forest, non-burned forest typically comprised most of hen annual and seasonal ranges, yet

burned and non-burned forest were generally used by hens in proportion to their availability.

Within annual and reproductive period ranges, hens used a diverse array of burned forest areas that varied in time-since-burn and burn frequency. In response to these burn regimes, hens exhibited habitat selection that varied among the spatiotemporal levels that we investigated. Time-since-burn influenced habitat selection at each level investigated but did not influence habitat selection during all reproductive periods. Burn frequency influenced habitat selection only within post-nesting home ranges and incubation core areas, and the areas that hens used more differed between the reproductive periods. Our results highlight the influence of prescribed fire on wild turkeys, and the importance of considering both temporal and spatial scales in analyses of habitat selection. Furthermore, the diversity of burned and non-burned forest used by hens across spatiotemporal scales emphasizes the importance of pyrodiversity for wildlife in a forested landscape, including the retention of non-burned forests as part of the forest mosaic.

INTRODUCTION

Across the United States, prescribed fire is becoming a common technique to manage natural landscapes (Melvin 2018), and land managers seek a better understanding of how burn regimes affect wildlife. Burn regimes aim to achieve specific objectives such as reducing unwanted or invasive plant species, wildfire prevention, and altering forest structure (Peterson and Reich 2001). By altering the frequency of burning or time-since-burn (i.e., burn regimes), land managers may also influence the use of these areas by wildlife (Martin et al. 2012, Lashley et al. 2015). With the increasing application of fire as a forest management tool, there is a growing need to identify how prescribed fire impacts wildlife.

Prescribed fire can affect wildlife species in diverse and complex ways, and how scientists study these responses is similarly diverse and complex. In birds, these effects are often measured in terms of abundance, diversity, and productivity after burning (Rodewald and Smith

1998, Aquilani et al. 2000). Prescribed fire effects may also be measured in the form of a behavioral response, such as habitat selection, which typically requires data that are abundant in both time and space. Studies of habitat selection can better inform land and wildlife managers about how, when, and why wildlife are using areas managed with prescribed fire. With this information, managers can develop fire prescriptions to provide conditions best suited for the wildlife that inhabit these areas. For example, researchers found that burning during the dry season immediately increased food availability for the endemic Florida bonneted bat (*Eumops floridanus*), a critically endangered species (Braun de Torrez et al. 2018). Alternatively, white-tailed deer (*Odocoileus virginianus*) avoided recently burned areas during the lactation period due to the lack of cover (Lashley et al. 2015). In northern California, black-backed woodpeckers (*Picoides arcticus*) exhibited habitat selection across a pyrodiverse landscape and selection was influenced by bird age (Stillman et al. 2019). To better understand the complex ways in which wildlife response to prescribed fire, it is important to consider how the characteristics of a fire may influence the many facets of a species ecology.

An important factor in achieving positive outcomes for wildlife conservation is a robust understanding of species' habitat requirements in the context of the ecosystem (Kelly et al. 2017). One example of a successful conservation outcome is the reintroduction of the wild turkey in North America (Williams 1991). During reintroduction efforts, biologists gained a thorough understanding of the habitat requirements of wild turkeys (Dickson 1992). Wild turkeys are generally linked to forest ecosystems, and throughout the annual cycle females shift habitat use in response to food and nesting requirements (Byrne et al. 2011, Pollentier et al. 2017). Nesting on the ground in upland hardwood forests, the Eastern wild turkey (*Meleagris gallopavo silvestris*) benefits from understory vegetation which provides cover from predators

during the incubation period (Badyaev 1995, Spears et al. 2007, Fuller et al. 2013). Herbaceous vegetation provides both cover from predation, and habitat for the invertebrates that turkey poults feed on during the brood-rearing period (Healy 1985, McCord et al. 2014). Therefore, prescribed fire is likely to affect wild turkey habitat use, particularly during the reproductive season.

The change in function and importance of vegetative cover for wild turkey hens during the reproductive season is well understood (Pollentier et al. 2017, Wood et al. 2019), yet in Midwestern hardwood forests the influence of prescribed fire on habitat use during the reproductive season remains unclear. Following a dormant season burn, herbaceous foraging opportunities may increase later in the reproductive season as the change in environmental conditions supports the regrowth of some understory plant species (Blake and Schuette 2000, Burton et al. 2011). For example, during the pre-nesting period turkey hens in Louisiana used pine forests burned within the past five months but did not nest in those areas (Yeldell et al. 2017). The recent burns may have provided suitable foraging opportunities during the pre-nesting period, and the absence of nesting in those areas suggests that recent burns did not provide habitat features that hens select for when choosing a nest site. Another study based in Georgia pine forests indicated that during the reproductive season hens exhibit pyrodiverse habitat selection during the reproductive season (Wood et al. 2019). The timing and frequency with which fire is applied to a landscape is necessary to consider in land and wildlife management plans. In the oak-hickory (Quercus spp.-Carya spp.) forests of the Midwest, however, the question of how burning will influence wild turkey habitat use remains unclear.

To evaluate habitat selection among individual female wild turkeys (hereafter "hens") within fire-managed oak-hickory forests, we conducted composition analyses at three

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spatiotemporal levels: annual home range, home range within reproductive periods, and core area within reproductive periods (see description of levels in section 3.3 below; Johnson 1980). At each spatiotemporal level, we first sought to determine if prescribed fire influenced habitat selection among wild turkey hens in oak-hickory forests (Martin et al. 2012, Yeldell et al. 2017), and predicted that hens would use forest areas managed with fire more relative to non-burned forest during the reproductive season. Second, we considered the burned areas of forest used by hens and hypothesized that burn regime, including burn frequency (number of burns during previous four years) and time-since-burn (number of growing seasons since burning), would influence selection among those areas by hens. We expected that during the reproductive season hens would exhibit greater use of areas with a low burn frequency (i.e., 1 occurrence), or areas that had not been recently burned (i.e., 1 or 2 growing seasons since burning).

STUDY AREA

We conducted this research during 2015 – 2017 in the Stephen A. Forbes Recreation Area (Forbes), located in south-central Illinois (88°46.7669101'W 38°43.6064637'N; Fig. 2.1). From 2015-2017, the mean max temp was 18.4°C, mean min temp was 7.7°C, and mean annual rainfall was 113.5 cm[2]. Within the Forbes park boundary, land cover is comprised of deciduous forest (751.6 ha, of which approximately 465 ha are oak-hickory), open water (220.4 ha and 29 km of shoreline), grass-pasture (58.6 ha), development (52.2 ha), agricultural fields (43.7 ha), and herbaceous wetlands (< 1 ha). Hickory (Carya spp.), elm (Ulmus spp.), and oak (Quercus spp.) were the most common trees at nest locations. Grassland species included big bluestem

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[2] The values listed are means of annual mean values from 2015-2017.

(*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), and little bluestem (*Schizachyrium scoparium*; T. Esker, pers. comm). The most common agricultural crops in the vicinity of the study area included corn (*Zea mays*), soy beans (*Glycine max*), and winter wheat (*Triticum aestivum*). To reduce invasive vegetation (e.g., bush honeysuckles (Lonicera spp.)) and encourage oak regeneration, prescribed fire was applied to portions of Forbes during fall through early spring of each year and burns ranged in size from 1 – 105 ha (mean = 32.5 ha; Fig. 2.2). Most burns occurred during February – April (n = 25), and others were conducted during October – November (n = 11). An additional 5 burns were conducted during August – September (each < 2 ha in size), and a single burn occurred during December. Non-burned areas had no record of burning since 1996 when forest management at the site was first documented.

METHODS

Animal capture

We captured wild turkeys using drop nets, baited with cracked corn, during January – March of 2015 – 2017. We fit each captured turkey with an aluminum rivet leg band (National Band and Tag Company, Newport, Kentucky), and determined age (juvenile or adult) using the shape, wear, and barring of the 9th and 10th primaries (Leopold 1943). Sex was determined using a combination of morphological features (e.g., caruncle coloration, beard presence/length, spur presence, and breast feather coloration; Pyle 2008). We fitted each hen with a 100-g MiniTrack GPS unit (µGPS; Lotek Wireless Inc., Ontario, Canada). All turkeys were processed and released at the captured site. We programmed each µGPS to record a location (accurate to 20 m) every two hours during daylight hours, and once at midnight (Cohen et al. 2018). Each µGPS was equipped with an accelerometer continuously measured the average rate of movement (per 5 min) in two directions (*x*: sideways/rotary; *y*: forward/backward; hereafter referred to as 'activity

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data'). We relocated hens once weekly using a 3-element Yagi antenna and a receiver (R-1000, 148-160 MHz, Communications Specialists Inc., Orange, CA, USA), and remotely downloaded all location and activity data using a Handheld Command Unit (Lotek Wireless Inc., Ontario, Canada). Remote downloads were possible at distances up to 500 m, and at that distance we presumed our presence did not significantly influence turkey movements. Capture and monitoring methods were approved by the University of Illinois at Urbana-Champaign Institutional Animal Care and Use Committee (Protocol #15010).

Hen and nest monitoring

We examined location and activity data of each hen to monitor habitat use and behavior. If locations indicated a hen was restricting daily movements, we then evaluated the activity data for that hen (Yeldell et al. 2017). We scanned the activity data for periods of inactivity during daylight hours, as indicated by x or y values of < 15. We assumed a hen was incubating when she remained inactive for at least three hours daily, and locations were restricted to a radius of ≤ 50 m. We assumed an incubation period of approximately 28 days (Paisley et al. 1998) and monitored each incubating hen for indications of nest abandonment, predation, or the successful hatching of eggs. We used ArcGIS Pro v.2.2.4 to create an approximate nest location for each nest that represented our best approximation of the center of the incubation hen location data during the initial days of incubation. When location data indicated the hen moved away from the nest location, and activity data were continuously active (x and y values > 15) throughout the day, we assumed nest incubation had terminated. Following signs of nest termination, we navigated to the approximate nest location, located the nest bowl, and evaluated the nest area for signs of abandonment, predation, or success. We determined nest fate based on egg conditions (i.e., abandoned: intact and whole; predated: crushed and scattered; successful hatch: intact and

in halves). We then located the female, regardless of apparent nest fate, and flushed her twice within the two-week period immediately following nest termination to determine presence of poults. If poults were detected, brood surveys were conducted once weekly up to 16 weeks post-hatch or until no poults were detected during two consecutive surveys (Yeldell et al. 2017).

Delineation and habitat composition of home-ranges

All location and activity data were managed in a PostgreSQL 10 database (Urbano and Cagnacci 2014), and all analyses were conducted using R (v3.5.1; Team 2016). All location data used in these analyses met two requirements: 1) location was recorded at a time between the capture/release date and the date of death (bird or μGPS) and 2) location was realistic within the landscape (e.g., not in open water) and relative to previous and successive locations (Urbano and Cagnacci 2014). We placed each location into one of four categories, including three reproductive periods (egg-laying, incubation, and post-nest), and a fourth category (flocking) representing the remainder of the annual cycle. Analysis of the flocking period is not reported here because our focus was on the reproductive season.

Activity data collected from each μGPS permitted us to estimate, to the nearest hour, when incubation began and ended (C. Parker, *in prep*). We defined the start of the incubation period as the date when a hen remained for at least three hours on the nest, and incubation terminated when hen activity data indicated continuous movement throughout the day. After defining the incubation period for each individual hen, we were able to define the hen-specific start and end dates for the other periods by which location records were categorized. For hens that renested following a failed attempt, the incubation period for our analyses was defined as the start of the first incubation period through the end of the renest incubation period. We pooled these data to avoid simultaneous use of data among the reproductive periods. To reduce

probability of abandonment among active nests we did not visit nest locations to determine clutch size. Instead, we defined the egg-laying period as the 10 days prior to the first day of incubation, assuming that birds are laying one egg per day. We acknowledge the egg-laying period varies as a function of actual clutch size and that an egg may not be laid every day. We considered a 10-day period to be a reasonable estimate for egg-laying considering that clutch size among turkeys can range widely (Little and Varland 1981, Green 1982, Pittman and Krementz 2016). For each hen with a successful nest, we defined post-nesting as the period up to 112 days following nest termination, which was based on 16 weekly brood flushes during which we sought to observe poults with hens. For unsuccessful nesting hens we set the post-nesting period as 112 days post-failure. For hens with no nest attempt, we set the post-nesting period as up to 112 days following the mean incubation end date of hens from the same capture flock. We evaluated habitat use by hens with unsuccessful or no nest attempts in the post-nesting analysis because hens often join other brood flocks if they themselves do not reattempt nesting (Little and Varland 1981, Byrne et al. 2011, M. Meador, personal communication). Therefore, the location data from unsuccessful or non-nesting hens may also represent post-nesting habitat. It is possible that nest attempts were not detected due to failure in the egg-laying phase, however only hens that exhibited incubation behavior (as detected in the location and activity data) were included in these analyses.

Flock- and individual-annual ranges were estimated using all hen locations, and individual- home ranges and core areas during reproductive periods were estimated using hen locations only from each of the respective reproductive periods for a given year. The minimum number of locations required for each range was 15, and the number of locations used to create ranges varied between 16 – 1738, with a mean of 382 locations. We created Brownian Bridge

Movement Models (BBMM) for each hen by year, and also by reproductive period x year (R

package adehabitatHR; Calenge 2006). Two parameters were specified in the models to account

for: 1) known location errors (*sig 2* = 20) and 2) motion variance related to the speed or mobility

of the animal (*sig 1* = 1.5). From the BBMM's, we derived flock ranges (95%) by year,

individual home ranges (95%) by year, and reproductive period ranges (home range: 95%; core

area: 50%) for each individual within a given year. Examples of these ranges for a single hen can

be found in the Appendix (Figs. A.1 and A.2).

We determined the forest management composition of each range by using ArcGIS Pro

v.2.2.4 to identify management areas that overlapped with each annual and seasonal range. For

each annual cohort of birds captured (i.e., 2015, 2016, 2017), we used year-specific management

data provided by the Illinois Department of Natural Resources to describe burn regimes. We

obtained land cover data from the National Land Cover Database (NLCD; Dewitz 2019). The

NLCD 2016 dataset has a resolution of 30 m. We extracted 'forest' category data from the

NLCD raster using the annual and seasonal ranges as masks. We contrasted the NLCD forest

data with the forest management data to identify non-burned forest habitat within each annual

and seasonal range. We then classified managed forest habitat by the number of growing seasons

that occurred since burning (time-since-burn; 0 – 3 years), and by burn frequency (1 – 4 burns

occurring within the four years prior to when we monitored a given hen).

Composition analyses

To answer the question of whether prescribed fire had a general influence on hen habitat

selection, we compared the composition of burned and non-burned forest within "used" areas to

those of "available" areas (Table 2.1). For the annual home range analysis, we defined used

habitat as the annual home range of a hen during a given year and defined available habitat as the

capture flock range of the same year. For both the home range and core area reproductive period analyses, used habitats were defined by the boundary of the home range or core area of the given reproductive period. Available habitats for both the home range and core area reproductive period analyses were defined by the boundary of a modified annual range that was created by merging all annual periods (flock and reproductive periods) for a given individual. The modified annual range fully encompassed the reproductive periods and provided an appropriate alternative to using the annual ranges created from the BBMMs, which did not always completely overlap reproductive period ranges due to the time-dependent nature of BBMMs. Next, we determined if hen habitat selection within burned portions of the forest was affected by burn regimes, and compared the composition of burned forest (i.e., time-since-burn: 0 – 3 years post-burn; burn frequency: 1 – 4 burns within the previous 4 years) within "used" and "available" burned areas. We compared the composition of "used" and "available" areas using the 'compana' function (adehabitatHS; Calenge 2006). We used Wilks Lambda (Λ) to evaluate overall habitat selection and t-tests to determine individual habitat rankings and used a *p*-value of 0.05 as a threshold for both tests. Habitat rankings indicate the use of habitats by hens relative to availability. We evaluated hen habitat selection for both questions at three spatiotemporal levels (Table 2.1).

RESULTS

Between two sites in the same study area (referred to as the 'Northern' and 'Southern' flocks; Fig. 2.1), we captured 47 hens (Northern flock = 40; Southern flock = 7), which we monitored and collected data from during 2015 – 2017. Among the captured hens we classified 24 as juvenile; 21 as adult; and for 2 individuals we were unable to determine age. We detected 31 nest attempts, of which 26 failed and 3 successfully hatched. For two nests, we were unable to determine the fate due to land access issues and μGPS malfunctions. Two unsuccessful nests

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were in forest that was burned during the previous year, and all other nests were located outside burn units in non-burned habitat.

The mean individual-annual home range size ($\bar{x} \pm$ SE) among all hens was 197.6 ± 13.5 ha (combined flocks; n = 62 annual ranges), 205.7 ± 15.8 ha (Northern flock; n = 48 annual ranges), and 154.35 ± 8.5 ha (Southern flock; n = 14 annual ranges). Land cover within the combined flock range (2575.3 ha) was composed of: deciduous forest (1622.2 ha; 62.9 %), grass-pasture (389.6 ha; 15.1 %), agricultural fields (301.2 ha; 11.7 %), open water (167 ha; 6.5 %), developed land (101.1 ha; 3.9 %), and wetlands (0.4 ha; .01 %). The mean home range (95%) sizes during the reproductive periods were: 75.9 ± 6.4 ha (egg-laying, n = 28), 53.9 ± 7.7 ha (incubation, n = 28), and 142.1 ± 15.1 ha (post-nesting, n = 33). The post-nesting period included 3 hens with broods, 16 hens with unsuccessful nests, 2 hens for which we were unable to determine nest fate, and 12 hens for which a nest attempt was not detected. The mean core area (50%) sizes during the reproductive periods were 15.4 ± 1.3 ha (egg-laying, n = 28), 5.2 ± 0.9 ha (incubation, n = 28), and 24.6 ± 2.6 ha (post-nesting, n = 33).

Prescribed fire influence on habitat selection within annual ranges

We evaluated the composition of burned and non-burned forest within the annual ranges of individual wild turkey hens and found each forest type used in proportion to what was available within the annual flock range (n = 29, $\Lambda = 0.90$, df = 1, p = 0.08; Fig. 2.3). Further analyses revealed that among only burned areas hen habitat selection was influenced by time-since-burn (n = 29, $\Lambda = 0.55$, df = 3, p < 0.001), but not burn frequency (n = 29, $\Lambda = 0.88$, df = 2, p = 0.16; Fig. 2.3). Hens appeared to use areas with one growing season since burning more than recent burns and areas that had experienced two or more growing seasons relative to what was available within the annual flock range (Table 2.2).

Prescribed fire influence on habitat selection within 95% reproductive period home ranges

Hens used burned and non-burned forest within reproductive period home ranges in proportion to what was available within the modified annual range during egg-laying ($n = 13$, $\Lambda = 0.86$, $df = 1$, $p = 0.15$), incubation ($n = 10$, $\Lambda = 0.87$, $df = 1$, $p = 0.23$), and post-nesting periods ($n = 22$, $\Lambda = 0.86$, $df = 1$, $p = 0.07$; Fig. 2.4). Time-since-burn influenced habitat selection among hens during the egg-laying period ($\Lambda = 0.48$, $df = 3$, $p = 0.02$), but not during the incubation ($\Lambda = 0.93$, $df = 3$, $p = 0.86$) or post-nesting periods ($\Lambda = 0.72$, $df = 3$, $p = 0.06$; Fig. 2.4). The habitat composition of hen ranges during the egg-laying period indicated greater use of areas that had experienced at least one growing season since burning, and less use of recently burned areas (during fall/winter prior to current reproductive season) based on the relative availability (Table 2.3). Burn frequency did not influence habitat selection among wild turkey hens during egg-laying ($\Lambda = 0.72$, $df = 2$, $p = 0.12$) and incubation periods ($\Lambda = 0.71$, $df = 2$, $p = 0.18$) but did so during the post-nesting period ($\Lambda = 0.69$, $df = 2$, $p = 0.02$; Fig. 2.4). Areas that were burned once during the previous four years were used most and areas burned three times were used least by hens during the post-nesting period (Table 2.4).

Prescribed fire influence on habitat selection within 50% reproductive period core areas

Hens used burned and non-burned forest within 50% reproductive period core areas in proportion to what was available within modified annual ranges during the egg-laying ($n = 7$, $\Lambda = 0.97$ $df = 1$, $p = 0.68$) and incubation periods ($n = 7$, $\Lambda = 0.84$, $df = 1$, $p = 0.28$; Fig. 2.5). Within post-nesting core areas, hens exhibited greater use of burned areas over non-burned areas ($n = 8$, $\Lambda = 0.42$, $df = 1$, $p = 0.008$). Further analysis of reproductive period core areas revealed that time-since-burn influenced selection by hens among burned areas during egg-laying ($\Lambda = 0.15$, $df = 3$, $p = 0.004$), but not during incubation ($\Lambda = 0.40$, $df = 3$, $p = 0.10$) or post-nesting ($\Lambda = 0.93$, $df =$

3, p = 0.90; Fig. 2.5). Areas burned during the current breeding year were used least by hens during egg-laying, while areas that had experienced two or three growing seasons since burning were used most (Table 2.5). Burn frequency influenced hen habitat selection within incubation core areas ($\Lambda = 0.21$, df = 2, p = 0.004), and hens exhibited greater use of areas that were burned two or three times over those burned once (Table 2.6; Fig. 2.5). Burn frequency did not appear to influence habitat selection within core areas during egg-laying ($\Lambda = 0.83$, df = 2, p = 0.53) or post-nesting ($\Lambda = 0.91$, df = 2, p = 0.69) periods.

DISCUSSION

As the use of prescribed fire as a forest management tool continues to expand, wildlife and land managers must consider the influence of burning on wildlife, such as wild turkeys, inhabiting the area being considered for management. While our results do not indicate that hens used burned forest more than non-burned forest in general, the hens in our study system did use burned forest areas differently during the reproductive season. Time-since-burn and burn frequency influenced where and when hens spent time during the reproductive season, and our results highlight the importance of considering spatial and temporal scales when evaluating the effects of land management on wildlife. Furthermore, the diversity of burned habitat used by hens across these temporal and spatial scales reinforces the perceived benefits of pyrodiversity for wildlife, including the importance of non-burned forests.

Non-burned forest

The data did not support our prediction that hens would use burned over non-burned forest, and non-burned forest represented a large proportion of the areas used by and available to wild turkey hens in our study. Our analyses revealed that burned and non-burned forest areas were used in proportion to availability, except for post-nesting core areas where burned areas

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were used more. This simple evaluation of burned versus non-burned forest underscores the importance of non-burned forests in a prescribed fire management scheme where wild turkeys are present. The value of non-burned forest is noticeably absent in other studies of turkey habitat selection in fire-managed systems (Martin et al. 2012, Kilburg et al. 2015). However, this is likely due to the nature of the questions investigated, analytical design, and perhaps ecosystem differences. In hardwood forests of Arkansas, Pittman and Krementz (2016) observed greater nest success among hens that nested in non-burned forest and concluded that the reintroduction of fire did not benefit turkeys in the study area. Although we did not have a sufficient sample size to evaluate the benefit of prescribed fire for turkeys in terms of nest success, most hens in our study nested in non-burned forest. Taken together, these results indicate that non-burned forests are an important component of forests managed with prescribed fire and emphasize the value of non-burned forest as priority habitat for Eastern wild turkeys.

Pyrodiversity

Our results are consistent with the habitat-complementation hypothesis of pyrodiversity which suggests that a species persistence is supported by a landscape comprised of multiple fire elements (Kelly et al. 2017). Turkey home ranges and core areas were composed of multiple fire elements. Our pyrodiverse landscape provided the heterogeneous vegetation structure needed by turkey hens during the reproductive season. During the egg-laying and incubation periods, hens exhibited greater use of areas that had experienced at least one growing season over current year burns. Less use of current year burns is contrary to the idea that hens would be attracted to those areas by the flush of spring growth after dormant season burns (Wilsey 1996, Meek et al. 2008). However, with fewer live shrubs and reduced understory foliage (i.e., 1.5 – 10m), recent burns may be unsuitable habitat for wildlife with young searching for cover (Blake and Schuette 2000).

For example, current-year burns were used less by white-tailed deer (*Odocoileus virginianus*) in North Carolina during the lactation period, when deer with fawns seek areas with sufficient cover from predators (similar to nesting or brood-rearing turkeys; Lashley et al. 2015). While hens included in our study may have used recent burns during the reproductive season, no hens nested within recently burned forest. Only two nest attempts (both unsuccessful) were in burned forest areas, and each had experienced one growing season prior to the time of nesting. The limited evidence of nesting within burned areas indicates that hens are less likely to nest in areas burned within the previous four years, but they are using burned areas that may provide foraging opportunities during the incubation period.

Burn regime influenced habitat selection among wild turkeys and the composition of burned areas used at different temporal scales. Similarly, Wood et al. (2018) found that hen habitat selection varied throughout the reproductive season, and hens exhibited habitat selection in response to time-since-burn and stand seral stage in pine forests. In our study, areas with a single growing season since burning were used more, likely because these areas support the growth of herbaceous understory vegetation that turkeys can use as forage and cover (Hutchinson et al. 2005). Following multiple growing seasons, however, vegetation density and cover may increase and the abundance of important forage plants (e.g., seed-bearing grasses, fruit-bearing forbs) may decline as woody shrubs and saplings limit the amount of light reaching these sun-loving plants (Hutchinson et al. 2005, Albrecht and McCarthy 2006). Diet composition data indicate that wild turkeys in Missouri consumed a large proportion of forbs and grasses (more than 40% of their diets) from mid-July through mid-October (Dalke et al. 1942), which generally falls into the post-nesting period of our analyses. The composition of post-nesting home ranges and core areas in our study included a greater proportion of areas with higher burn

frequencies. While these areas were used in proportion to their availability, the use of these frequently burned areas throughout the annual cycle suggests their importance for wild turkeys during the reproductive periods, presumably for foraging.

Habitat selection outside the reproductive period

Here we focused on habitat selection during the reproductive season, but we would be remiss to ignore habitat selection that occurs before and after reproduction. As foraging largely governs space use by wild turkeys outside the reproductive season we would expect that food availability dictates where turkeys spend their time (Thomas 1950). During fall and winter, acorns and other hard mast represent an important component of the turkey's diet (Dalke et al. 1942), yet the impact that burning may have on the availability and nutrition of these forage for wildlife remains unclear. Germination rates of acorns within the leaf litter layer are reduced following a prescribed fire (Greenberg et al. 2012). A reduction in acorn germination rates may indicate that those acorns lose some value as a nutritional resource for wildlife but to our knowledge this has not yet been tested. Alternatively, burning can provide easier access to acorns within the duff or soil layer by eliminating leaf litter (Greenberg et al. 2012). Ultimately, further study is needed to understand how prescribed fire influences food resources for wildlife.

Locating productive foraging areas may require less effort during the non-breeding season when turkeys forage in flocks, from which members can access social information that increases individual foraging success (Clark and Mangel 1984). Another benefit to flocking behavior is higher survival rates among hens when compared to the reproductive period when hens incubate nests and forage independently (Humberg et al. 2009, Pollentier et al. 2014b). This influence of group behavior violates the assumption for composition analyses that individuals are acting independently (Calenge 2006). For this reason, we chose not to include analyses of

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individual habitat selection during the flocking period. However, habitat selection that occurs during the flocking period is inherently incorporated in the individual-annual analyses because the individual-annual ranges and the flock-annual ranges include year-round data.

Sex-specific habitat selection

The habitat selection we observed among wild turkey hens may not apply to male turkeys. Males generally remain in flocks throughout the entire year (Watts and Stokes 1971), and in central Mississippi did not exhibit variation in habitat use throughout the year (Miller et al. 2001). Because wild turkeys use a variety of habitat and food types, we would not expect males in hardwood forest stands to exhibit shifts in habitat use except during the reproductive season when locating, displaying for, and trying to mate with females. Following the mating period, male turkeys play no role in nest incubation or brood rearing, during which time hens must balance nutrition acquisition with predation risk. Given this difference in reproductive behavior and the vastly different influence males have on population dynamics, we would not expect male habitat selection to mirror that of females (Pollentier et al. 2014a).

CONCLUSIONS

Prescribed fire played an important role in shaping habitat selection among wild turkey hens. Pyrodiversity, here represented by time-since-burn and burn frequency, provided hens in our study area with a mosaic of managed habitat. Non-burned areas within this managed forest proved to be an important habitat component for hens during reproduction. Selection for and against different types of burned forest varied among spatial and temporal scales, and this variation emphasizes the importance of scale when considering the influence of management practices on wildlife habitat selection. For those interested in managing a forested landscape for wild turkeys, we recommend: 1) develop burn prescriptions that produce a blend of time-since-

burn and burn frequencies, and 2) retain some non-burned forest which may be used for nesting, as refuge by turkeys and other wildlife during burning events, and as places where turkeys can find forage items that are not burn-tolerant.
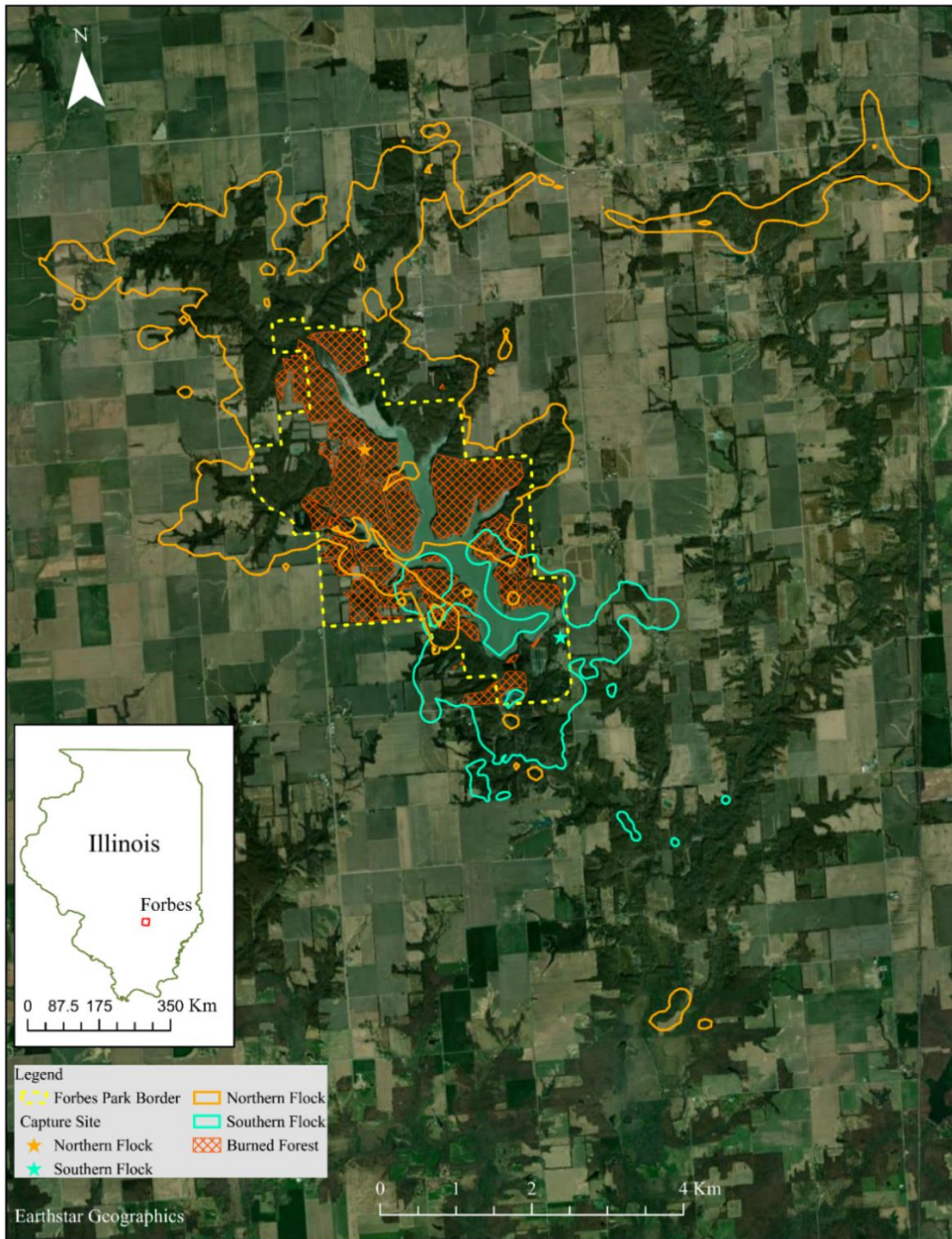
Figure 2.1. Boundaries of Stephen A. Forbes State Recreation Area (dashed yellow line), Eastern wild turkey flock ranges (solid lines), and burned forest (crosshatched areas) in Kinmundy, Illinois, USA. The flock ranges and burned forest areas are merged across years in this figure. Stars represent the locations where Northern & Southern turkey flocks were captured during 2015 - 2017. Inset map displays the park location (red line) within the state of Illinois (green line).
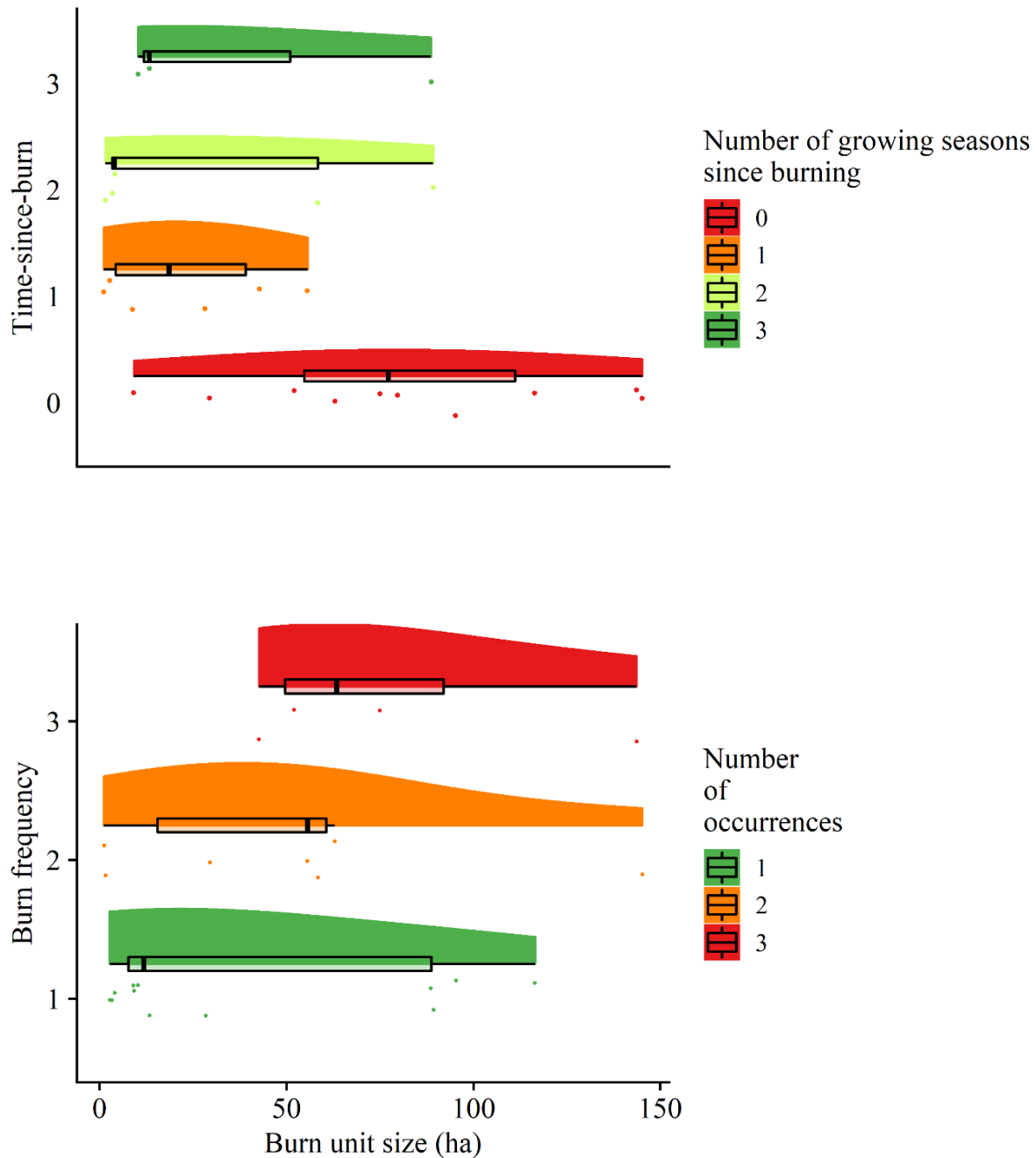
Figure 2.2. Rain cloud plot of burn unit sizes (ha) categorized by time-since-burn, or the number of growing seasons since burning within the previous four years (top panel). Rain cloud plot of burn unit sizes (ha) categorized by burn frequency, or the number of burns within four years (bottom panel). The "clouds" illustrate the probability distribution of burn sizes, the "rain" illustrates the raw burn unit sizes, and the box plots provide additional statistics describing burn sizes.
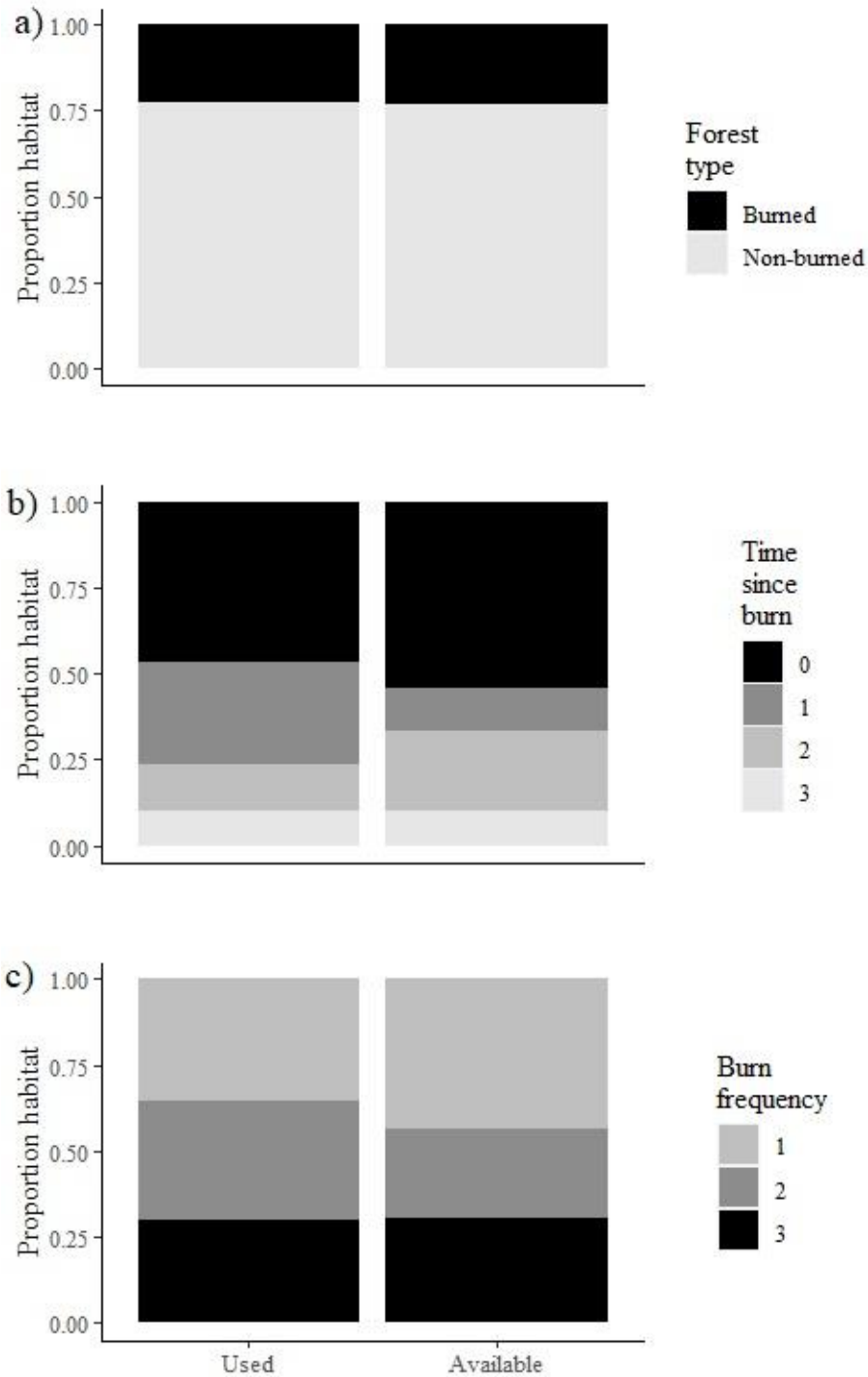
Figure 2.3. Side by side comparisons of individual annual range compositions (Used) and flock annual range compositions (Available) among all years, 2015 – 2017. Habitats illustrated included: a) burned and non-burned forest; b) the number of growing seasons a burned area experienced prior to the current year; c) the number of burns that occurred in an area within the previous four years.
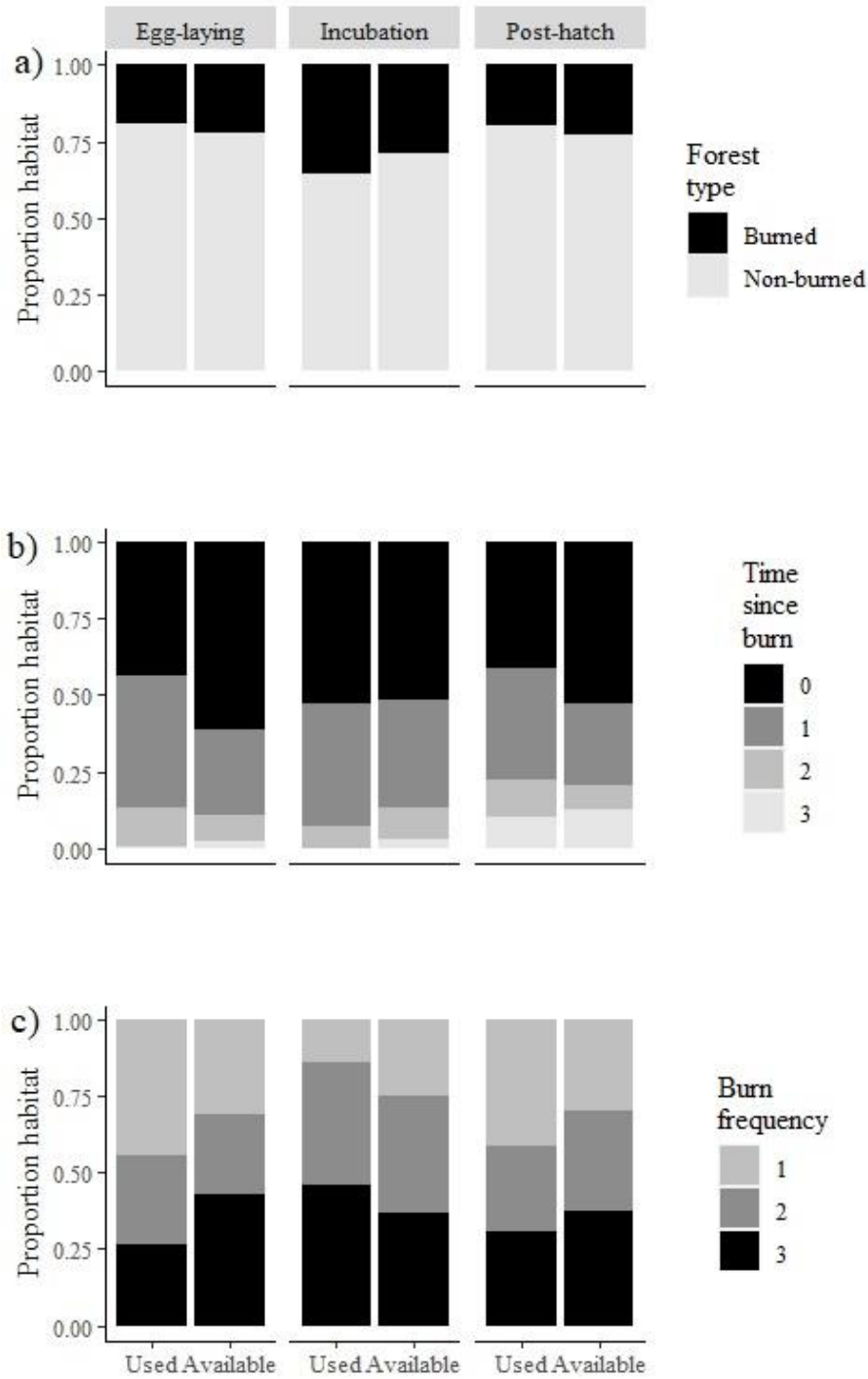
Figure 2.4. Side by side comparisons of reproductive period home range (95%) compositions (Used) and modified annual range compositions (Available) among all years, 2015 – 2017. Habitats illustrated included: a) burned and non-burned forest; b) the number of growing seasons a burned area experienced prior to the current year; c) the number of burns that occurred in an area within the previous four years.
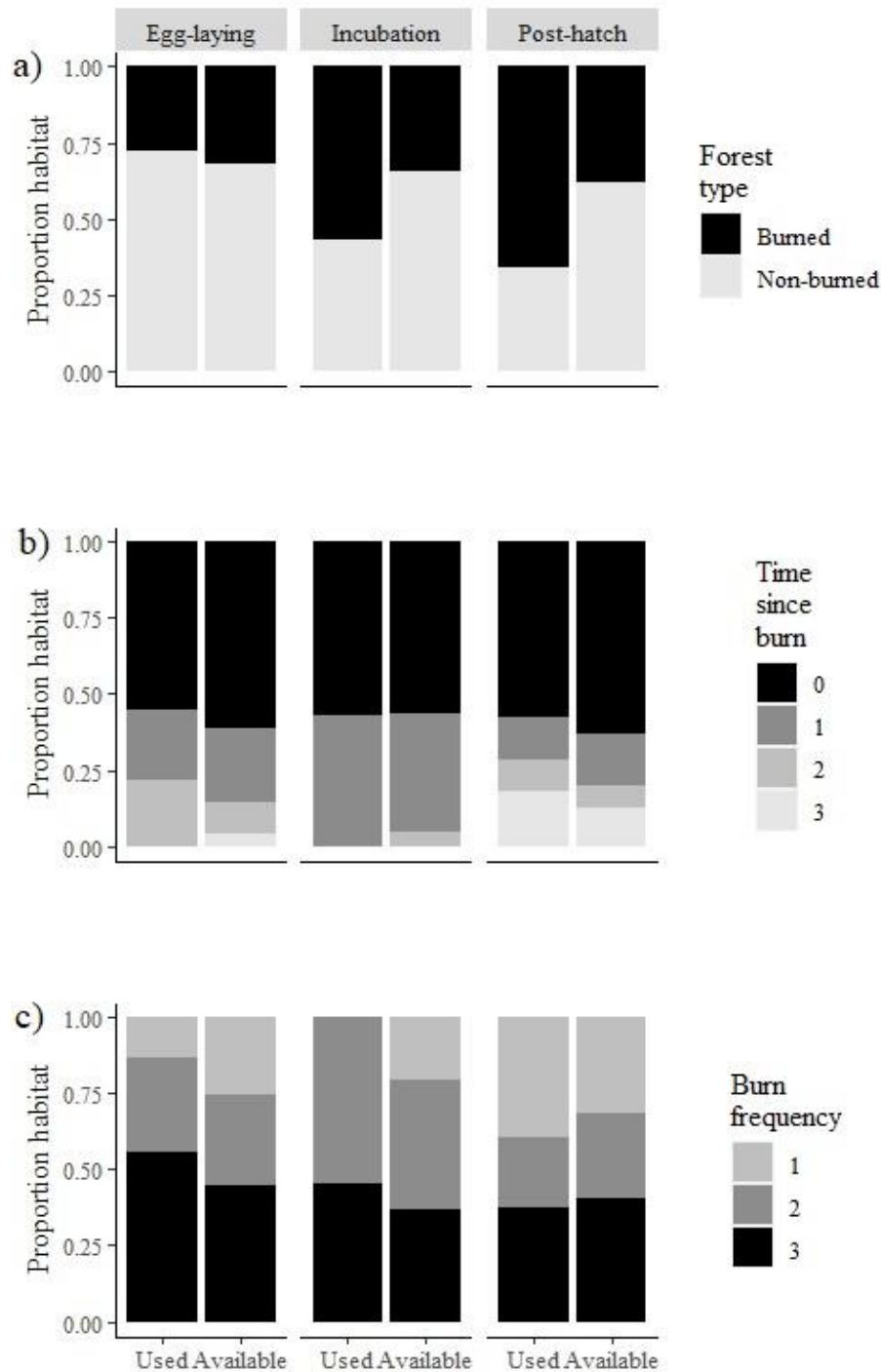
Figure 2.5. Side by side comparisons of reproductive period core area (50%) compositions (Used) and modified annual range compositions (Available) among all years, 2015 – 2017. Habitats illustrated included: a) burned and non-burned forest; b) the number of growing seasons a burned area experienced prior to the current year; c) the number of burns that occurred in an area within the previous four years.

Table 2.1. Spatiotemporal levels at which composition analyses were conducted for Eastern wild turkeys in south-central Illinois, USA. For each level, we described the habitat "used" by individual hens and the habitat "available" to individual hens for each year, from 2015 - 2017.

Comparison Level	Used	Available
Annual	Annual home range	Annual flock range
Reproductive period home range (95%)	Reproductive period home range:	
	Egg-laying	Modified annual range[3]
	Incubation	Modified annual range
	Post-nesting	Modified annual range
Reproductive period core area (50%)	Reproductive period core area:	
	Egg-laying	Modified annual range
	Incubation	Modified annual range
	Post-nesting	Modified annual range

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[3] The 'modified annual range' for each hen represents a merged range that includes each of the reproductive period 95% home ranges and the individual's flock-period range for the same year.

Table 2.2. Pair-wise comparison of burned areas (categorized by time-since-burn) within annual ranges (95%) of individual wild turkey hens at Stephen A. Forbes State Recreation Area, Illinois, 2015 – 2017. Within rows, a + indicates that the habitat was used more than the habitat in the column relative to availability, and a – indicates that the habitat was used less than the habitat in the column relative to availability. Triple signs indicate statistical significance of the relationship at α = 0.05. The rank column indicates the relative rank of use among burn categories (0 = least used, 3 = most used).

Time-since-burn (years)	0yr	1yr	2yr	3yr	Rank
0yr	0	---	+	-	1
1yr	+++	0	+++	+++	3
2yr	-	---	0	---	0
3yr	+	---	+++	0	2

Table 2.3. Pair-wise comparison of burned areas (categorized by time-since-burn) within 95% reproductive period home ranges of wild turkey hens at Stephen A. Forbes State Recreation Area, Illinois, 2015 – 2017. Within rows, a + indicates that the habitat was used more than the habitat in the column relative to availability, and a – indicates that the habitat was used less than the habitat in the column relative to availability. Triple signs indicate statistical significance of the relationship at α = 0.05. The rank column indicates the relative rank of use among burn categories (0 = least used, 3 = most used).

Egg-laying	0yr	1yr	2yr	3yr	Rank
0yr	0	-	---	-	0
1yr	+	0	-	+	2
2yr	+++	+	0	+	3
3yr	+	-	-	0	1
Incubation	0yr	1yr	2yr	3yr	Rank
0yr	0	-	+	+	2
1yr	+	0	+	+	3
2yr	-	-	0	-	0
3yr	-	-	+	0	1
Post-nesting	0yr	1yr	2yr	3yr	Rank
0yr	0	---	---	-	0
1yr	+++	0	+	+	3
2yr	+++	-	0	+	2
3yr	+	-	-	0	1

Table 2.4. Pair-wise comparison of burned areas (categorized by burn frequency) within the 95% reproductive period home ranges of wild turkey hens at Stephen A. Forbes State Recreation Area, Illinois, 2015 – 2017. Within rows, a + indicates that the habitat was used more than the habitat in the column relative to availability, and a – indicates that the habitat was used less than the habitat in the column relative to availability. Triple signs indicate statistical significance of the relationship at $\alpha = 0.05$. The rank column indicates the relative rank of use among burn categories (0= least used, 2 = most used).

Egg-laying	1	2	3	Rank
1	0	+	+	2
2	-	0	+	1
3	-	-	0	0
Incubation	1	2	3	Rank
1	0	-	-	0
2	+	0	-	1
3	+	+	0	2
Post-nesting	1	2	3	Rank
1	0	+	+++	2
2	-	0	+	1
3	---	-	0	0

Table 2.5. Pair-wise comparison of burned areas (categorized by time-since-burn) within the 50% reproductive period core areas of wild turkey hens at Stephen A. Forbes State Recreation Area, Illinois, 2015 – 2017. Within rows, a + indicates that the habitat was used more than the habitat in the column relative to availability, and a – indicates that the habitat was used less than the habitat in the column relative to availability. Triple signs indicate statistical significance of the relationship at $\alpha = 0.05$. The rank column indicates the relative rank of use among burn categories (0 = least used, 3 = most used).

Egg-laying	0yr	1yr	2yr	3yr	Rank
0yr	0	-	-	-	0
1yr	+	0	---	-	1
2yr	+	+++	0	+	3
3yr	+	+	-	0	2

Incubation	0yr	1yr	2yr	3yr	Rank
0yr	0	+	+	-	2
1yr	-	0	+	-	1
2yr	-	-	0	-	0
3yr	+	+	+	0	3

Post-nesting	0yr	1yr	2yr	3yr	Rank
0yr	0	-	-	-	0
1yr	+	0	-	+	2
2yr	+	+	0	+	3
3yr	+	-	-	0	1

Table 2.6. Pair-wise comparison of burned areas (categorized by burn frequency) within the 50% reproductive period core areas of wild turkey hens at Stephen A. Forbes State Recreation Area, Illinois, 2015 – 2017. Within rows, a + indicates that the habitat was used more than the habitat in the column relative to availability, and a – indicates that the habitat was used less than the habitat in the column relative to availability. Triple signs indicate statistical significance of the relationship at α = 0.05. The rank column indicates the relative rank of use among burn categories (0= least used, 2 = most used).

Egg-laying	1	2	3	Rank
1	0	-	-	0
2	+	0	+	2
3	+	-	0	1

Incubation	1	2	3	Rank
1	0	---	---	0
2	+++	0	-	1
3	+++	+	0	2

Post-nesting	1	2	3	Rank
1	0	+	+	2
2	-	0	+	1
3	-	-	0	0

REFERENCES

Albrecht, M. A., and B. C. McCarthy. 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. Forest Ecology and Management **226**:88-103.

Aquilani, S. M., D. C. LeBlanc, and T. E. Morrell. 2000. Effects of prescribed surface fires on ground- and shrub-nesting neotropical migratory birds in a mature Indiana oak forest, USA. Natural Areas Journal **20**:317-324.

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

Blake, J. G., and B. Schuette. 2000. Restoration of an oak forest in east-central Missouri: Early effects of prescribed burning on woody vegetation. Forest Ecology and Management **139**:109-126.

Braun de Torrez, E. C., H. K. Ober, and R. A. McCleery. 2018. Activity of an endangered bat increases immediately following prescribed fire. The Journal of Wildlife Management **82**:1115-1123.

Burton, J. A., S. W. Hallgren, S. D. Fuhlendorf, and D. M. Leslie. 2011. Understory response to varying fire frequencies after 20 years of prescribed burning in an upland oak forest. Plant Ecology **212**:1513-1525.

Byrne, M. E., M. J. Chamberlain, and F. G. Kimmel. 2011. Seasonal space use and habitat selection of female wild turkeys in a Louisiana bottomland forest. Pages 8-14 *in* Proceedings of the Southeastern Association of Fish and Wildlife Agencies.

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

Clark, C. W., and M. Mangel. 1984. Foraging and flocking strategies: Information in an

    uncertain environment. The American Naturalist **123**:626-641.

Cohen, B. S., T. J. Prebyl, B. A. Collier, and M. J. Chamberlain. 2018. Home range estimator

    method and GPS sampling schedule affect habitat selection inferences for wild turkeys.

    Wildlife Society Bulletin **42**:150-159.

Dalke, P. D., W. K. Clark, Jr., and L. J. Korschgen. 1942. Food habit trends of the wild turkey in

    Missouri as determined by dropping analysis. The Journal of Wildlife Management

    6:237-243.

Dewitz, J. 2019. National Land Cover Database (NLCD) 2016 Land Cover Science Product.*in* U.

    S. G. Survey, editor. U.S. Geological Survey - ScienceBase, Sioux Falls, SD.

Dickson, J. G. 1992. The wild turkey: biology and management. Stackpole Books.

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.

Green, H. E. 1982. Reproductive-behavior of female wild turkeys in northern lower Michigan.

    Journal of Wildlife Management **46**:1065-1071.

Greenberg, C. H., T. L. Keyser, S. J. Zarnoch, K. Connor, D. M. Simon, and G. S. Warburton.

    2012. Acorn viability following prescribed fire in upland hardwood forests. Forest

    Ecology and Management **275**:79-86.

Healy, W. M. 1985. Turkey poult feeding activity, invertebrate abundance, and vegetation

    structure. The Journal of Wildlife Management **49**:466-472.

Humberg, L. A., T. L. Devault, and O. E. Rhodes, Jr. 2009. Survival and cause-specific mortality

    of wild turkeys in northern Indiana. American Midland Naturalist **161**:313-322.

Hutchinson, T. F., R. E. J. Boerner, S. Sutherland, E. K. Sutherland, M. Ortt, and L. R. Iverson. 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. Canadian Journal of Forest Research **35**:877-890.

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

Kelly, L. T., L. Brotons, and M. A. McCarthy. 2017. Putting pyrodiversity to work for animal conservation. Conservation Biology **31**:952-955.

Kilburg, E. L., C. E. Moorman, C. S. DePerno, D. Cobb, and C. A. Harper. 2015. Wild turkey prenesting-resource selection in a landscape managed with frequent prescribed fire. Southeastern Naturalist **14**:137-146.

Lashley, M. A., M. C. Chitwood, R. Kays, C. A. Harper, C. S. DePerno, and C. E. Moorman. 2015. Prescribed fire affects female white-tailed deer habitat use during summer lactation. Forest Ecology and Management **348**:220-225.

Leopold, A. S. 1943. The molts of young wild and domestic turkeys. The Condor **45**:133-145.

Little, T. W., and K. L. Varland. 1981. Reproduction and dispersal of transplanted wild turkeys in Iowa. The Journal of Wildlife Management **45**:419-427.

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

McCord, J. M., C. A. Harper, and C. H. Greenberg. 2014. Brood cover and food resources for wild turkeys following silvicultural treatments in mature upland hardwoods. Wildlife Society Bulletin **38**:265-272.

Meek, M. G., S. M. Cooper, M. K. Owens, R. M. Cooper, and A. L. Wappel. 2008. White-tailed

    deer distribution in response to patch burning on rangeland. Journal of Arid

    Environments **72**:2026-2033.

Melvin, M. A. 2018. National prescribed fire use survey report.

Miller, D. A., L. M. Conner, B. D. Leopold, and G. A. Hurst. 2001. Spatial fidelity of wild

    turkeys between the seasons in central Mississippi. Pages 475-487 *in* Proceedings of the

    Fifty-Fifth Annual Conference of the Southeastern Association of Fish and Wildlife

    Agencies.

Paisley, R. N., R. G. Wright, J. F. Kubisiak, and R. E. Rolley. 1998. Reproductive ecology of

    eastern wild turkeys in southwestern Wisconsin. The Journal of Wildlife Management

    62:911-916.

Peterson, D. W., and P. B. Reich. 2001. Prescribed fire in oak savanna: Fire frequency effects on

    stand structure and dynamics. Ecological Applications **11**:914-927.

Pittman, H. T., and D. G. Krementz. 2016. Impacts of short-rotation early-growing season

    prescribed fire on a ground nesting bird in the Central Hardwoods region of North

    America. PloS one **11**:e0147317.

Pollentier, C. D., S. D. Hull, and R. S. Lutz. 2014a. Eastern wild turkey demography: Sensitivity

    of vital rates between landscapes. The Journal of Wildlife Management **78**:1372-1382.

Pollentier, C. D., R. S. Lutz, and D. Drake. 2017. Female wild turkey habitat selection in mixed

    forest-agricultural landscapes. The Journal of Wildlife Management **81**:487-497.

Pollentier, C. D., R. S. Lutz, and S. D. Hull. 2014b. Survival and productivity of eastern wild

    turkey females in contrasting landscapes in Wisconsin. The Journal of Wildlife

    Management **78**:985-996.

Pyle, P. H., Steve N.G.; Ruck, Siobhan; Desante, David F. 2008. Identification guide to North
American birds, Part II Anatidae to Alcidae. Slate Creek Press, Point Reyes Station,
California.

Rodewald, P. G., and K. G. Smith. 1998. Short-term effects of understory and overstory
management on breeding birds in Arkansas oak-hickory forests. The Journal of Wildlife
Management **62**:1411-1417.

Spears, B. L., M. C. Wallace, W. B. Ballard, R. S. Phillips, D. P. Holdstock, J. H. Brunjes, R.
Applegate, M. S. Miller, and P. S. Gipson. 2007. Habitat use and survival of preflight
wild turkey broods. The Journal of Wildlife Management **71**:69-81.

Stillman, A. N., R. B. Siegel, R. L. Wilkerson, M. Johnson, M. W. Tingley, and L. Brudvig.
2019. Age-dependent habitat relationships of a burned forest specialist emphasise the role
of pyrodiversity in fire management. Journal of Applied Ecology **56**:880-890.

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

Thomas, C. H. 1950. Relationships of wild turkey social and spatial behavior to management.

Urbano, F., and F. Cagnacci. 2014. Spatial database for GPS wildlife tracking data. Springer.

Watts, C. R., and A. W. Stokes. 1971. The social order of turkeys. Scientific American **224**:112-
119.

Williams, L. E. 1991. Wild Turkey Country. NorthWord Press, Minnetonka, Minnesota.

Wilsey, B. J. 1996. Variation in use of green flushes following burns among African ungulate
species: the importance of body size. African Journal of Ecology **34**:32-38.

Wood, J. D., B. S. Cohen, L. M. Conner, B. A. Collier, and M. J. Chamberlain. 2019. Nest and brood site selection of eastern wild turkeys. The Journal of Wildlife Management **83**:192-204.

Wood, J. D., B. S. Cohen, T. J. Prebyl, L. M. Conner, 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, T. J. Prebyl, B. A. Collier, and M. J. Chamberlain. 2017. Prescribed fire influences habitat selection of female eastern wild turkeys. The Journal of Wildlife Management **81**:1287-1297.

CHAPTER 3: DETECTING AND QUANTIFYING INCUBATION BEHAVIOR OF WILD TURKEYS

ABSTRACT

Bird incubation behavior remains a relatively understudied aspect of nesting ecology and for many species our understanding of incubation remains limited. Among some species, direct observation of nesting behavior may be possible, however, more cryptic species such as wild turkeys (*Meleagris gallopovo*) are sensitive to human presence near the nest and very limited information about their incubation behavior exists. Here, I remotely monitored the movement of wild turkey hens using micro-GPS units during the reproductive season and then described incubation behavior using accelerometer-produced activity data that I classified into behavioral states using hidden Markov models. I classified activity data from 43 incubating turkeys (53 nest attempts) into 4 behavioral states and used those states to describe the incubation behavior of Eastern wild turkeys in Illinois during 2015 – 2018. I discovered partial incubation behavior among all nest attempts that lasted from 1 – 6 days prior to the onset of continuous incubation. During the incubation period, incubation activity began before noon more often than after noon. Among nest attempts, I detected variation in daily frequency of recesses ($\bar{x} = 1.3 \pm 0.7$), daily total time in recess ($\bar{x} = 42.8 \pm 47.8$ min) and the duration of recess ($\bar{x} = 45.3 \pm 30.7$ min). Daily recess frequency increased with nest age and did not differ between second year and after second year hens. Afternoon recesses occurred more frequently than morning recesses. Recess duration declined with increasing nest age but was not influenced by hen age or when the recess began (morning vs. afternoon). This analysis provided basic, descriptive information about the incubation behavior of Eastern wild turkeys that will provide a means for comparison with future

studies and identified temporal factors that influence turkey incubation behavior which may have important implications for harvest season management.

INTRODUCTION

Parental behavior during the nesting period is a form of reproductive investment and for many species is incredibly challenging to quantify (Brown et al. 2013). A form of reproductive investment, parental behavior is one way that birds can increase fitness (Hohman 1986, Fontaine and Martin 2006, Drake et al. 2018). Incubation represents one of the most important parental behaviors because it influences egg hatchability (King'Ori 2011), quality of young (DuRant et al. 2012, DuRant et al. 2013), and energetic costs to the incubating parent(s) (Nord and Williams 2015). Many factors can influence incubation behavior, such as nesting habitat (Hohman 1986, Amininasab et al. 2016), climate conditions (Wiebe and Martin 1997), and energetic requirements of the incubating parent (Steven and Raveling 1987, Deeming 2002). For example, the incubating parent may adjust the frequency or duration of recesses away from the nest to regulate body or egg temperature, obtain food or water, or reduce predation risk to itself or the nest (Conway and Martin 2000, Fontaine and Martin 2006, Nord and Cooper 2020).

A major challenge in studying incubation behavior is the inability to continuously monitor nests (Smith et al. 2015). Through direct observation researchers may witness subtle behaviors that might otherwise go undetected when using remote detection or data interpretation techniques (Smith et al. 2015). However, direct observations are not feasible for all species due to inaccessible nest locations, sensitivity of incubating individuals to observation, and the time and labor involved in collecting observations (Smith et al. 2015). Moreover, direct observation can influence the behavior of incubating individuals, attract predators to the nest site, and is subject to observer error and variation among observers (Smith et al. 2015, Meixell and Flint 2017).

Technological advances during recent decades have increased the capability of researchers to monitor and study wildlife behavior (Wall et al. 2014). A variety of remote monitoring tools have been developed specifically for monitoring incubation behavior. While some tools measure nest attendance, such as perch switches, video cameras, and PIT (passive integrated transponder) tags; *i*Buttons® (Maxim Integrated Products 2014) and other pressure and temperature sensors in dummy eggs enable researchers to detect incubation by recording when an adult contacts eggs in the nest (Wang and Beissinger 2011). Researchers have also used Global Positioning System (GPS) units to monitor nest attendance, and more recent units include accelerometers, allowing researchers to pair location data with activity data. Among the most novel applications each of these tools provides is the ability to detect unobservable behaviors (Brown et al. 2013, Campbell et al. 2013). Monitoring wildlife behavior without exerting observer influence on behaviors of interest can be challenging. Deploying these devices on wildlife provides the opportunity to monitor activity when direct observation is not feasible (Nathan et al. 2012, Leos-Barajas et al. 2017), and to obtain data that are meaningful and quantifiable.

Due to the fine temporal resolution over which data are recorded by *i*Buttons and GPS units, for example, managing, storing, and analyzing large quantities of data quickly becomes a challenge (Body et al. 2012, Urbano and Cagnacci 2014). However, with recent advances in statistical modeling techniques it is possible to detect unobserved behavior patterns using machine learning (Nathan et al. 2012). The use of hidden Markov models (hereafter 'HMMs'), a type of machine learning, is increasing in popularity in the field of ecology because it permits behavioral analysis without the training dataset that is often required by other machine learning models (e.g., K-nearest neighbor; Bidder et al. 2014). Challenges associated with using HMMs

include selecting appropriate software, determining the number of states, parameter estimation, and state interpretation (McClintock et al. 2020). HMMs can be used for behavioral state prediction and to evaluate drivers of behavior (Leos-Barajas et al. 2017). Computational challenges notwithstanding, HMMs are a boon for researchers interested in studying animal behavior, particularly among cryptic or geographically remote species (Campbell et al. 2013, Patterson et al. 2019, Wang 2019).

Wild turkeys (*Meleagris gallopovo*) are a gregarious species outside the reproductive season and are typically easy to observe from a distance (Dickson 1992). However, with the onset of breeding, hens become quite cryptic and are challenging to observe during the nesting period (Williams Jr et al. 1971, Dickson 1992). Although the population growth of wild turkeys is highly sensitive to nest success among breeding hens, our understanding of hen behavior during the incubation period remains unclear. To date, knowledge of turkey incubation behavior is limited to a few studies, including recent studies with reasonable sample sizes (n > 10 nests; Bakner et al. 2019, Lohr et al. 2020, Spohr 2001). Earlier research based on direct observation of incubating turkey hens generally indicated that individuals varied in recess frequency, took recesses during all hours of the day, and noted that recess length may be influenced by climate (Williams Jr et al. 1971, Green 1982). For example, hens in Michigan took briefer recesses than hens in Florida, where the warmer temperatures may slow egg cooling while hens are off the nest (Williams Jr et al. 1971, Green 1982). More recent studies of turkey incubation behavior were based on hourly GPS location data. Researchers in the southeastern United States found that hens recessed, on average, more than once per day (Bakner et al. 2019, Lohr et al. 2020), and increased recess duration led to reduced nest survival (Lohr et al. 2020). The incubation behavior among turkeys in the southeast United States may differ from hens that live in different climates

and ecosystems, such as the upland hardwood forests of the Midwest, and activity data with finer temporal resolution (e.g., 5 min) can provide more precise estimates of time engaged in recess activities.

Improving our understanding of wild turkey behavior during the reproductive period will provide wildlife managers with information (e.g., length of continuous incubation period, timing of recess bouts) that can be used to adjust harvest season lengths and timing (e.g., morning only vs. daylight hours). By adjusting the temporal extent of the harvest season and daily hunting hours, managers may be able to reduce potential impacts of the harvest season, such as hen-harvest, during the incubation period. Therefore, I used accelerometer-derived activity data to describe the incubation behavior among Eastern wild turkey (*Meleagris gallopovo silvestris*) hens in Illinois. Using hidden Markov models, I classified activity data into behavioral states representing different activity levels exhibited by hens during the incubation period. I described incubation behavior (i.e., frequency, timing, and duration of incubation recesses) among turkey hens, without direct observation, to contribute to the further understanding of incubation behavior in this cryptically-nesting species. I assessed variability in daily recess frequency, and the timing and duration of incubation recesses as a function of hen age, nest age, and time of day (morning vs. afternoon).

STUDY AREA

I captured and remotely monitored Eastern wild turkeys among three study areas across Illinois which included: Stephen A. Forbes State Recreation Area in Kinmundy, IL (hereafter 'Forbes'; two sites); Lake Shelbyville area (hereafter 'Shelbyville'; three sites); and Western Illinois (three sites; hereafter 'W. IL.'). Individual sites within each study area represent separate locations where I captured and monitored turkeys (Fig. 3.1). All capture sites in Forbes and

Shelbyville were located on public lands. Capture sites in W. IL and many nest locations, among all study areas, occurred on private land. All study areas consisted of oak-hickory (*Quercus* spp.-*Carya* spp.) forests, agricultural row-crops (e.g., corn (*Zea mays*) and soy beans (*Glycine max*)), grassland, and pasture.

Forbes is a 1256 ha multiuse recreation area that includes 465 ha of oak-hickory forest, open water (29 km of shoreline), grass-pasture, agricultural fields, and herbaceous wetlands (Parker et al. 2021). Land managers used a combination of prescribed fire and selective thinning to reduce invasive vegetation and to encourage regeneration of oak species.

Shelbyville is a vast patchwork of private and public land that includes developed recreation sites, 276 kilometers of shoreline, and wildlife management areas amid ≥1000 ha of upland forest comprised of oak, hickory, and maples (*Acer* spp.). Land managers encouraged regeneration of oak species and managed invasive vegetation using selective tree thinning, prescribed fire, mechanical shrub removal, and aerial herbicide application.

W. IL. includes three private properties (i.e., Buckeye, McAllister, and Syrcle) located in Pike County. The capture site at Syrcle property is a cattle grazing area; however, the surrounding landscape includes large, forested areas and agricultural cropland. The Buckeye property is an area managed for hunting and fishing recreation. Food plots (e.g., sunflowers and radishes) were part of the area and varied among years. The general landscape surrounding Buckeye included forest, grassland/pasture, and agricultural cropland. The McAllister property was also managed for hunting and fishing opportunities and included managed food plots (e.g., corn). The landscape surrounding McAllister included forest, grassland/pasture, and agricultural cropland.

METHODS

Turkey capture and tagging

During January – March of 2015 – 2018 I captured female Eastern wild turkeys using drop nets and air cannons that were baited with cracked corn. I banded each hen on the tarsus with an aluminum rivet band (National Band and Tag Company, Newport, Kentucky), and determined age (second-year vs. after second year) based on the shape, wear, and barring of the 9th and 10th primaries (Leopold 1943, Pyle 2008). Each captured hen was fitted with a 100-g (~2 % of body weight) MiniTrack GPS unit (µGPS; Lotek Wireless Inc., Ontario, Canada), and I programmed each µGPS to record a location (accurate to 20 m) every two hours during daylight hours, and once at midnight (Cohen et al. 2018). Accelerometer data (x and y) were recorded as mean values across 5-minute intervals. *X*-values represented sideways/rotary movement and *y*-values represented forward/backward movement. Activity values ranged from 0 – 255 (unitless values) and provided a gradient of activity levels (0: no activity; 255: high activity). Once weekly for the duration of the life of the µGPS I relocated hens using a 3-element Yagi antenna and a receiver (R-1000, 148-160 MHz, Communications Specialists Inc.) to remotely download all location and activity data using a Handheld Command Unit (Lotek Wireless Inc., Ontario, Canada). Remote downloads were conducted at the farthest location that communication with the µGPS was possible (up to 500 m), where I presumed my presence did not influence turkey behavior. These methods were approved by the University of Illinois at Urbana-Champaign Institutional Animal Care and Use Protocol (#15010).

Virtual monitoring of nests

To determine when nesting behaviors began and ended for each hen, I examined location and movement data following each weekly data download as described in Chapter 2 (Parker et

al. 2021). When location data for an individual indicated restricted daily movements, I then evaluated the movement data for that hen (Yeldell et al. 2017). I scanned the movement data for bouts of inactivity (*x* and *y* values of < 15) during daylight hours. I assumed incubation began when a hen remained inactive for approximately 2.5 - 3 hours daily (partial incubation), and daily locations became restricted to a radius generally ≤ 50 m. I acknowledge that nests failing in the egg-laying stage may have been missed, however, I included only nest attempts that experienced continuous incubation in this analysis to study recess behavior during that period. I monitored each nest attempt for indications of nest abandonment, predation, or a successful hatch. I assumed an incubation period of 28 days (Paisley et al. 1998), and that incubation ceased when location data indicated the hen moved away from the nest location and movement data (x and y values > 15) indicated continuous motion throughout the day. When incubation ceased, I verified the nest location in the field using a central GPS point from the location data and searched the nest site for indications of abandonment, predation, or success. I determined nest fate based on egg conditions (i.e., abandoned: intact and whole; predated: crushed and scattered; successful hatch: intact and in halves). I then located the female and flushed her twice within the two-week period immediately following nest termination to determine presence of poults. A nest attempt was considered successful if at least one poult was present with the tagged hen.

Detection of behavior states

Wild turkey hens are notoriously cryptic during the reproductive season, which prohibits prolonged periods of observation. Therefore, I used hidden Markov models, a type of unsupervised machine learning, to detect changes in behavioral states (Leos-Barajas et al. 2017, McClintock et al. 2020). HMMs are stochastic time-series models that assume the observed time series (in this study – accelerometer data), is driven by an unobservable state process (e.g., some

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behavioral state; Leos-Barajas et al. 2017). For further details on HMMs and their usage see Leos-Barajas et al. (2017), McClintock and Michelot (2018), and McClintock et al. (2020). To focus on behavior occurring during the continuous incubation period, I used the start and end dates of continuous incubation for each nest attempt to select activity and location data from that period. I calculated an additional measure of activity "z", by summing of x and y values, to provide a metric of total body movement. I visualized z data in a histogram and specified a gamma distribution for the state-dependent observation process (McClintock et al. 2020). These models require distribution-dependent summary statistics from windows (one for each assumed state) of the observed data that accentuate the differences in observed acceleration measurements (Leos-Barajas et al. 2017). Based on my interpretation of activity levels among tagged hens throughout this study, I made biologically-informed assumptions and concluded that four behavioral states occurred with the activity data. For example, nocturnal z levels remained at or close to zero indicating no movement (i.e., sleeping). In the hour after hens were released following capture, hen z values were as large as 373, which indicates flying or running, which I observed occurring as the hens moved away from the release site. Given these two extremes (no activity vs. high activity), I felt it was reasonable to assume two additional states of "low activity" and "medium activity", such that our model-states represent a gradient of activity levels. I derived the initial parameter values (mean, standard deviation, and proportion of zero values) required to create an HMM (Table 3.1) by visually examining hen data. I created a pseudo-design matrix to prevent label-switching among behavioral states (McClintock and Michelot 2018). I did not make any assumptions about transition probabilities between activity levels. I used the 'fitHMM' function of the 'momentuHMM' package in R to create a set of competing HMMs (McClintock and Michelot 2018). To improve the estimates of starting

parameters for each state, I fit multiple models using different parameters and selected the model with the lowest value of the maximum log-likelihood (Table 3.). Then I created a set of five competing models that included covariates that I expected to influence change between behavioral states (Table 3.). Due to the high proportion of zeros in my data, evaluations of model fit using pseudo residual QQ plots were unclear. Therefore, I relied on Akaike's Information Criterion (AIC) and selected the model with the smallest AIC value (Table 3.). All models and analyses were conducted using the statistical software R (v.4.0.4; R Core Team 2016).

Behavior state validation

To validate the behavioral state classifications (herafter 'states') derived from the HMM model, I associated the location data that were recorded during the incubation period with classified activity data that occurred within a time interval of 10 minutes (5 minutes before and after) of a given location record (Fig. 3.2). I assumed a 10-minute window was a reasonable period to validate states with respect to a hen's location (on or away from the nest). I applied a spatial filter to the joined location-activity data and labeled data as: 1) "recess" - data points that were > 20 m from the nest location and did not occur on the first or last day of incubation; 2) "incubation" - data points that were ≤ 20 m of the nest location and did not occur on the first or last day of incubation. I summarized the counts of states by behavior, incubation or recess, and then conducted a Pearson's chi-squared test to assess the relationship between states and behaviors. Next, I plotted the residuals of the chi-squared test in a correlation plot to examine the relative contribution of states to the relationship between behaviors and states (Fig. 3.3). While foraging, turkeys may continue to slowly walk or they may remain at a location moving very little, and this would lead to some low state values (1 – 2) observed in the "recess" labeled data. Likewise, hens depart from the nest by flying or walking, and this produces some larger state

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values (3 or 4) in the "incubation" labeled data. Therefore, based on these correlation values, I labeled records with HMM states 3-4 as 'active' states and HMM states 1-2 as 'inactive' states in the full classified dataset.

Analysis of incubation behaviors

Information on partial incubation among wild turkeys is generally lacking, so I calculated summary statistics to describe the partial and continuous incubation periods observed among Eastern wild turkey hens. I defined the first day of partial incubation as the day in which a hen remained on the nest for at least 2.5 hours, and the last day when the hen remained on the nest overnight for the first time. I grouped successive records with the same activity status ('active' or 'inactive') into bouts and recorded the start and end timestamps of each activity bout. I calculated the duration in minutes for each activity bout (Fig. 3.4). Data from the last day the nest was active are not included in analyses of recess behavior because hens incubated only for a portion of those days and I would be unable to distinguish an actual recess from behavior associated with the hatching period or nest predation, and subsequent departure.

I calculated the frequency, duration, and total time spent on the nest during the partial incubation period, and the same metrics for time spent off the nest (i.e., recess) during the continuous incubation period for each nest attempt. Analyses of nest attendance during the partial incubation period mirror the model format described here for incubation recess, with metrics of nest attendance as the response variable. For comparison with previous studies of turkey incubation, I examined variation in daily recess frequency among nest attempts using a generalized linear model, created with daily recess frequency as the response variable, nest attempt ID as the predictor variable, and a Poisson distribution (Bates et al. 2015). I conducted a chi-square test on the model to determine if there was a general effect of nest attempt on daily

recess frequency. I examined effects of nest and hen age on daily recess frequency using a generalized linear mixed model that included nest attempt as a random variable (Table 3.4).

I examined variation in the timing of recess bouts by summarizing the start time of bouts according to when they began relative to 12:00. I evaluated the influence of nest attempt ID on the start time of recess activity before or after 12:00 (i.e., AM or PM) using a generalized linear model with a Poisson distribution, "AM" or "PM" as a binary response variable, and nest attempt ID as the predictor variable (Table 3.4).

I evaluated the variation in recess bout duration among nest attempts, generally, by conducting a chi-square test. Then I examined recess duration as a function of nest age (days of continuous (or partial) incubation), hen age (second year or after second year) and start time of activity relative to noon (i.e., AM or PM). I fit linear mixed models of recess duration including each factor (nest age, hen age, start time) as predictor variables in separate models and nest attempt ID as a random variable (Table 3.4). Standard deviations are reported for all mean values throughout the results unless specified otherwise.

RESULTS

I monitored 62 nest attempts by 50 female wild turkeys during 2015 – 2018 across Illinois. Of these attempts I censored 7 nests for which I was unable to obtain activity data and two attempts that never reached continuous incubation. From 53 nest attempts I collected 206,454 activity data points and 16,323 location points from which I described 627 incubation recesses during 738 nest days.

Model validation

        I used 12,248 activity records that were recorded within 5 minutes before or 5 minutes after a location record to validate the state classification of the HMM model. Of these data, 11,277 were located at the nest location or within 20 m of the nest and were coded as "incubation" and 971 records were detected > 20 m from the respective nest location and were coded as "recess". The difference in mean state values between records classified as 'incubation' or 'recess' was 1.06 (95% CI:1.03-1.09) and I was able to determine that the distribution of states between "incubation" and "recess" was not random ($X^2 = 3611$, df = 3, p < 0.0001). Higher state values (3 & 4) were more closely associated with "recess" records, while lower state values (1 & 2) were more closely associated with "incubation" records (Fig. 3.3). Based on these results, the classifications determined by the HMM were deemed appropriate for our goals of describing incubation behavior among wild turkeys.

Incubation period

        I detected partial incubation bouts starting 1 - 6 days prior to the first occasion a hen remained on its nest overnight and began continuous incubation (Fig. 3.5). Including partial incubation days, the mean length of incubation was 17 ± 10.5 days, and the mean length of continuous incubation was 14.9 ± 10.4 days. The mean ordinal date of the start of continuous incubation was 126 ± 13.9 days (May 6th), and the mean ordinal date of the start of partial incubation was 124 ± 13.8 days (May 4th). During the continuous incubation period I detected 627 recess bouts of nest attendance.

        During partial incubation days, periods of inactivity or low activity that I presumed to be incubation behavior, ranged from $1 - 14$ hours ($\bar{x} = 3.5 \pm 1.3$ hrs; Fig. 3.6). On average, hens incubated the nest 1.2 ± 0.5 times per day. Hens started incubation before noon more often than

in the afternoon (β = -1.5, se = 0.2, p < 0.001), and the observed mean frequency of morning

incubation bouts was 1.03 ± 0.2 and was 0.2 ± 0.4 in the afternoon. Second year and after second

year hens did not differ in daily incubation frequency (β = -0.06, se = 0.2, p = 0.7). On average,

incubation bouts increased in length (hrs) with increasing nest age (β = 0.3, df = 214, p < 0.001;

Fig. 3.7), and incubation bouts started before noon lasted longer than those started in the

afternoon (β_{PM} = -5.1, se = 0.1, p < 0.001).

Daily recess frequency

On average, incubating hens took 1.3 daily recesses (SD = 0.7) and the number of daily

recesses ranged between 0 – 5. On average, hens recessed at least once per day on 9.1 out of 14.9

days of continuous incubation. Only five nest attempts, each by a different hen, took a recess on

each day of continuous incubation. I detected general variation in daily recess frequency among

nest attempts (X^2 = 70.2, df = 52, p = 0.05). Relative to a single daily recess, 2 or more daily

recesses was less likely to occur (β_2 = -0.8^4, β_3 = -1.2^1, β_4 = -2.1^1, β_5 = -2.5^1). Second year and

after second year hens did not exhibit a detectable difference in daily recess frequency (β_{ASY} = -

0.08, se = 0.1, p = 0.5). Recess frequency increased with increasing nest age (β = 0.02, se =

0.005, p < 0.001; Fig. 3.8).

Recess timing

Among all hens, recesses occurred both in the morning and afternoon throughout the

incubation period. On average, recesses started at 12.8 ± 3.6 hours (Fig. 3.9). The mean hour of

morning recess initiations was 8.6 ± 2.7 hours, and the mean hour of afternoon recess initiations

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[4] Effect significantly different from zero at α = 0.05.

was 14.7 ± 1.9. Hens started recesses more frequently in the afternoon ($\bar{x}$ = 0.57 daily recesses, 95% CI: 0.5, 0.6) than in the morning ($\bar{x}$ = 0.3 daily recesses, 95% CI: 0.2, 0.3).

Recess duration

Recess duration varied among nest attempts (X^2 = 233, df = 52, p < 0.001). The mean recess duration among incubating hens was 45.3 ± 30.7 minutes and ranged from 5 - 325 minutes. No difference was detected in recess duration between morning ($\bar{x}$ = 50.5 min, 95% CI: 44, 56.9). and afternoon-initiated recesses ($\bar{x}$ = 47.7 min, 95% CI: 41.8, 53.6). No difference was detected in recess duration between second year ($\bar{x}$ = 46.1 min, 95% CI: 35.3, 56.9). and after-second year hens ($\bar{x}$ = 49.7 min, 95% CI: 43.0, 56.4). Recess duration decreased within nest age (β = -0.5, se = 0.1, p < 0.001).

Total daily recess time was 42.8 ± 47.8 min) and varied among nest attempts (X^2 = 94, df = 52, p = 0.0003). Total daily recess time increased as nest age increased (β = 0.01, se = 0.003, p = 0.007; Fig. 3.10). Hen age did not influence the total time hens spent in recess each day (β_{ASY} = 0.04, se = 0.09, p = 0.7).

DISCUSSION

Here I demonstrated the use of HMMs to classify accelerometer data that were recorded during a discrete biological period. The HMM-derived classifications permitted me to describe and evaluate incubation behavior among Eastern wild turkeys in Illinois. I found that among nest attempts there was variation in the daily frequency, bout duration, and total daily time spent in recess. There was also noticeable variation in the timing of recess bouts. the data indicated that hens initiated recesses more frequently in the afternoon, and daily frequency increased with nest age.

An exciting result of this research was the detection of partial incubation behavior. Williams Jr et al. (1971) described partial incubation behavior among Osceola wild turkeys in Florida using data collected from direct observations of nests. Due to logistical constraints associated with direct observations, Williams Jr et al. (1971) was only able to observe 7 nests, whereas this remote technique allowed me to detect and describe this behavior for all 53 nest attempts. To my knowledge, no modern research of wild turkey incubation behavior has described partial incubation. Also known as "brooding", "nonrhythmic incubation", "intermittent incubation", and "nest attendance", nest attendance prior to the onset of continuous or full incubation is common among many bird species and may serve several functions (Wang and Beissinger 2011). The measures of nest attendance I reported among wild turkey nests do not permit tests of predictions about the function(s) that partial incubation may have served, however, I list here several potential functions that would be interesting avenues for future research. Functions of partial incubation that do not require the transfer of heat between the incubating adult and eggs include benefits to adult condition/survival as a function of nest-site concealment and favorable microclimate (Wiebe and Martin 1998), and protection of nest against egg loss or brood parasitism (Wang and Beissinger 2011). Although reports of brood parasitism of wild turkey nests are uncommon (but see Schmutz 1988 and Krakauer 2003), it is possible that in areas where potential brood parasites are present, hens may spend more time on the nest to protect their investment (Petrie and Møller 1991). A function of partial incubation that may involve heat transfer between the incubating adult and eggs to protect eggs from direct environmental exposure (Brown and Downs 2003).

While the focus of this research was on the reproductive period of wild turkeys, classified accelerometer data from HMMs has also been used to examine activity levels of blacktip reef

sharks (*Carcharhinus melanopterus*) in response to temporal and tidal inputs (Leos-Barajas et al. 2017), soaring behavior of Verreaux's eagle (*Aquila verreauxii*) as a function of atmospheric conditions (Leos-Barajas et al. 2017), and different behavioral states among seabirds (Patterson et al. 2019). This avenue of research on cryptic wildlife and behaviors, particularly during a reproductive season, may provide wildlife scientists with data that can be used in tests of predictions to address questions such as: does the species make trade-offs between current and future fitness? Does the behavior influence life history traits (e.g., reproductive effort, survival rates)? To my knowledge, this is the first use of HMMs to describe nest attendance behavior for breeding birds and I believe this technique will provide scientists with a useful tool for future research.

An important takeaway from working through this method is that single data types may provide unreliable indications of behavior. During the validation process I discovered many location records that occurred on the nest were associated with activity states 3 and 4. I found that high activity levels associated with location data at the nest-site were in fact indicative of the hen departing from the nest (i.e., the start of a recess bout). As a result, it may not be as accurate to estimate time spent on the nest based solely on location data at the nest site (Bakner et al. 2019, Lohr et al. 2020). I had also expected low levels of activity to indicate incubation. However, hen movement levels were often reduced at locations away from the nest following the initial recess departure. I would expect to see similar patterns between location and activity states in other scenarios when an animal leaves a roost or den location to forage. Therefore, I encourage researchers interested in evaluating movement behavior to use location and activity data in tandem (when possible) to ensure reliable inferences are made.

In this study I used a combination of location and activity data, along with HMMs to detect behavior states among incubating wild turkeys. My intention throughout this study was to influence hen behavior as little as possible. From personal experience, and documentation of observer-induced abandonment among wild turkey nesting studies (Badyaev 1995, Byrne and Chamberlain 2013), I presumed any attempts to obtain continuous behavior data would likely influence hen behavior and at worst result in abandonment. HMMs provided an alternative to other machine-learning-based techniques and do not require observational data or training data. However, a basic understanding of the ecology of the species, at a minimum, is required to implement and interpret HMMs. The modeling process was time-intensive and required a steep learning curve yet provided me with a technique to work with remotely collected data to describe unobserved behavior. I encourage researchers interested in behavior analysis, particularly of cryptic species or unobservable behaviors, to consider adding HMMs to their analytical toolkit.

TABLES AND FIGURES

Table 3.1. Parameters of best fitting hidden Markov model used to classify behavioral states of Eastern wild turkey hens during the incubation period in south-central Illinois, USA during 2015 - 2018.

State	Mean	SD	Zeromass[1]	Presumed activity
1	2.28	1.42	0.98	inactive - sleep/incubation/self & nest maintenance
2	8.33	6.89	0.45	low activity - walking/foraging
3	61.32	34.37	0.00	medium activity - walking/running
4	151.77	60.95	0.00	high activity - running/flying

[1] The zeromass parameter represents the proportion of zero values in the data.

Table 3.2. List of hidden Markov models evaluated for classifying incubation period behaviors among Eastern wild turkeys in Illinois, USA during 2015 - 2018.

Model	Formula	Description
1	cosinor (hr, period = 24)	A cyclical function that assumes 24 hr periodicity
2	incubation day	e.g., 1, 2, 3…37
3	temperature	recorded at the same time interval as accelerometer data
4	temperature + incubation day	
5	cosinor (hr, period = 24) + incubation day	

Table 3.3. Results of hidden Markov model comparison predicting behavioral states among incubating Eastern wild turkey hens in Illinois, during 2015 - 2018.

Model	AIC	weight	ΔAIC
5	481884.15	1.00	0.00
1	481943.71	0.00	59.56
2	484032.45	0.00	2148.30
Null	484441.35	0.00	2557.20
4	485067.61	0.00	3183.46
3	485375.61	0.00	3491.46

Table 3.4. Model type and formula structure for models of incubation and recess bouts detected among Eastern wild turkeys in Illinois, USA during 2015 - 2018.

Model type	Response	Predictor	Random	Distribution
GLM[1]	Daily bout frequency	Nest attempt ID		Poisson
GLMM[2]	Daily bout frequency	Hen age	Nest attempt ID	Poisson
	Daily bout frequency	Nest age (days)	Nest attempt ID	Poisson
GLM[1]	Bout start time (AM/PM)	Nest attempt ID		Binomial
GLMM[2]	Daily AM/PM bout frequency	AM/PM	Nest attempt ID	Poisson
GLM[1]	Bout duration (hrs)	Nest attempt ID		Normal
LMM[3]	Bout duration (hrs)	Bout start time	Nest attempt ID	Normal
	Bout duration (hrs)	Nest age (days)	Nest attempt ID	Normal
	Bout duration (hrs)	AM/PM	Nest attempt ID	Normal

[1] Generalized linear model

[2] Generalized linear mixed model
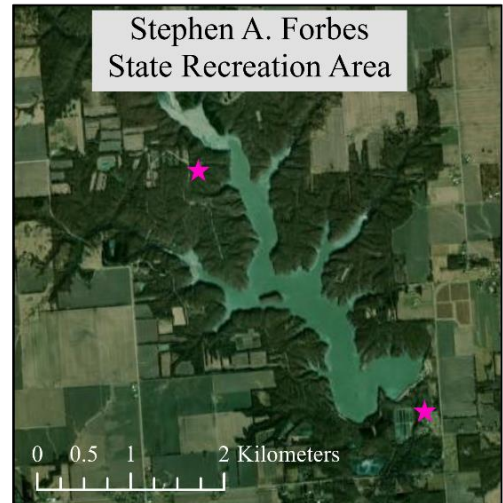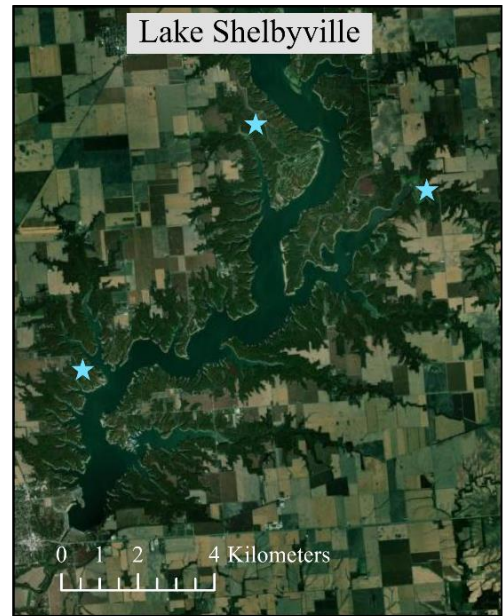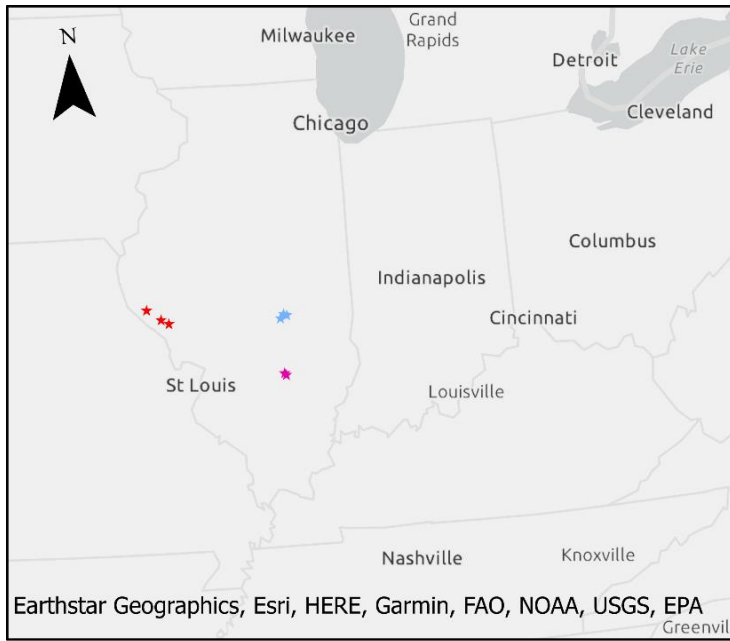
[3] Linear mixed model

Figure 3.1. Map of study areas in Illinois, USA where Eastern wild turkeys were captured and monitored during 2015 - 2018.
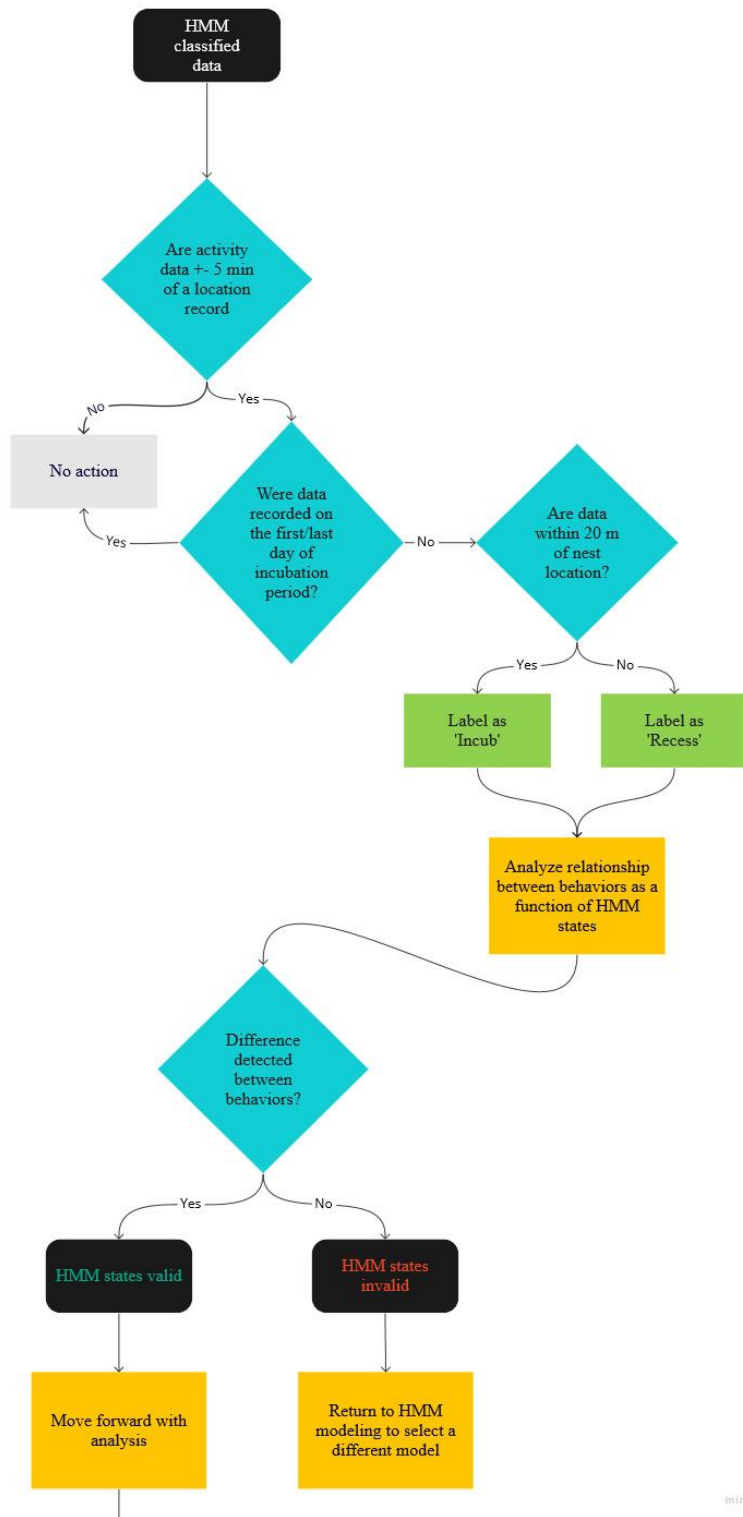
Figure 3.2. Workflow used to validate hidden Markov model-defined states of activity data collected from Eastern wild turkeys in Illinois, USA during 2015 - 2018.
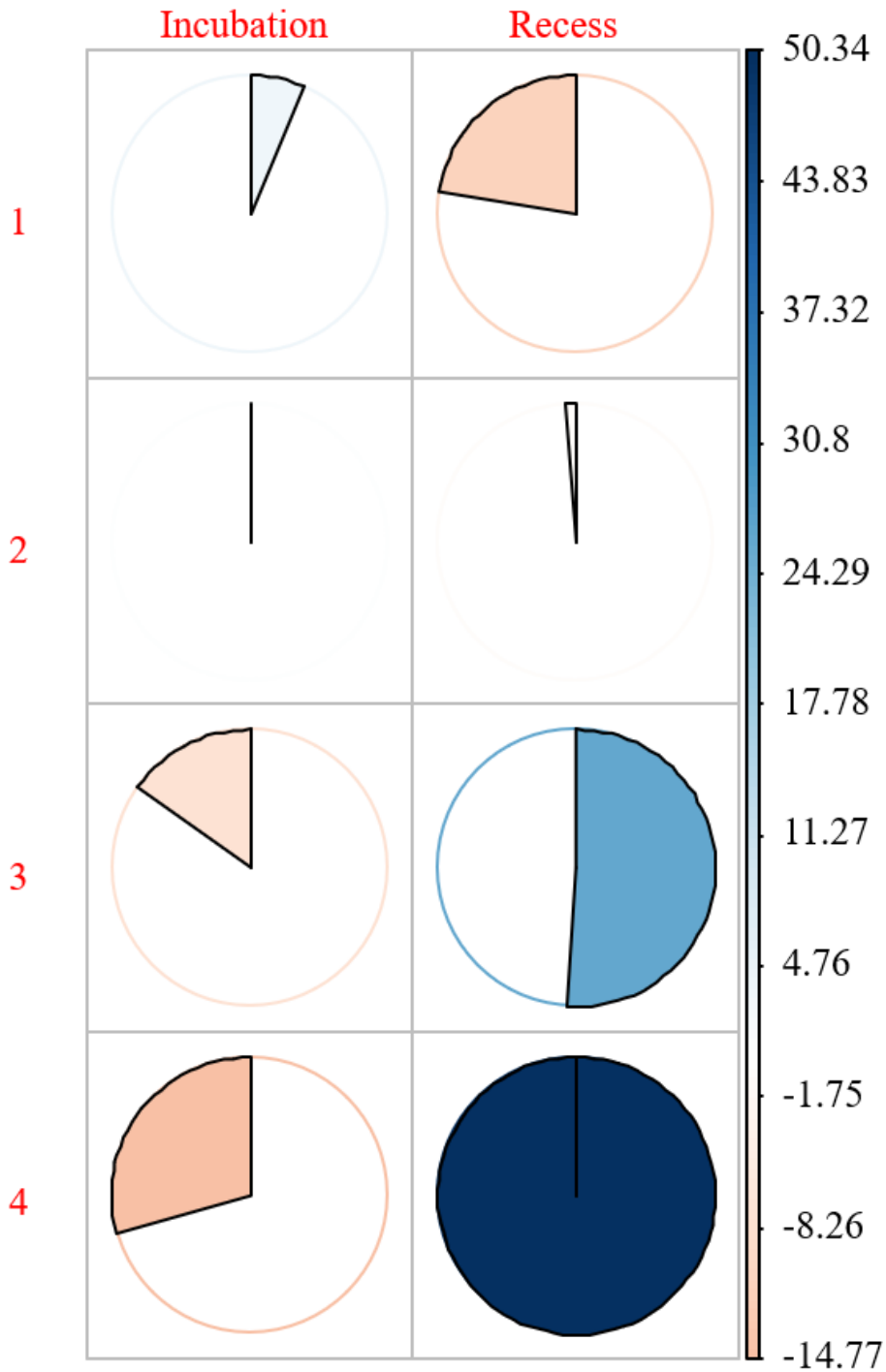
Figure 3.3. Correlation plot of residual values from chi-squared test of the relationship between location-based behaviors (incubation and recess) and behavioral states (1 - 4). Values along the color-gradient indicate the relative contribution of each behavioral state to the relationship ($p < 0.0001$) detected between behaviors and behavioral states.

Figure 3.4. Workflow used to summarize hidden Markov model-defined states of activity data collected from incubating Eastern wild turkey hens in Illinois, USA during 2015 - 2018.
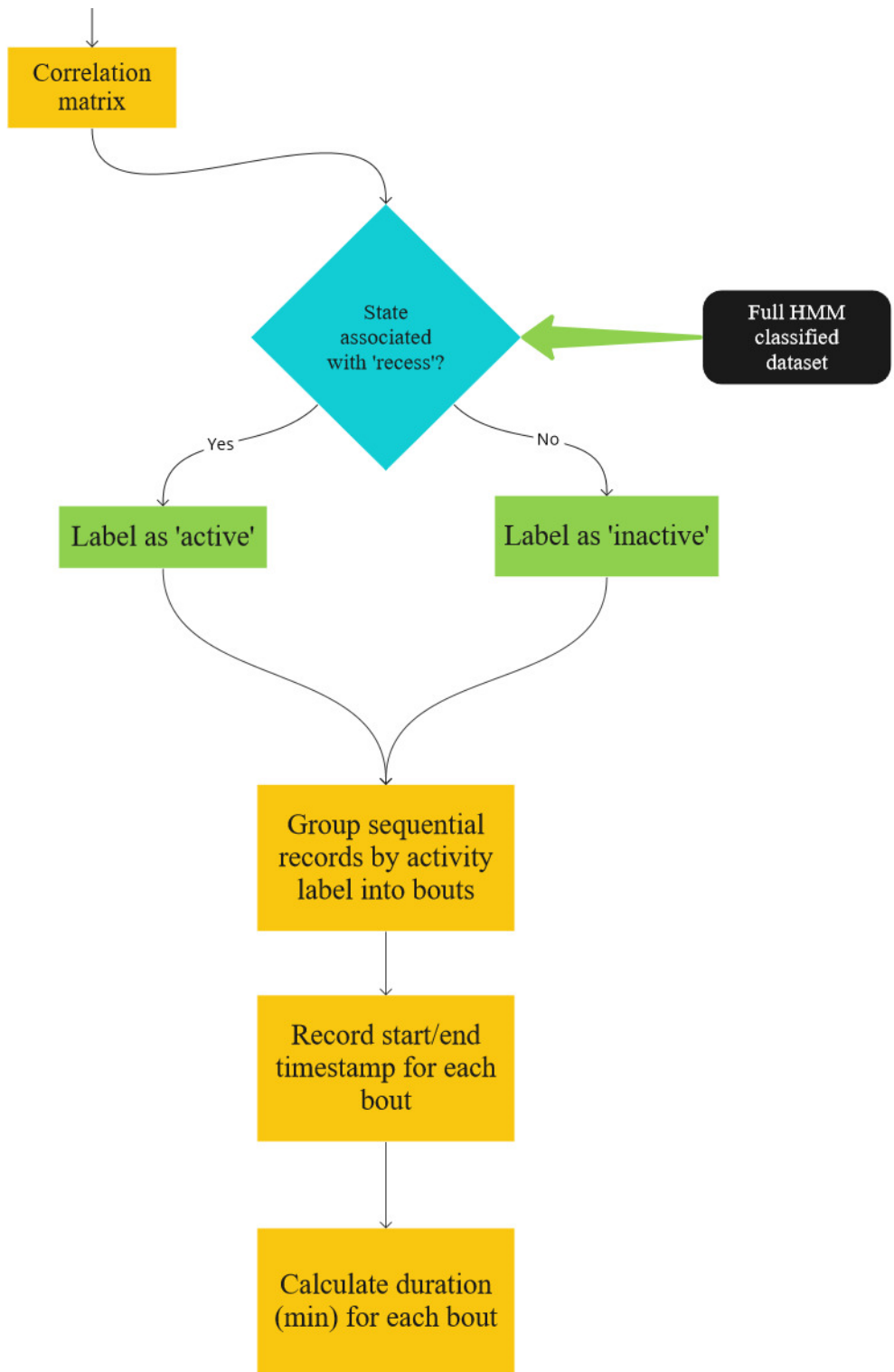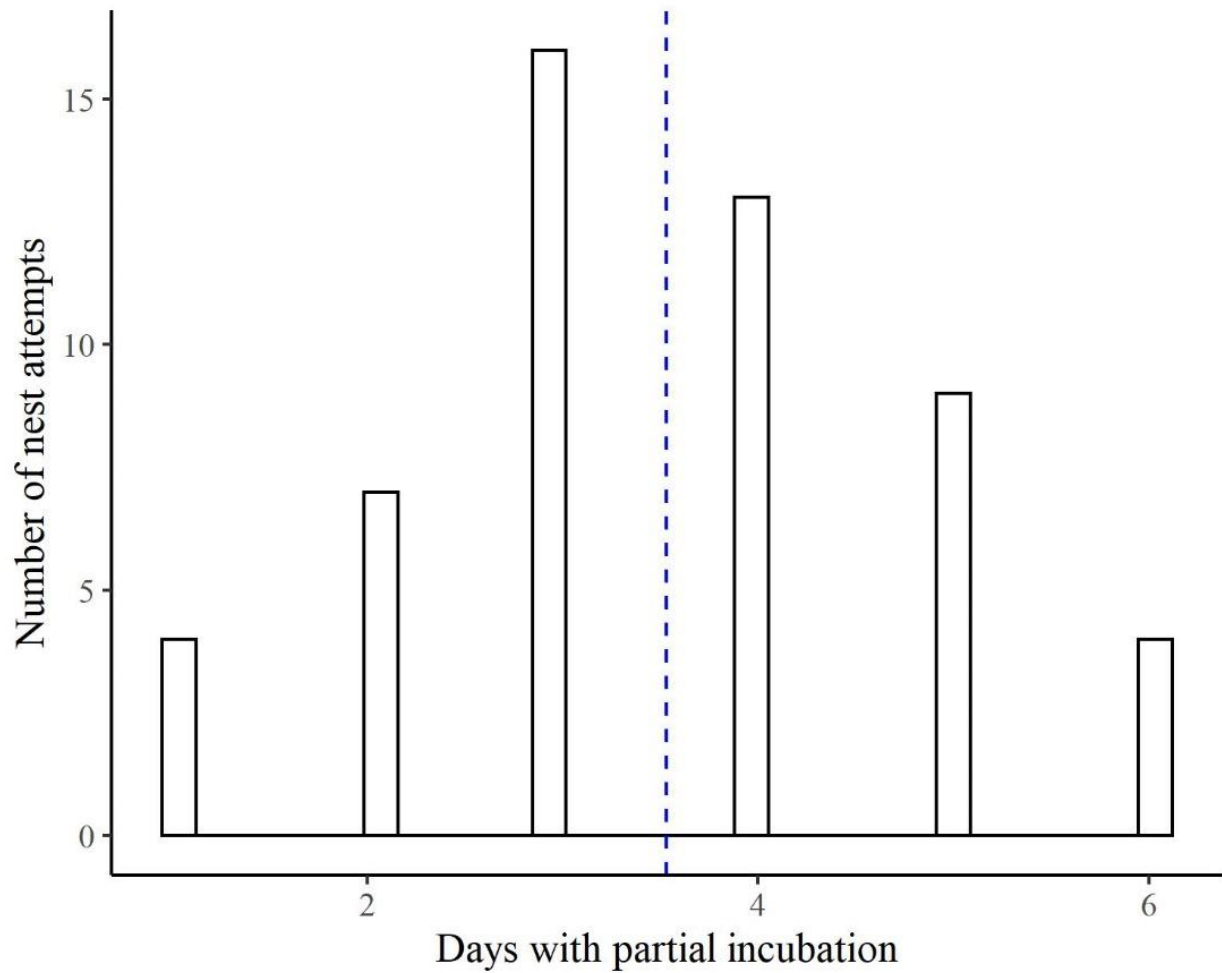
Figure 3.5. Histogram of the partial incubation period (days) prior to the first night a hen remained on the nest overnight among wild turkey nests monitored across Illinois during 2015 – 2018. Dashed blue line represents the mean number of days ($\bar{x} = 3.5 \pm 1.3$) a nest was partially incubated prior to the start of overnight incubation.
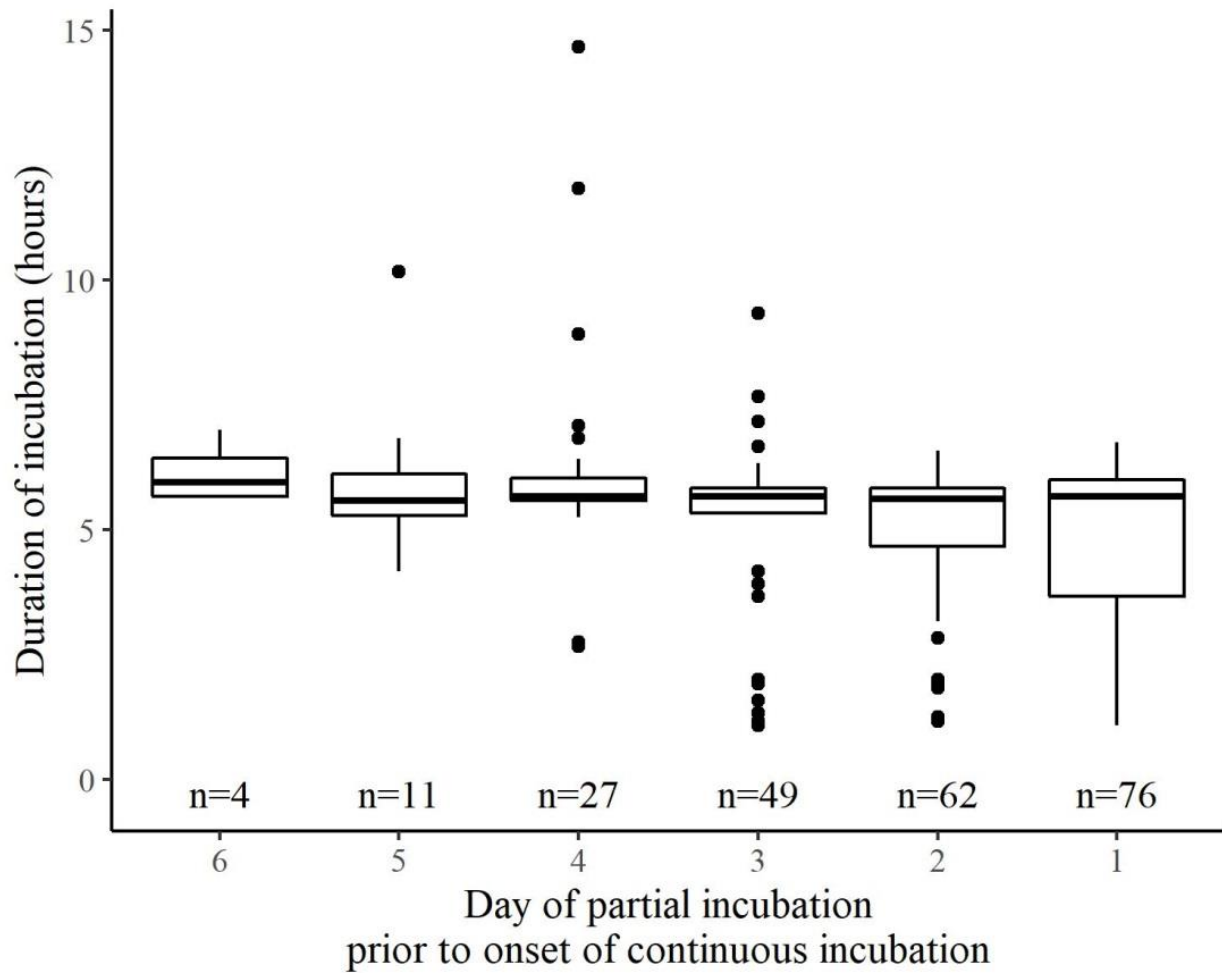
Figure 3.6. Boxplots illustrating the duration of partial incubation bouts for each day prior to the onset of continuous incubation among Eastern wild turkey nests in Illinois, during 2015 - 2018. Sample sizes along the x-axis indicate the number of partial incubation bouts detected on that day prior to continuous incubation. The number of nest attempts included in each day prior to onset of continuous incubation were: day 6 (4); day 5 (11); day 4 (26); day 3 (40); day 2 (49); and day 1 (53).
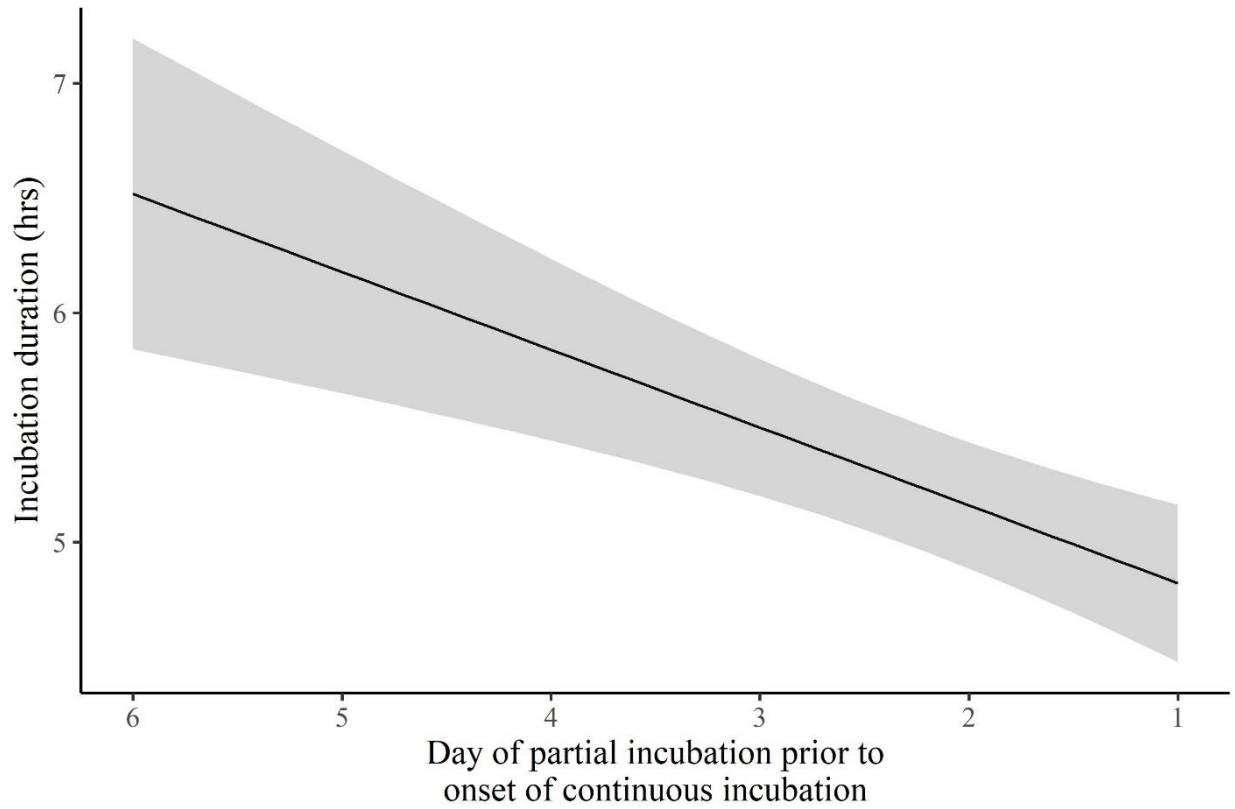
Figure 3.7. Predicted duration of incubation bouts as a function of number of days prior to the start of continuous during the partial incubation period among Eastern wild turkeys in Illinois, during 2015 - 2018.
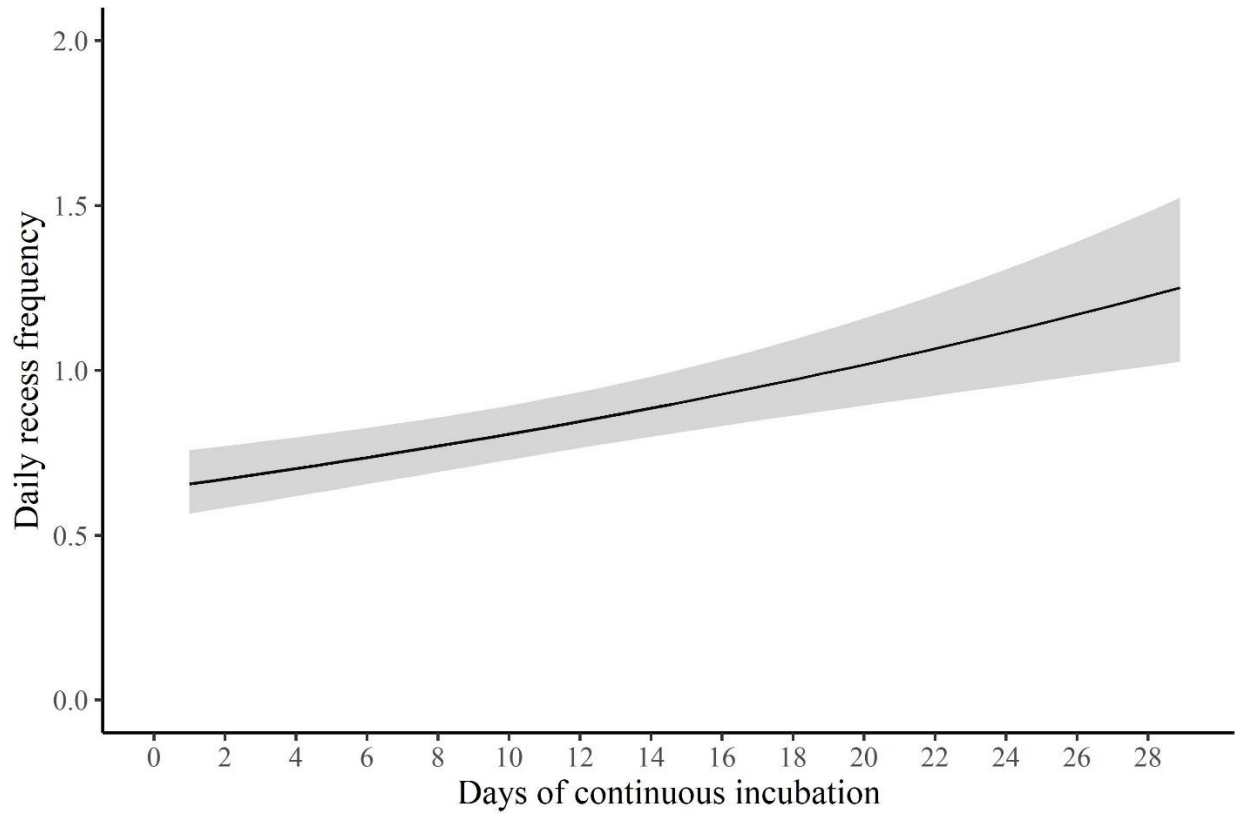
Figure 3.8. Predicted daily recess frequency as a function of days of continuous incubation among all nest attempts by Eastern wild turkeys in Illinois, during 2015 - 2018. Gray shading indicates 95% confidence intervals.
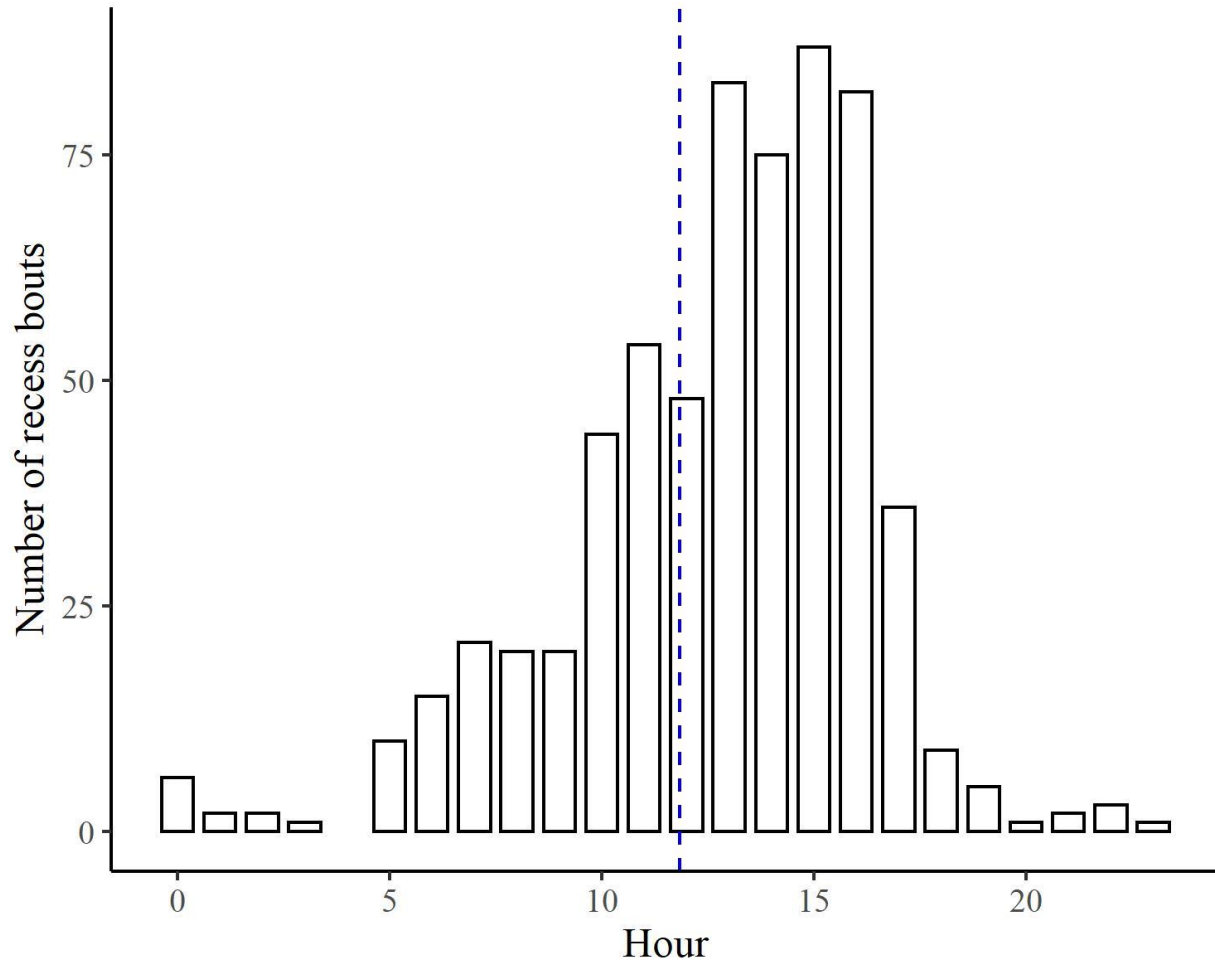
Figure 3.9. Hourly start of recess activity among incubating Eastern wild turkey hens across Illinois, during 2015 - 2018.

Figure 3.10. Predicted daily cumulative time (hours) spent in recess as a function of days of continuous incubation among Eastern wild turkey hens in Illinois, during 2015 - 2018.

REFERENCES

Amininasab, S. M., S. A. Kingma, M. Birker, H. Hildenbrandt, and J. Komdeur. 2016. The effect
of ambient temperature, habitat quality and individual age on incubation behaviour and
incubation feeding in a socially monogamous songbird. Behavioral Ecology and
Sociobiology **70**:1591-1600.

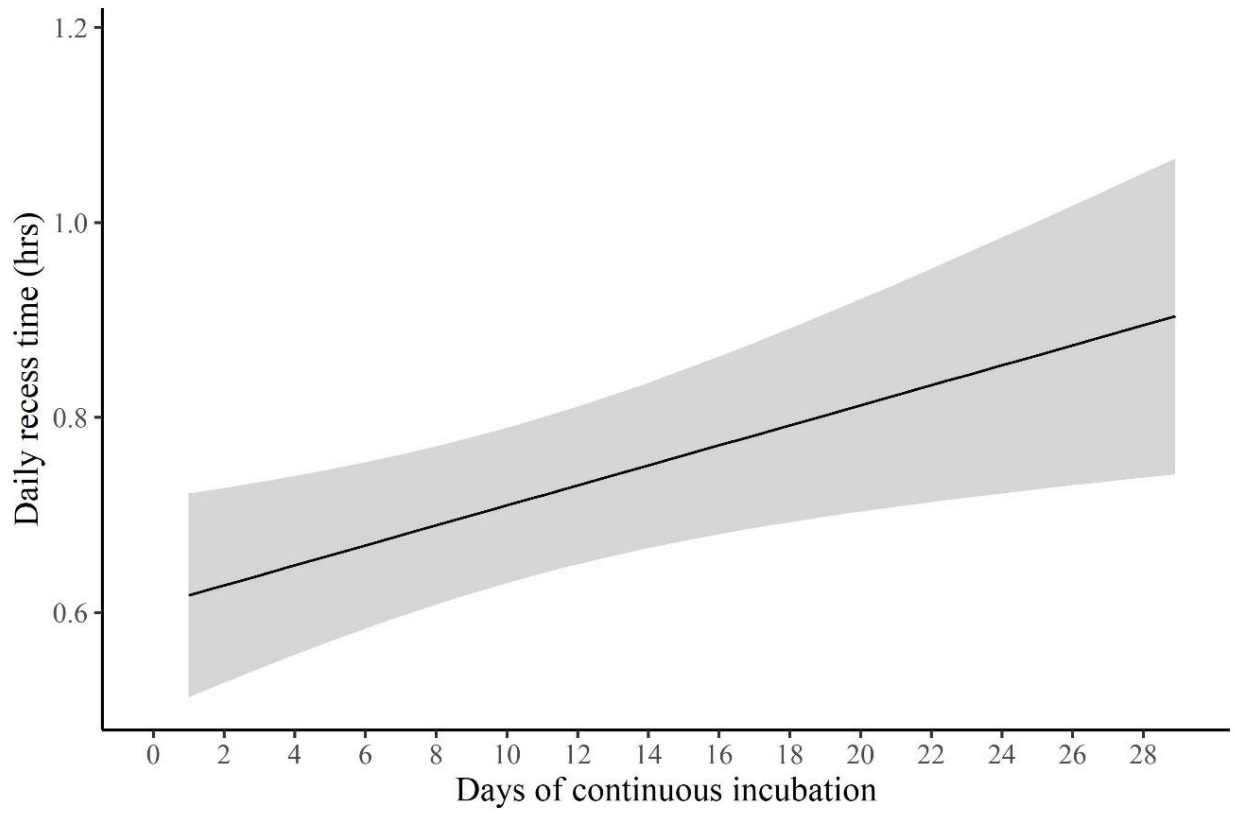Badyaev, A. V. 1995. Nesting habitat and nesting success of eastern wild turkeys in the Arkansas
Ozark Highlands. Condor **97**:221-232.

Bakner, N. W., L. R. Schofield, C. Cedotal, M. J. Chamberlain, and B. A. Collier. 2019.
Incubation recess behaviors influence nest survival of wild turkeys. Ecology and
Evolution **9**:14053-14065.

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

Bidder, O. R., H. A. Campbell, A. Gomez-Laich, P. Urge, J. Walker, Y. Cai, L. Gao, F.
Quintana, and R. P. Wilson. 2014. Love thy neighbour: automatic animal behavioural
classification of acceleration data using the K-nearest neighbour algorithm. PloS one
9:e88609.

Body, G., R. B. Weladji, and Ø. Holand. 2012. The recursive model as a new approach to
validate and monitor activity sensors. Behavioral Ecology and Sociobiology **66**:1531-
1541.

Brown, D. D., R. Kays, M. Wikelski, R. Wilson, and A. P. Klimley. 2013. Observing the
unwatchable through acceleration logging of animal behavior. Animal Biotelemetry **1**:20.

Brown, M., and C. T. Downs. 2003. The role of shading behaviour in the thermoregulation of
breeding crowned plovers (*Vanellus coronatus*). Journal of Thermal Biology **28**:51-58.

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

Campbell, H. A., L. Gao, O. R. Bidder, J. Hunter, and C. E. Franklin. 2013. Creating a behavioural classification module for acceleration data: using a captive surrogate for difficult to observe species. The Journal of Experimental Biology. **216**:4501-4506.

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

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

Deeming, C. 2002. Avian incubation: behaviour, environment and evolution. Oxford University Press, Oxford.

Dickson, J. G. 1992. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, PA.

Drake, K. L., R. T. Alisauskas, and A. M. Calvert. 2018. Experimental test for a trade-off between successful nesting and survival in capital breeders with precocial offspring. The Auk:637-646.

DuRant, S. E., W. A. Hopkins, D. M. Hawley, and G. R. Hepp. 2012. Incubation temperature affects multiple measures of immunocompetence in young wood ducks (*Aix Sponsa*). Biology letters **8**:108-111.

DuRant, S. E., W. A. Hopkins, G. R. Hepp, and J. R. Walters. 2013. Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. Biological Reviews **88**:499-509.

Fontaine, J. J., and T. E. Martin. 2006. Parent birds assess nest predation risk and adjust their

        reproductive strategies. Ecology Letters **9**:428-434.

Green, H. E. 1982. Reproductive-behavior of female wild turkeys in northern lower Michigan.

        Journal of Wildlife Management **46**:1065-1071.

Hohman, W. L. 1986. Incubation rhythms of ring-necked ducks. Condor **88**:290-296.

King'Ori, A. 2011. Review of the factors that influence egg fertility and hatchability in poultry.

        International Journal of poultry science **10**:483-492.

Krakauer, A. 2003. California quail lays egg in wild turkey nest. Western Birds **34**:169-170.

Leopold, A. S. 1943. The molts of young wild and domestic turkeys. The Condor **45**:133-145.

Leos-Barajas, V., T. Photopoulou, R. Langrock, T. A. Patterson, Y. Y. Watanabe, M.

        Murgatroyd, and Y. P. Papastamatiou. 2017. Analysis of animal accelerometer data using

        hidden Markov models. Methods in Ecology and Evolution **8**:161-173.

Lohr, A. K., J. A. Martin, G. T. Wann, B. S. Cohen, B. A. Collier, and M. J. Chamberlain. 2020.

        Behavioral strategies during incubation influence nest and female survival of wild

        turkeys. Ecology and Evolution **10**:11752-11765.

McClintock, B. T., R. Langrock, O. Gimenez, E. Cam, D. L. Borchers, R. Glennie, and T. A.

        Patterson. 2020. Uncovering ecological state dynamics with hidden Markov models.

        Ecology Letters **23**:1878-1903.

McClintock, B. T., and T. Michelot. 2018. momentuHMM: R package for generalized hidden

        Markov models of animal movement. Methods in Ecology and Evolution **9**:1518-1530.

Meixell, B. W., and P. L. Flint. 2017. Effects of industrial and investigator disturbance on

        Arctic-nesting geese. The Journal of Wildlife Management **81**:1372-1385.

Nathan, R., O. Spiegel, S. Fortmann-Roe, R. Harel, M. Wikelski, and W. M. Getz. 2012. Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. The Journal of Experimental Biology. **215**:986-996.

Nord, A., and C. B. Cooper. 2020. Night conditions affect morning incubation behaviour differently across a latitudinal gradient. Ibis **162**:827-835.

Nord, A., and J. B. Williams. 2015. The energetic costs of incubation. Pages 152-170 Nests, eggs, and incubation: new ideas about avian reproduction. Oxford University Press, USA.

Paisley, R. N., R. G. Wright, J. F. Kubisiak, and R. E. Rolley. 1998. Reproductive ecology of eastern wild turkeys in southwestern Wisconsin. The Journal of Wildlife Management **62**:911-916.

Parker, C., W. M. Schelsky, L. Garver, and J. P. Hoover. 2021. Pyrodiversity matters: wild turkey habitat selection in a fire managed landscape. Forest Ecology and Management.

Patterson, A., H. G. Gilchrist, L. Chivers, S. Hatch, and K. Elliott. 2019. A comparison of techniques for classifying behavior from accelerometers for two species of seabird. Ecology and Evolution **9**:3030-3045.

Petrie, M., and A. Møller. 1991. Laying eggs in others' nests: intraspecific brood parasitism in birds. Trends in Ecology & Evolution **6**:315-320.

Pyle, P. H., Steve N.G.; Ruck, Siobhan; Desante, David F. 2008. Identification Guide to North American birds, Part II Anatidae to Alcidae. Slate Creek Press, Point Reyes Station, California.

Schmutz, J. A. 1988. Ring-necked Pheasant parasitism of Wild Turkey nests. The Wilson Bulletin **100**:508-509.

Smith, J., C. Cooper, S. Reynolds, D. Deeming, and S. Reynolds. 2015. Advances in techniques to study incubation. Pages 179-195. Nests, eggs, and incubation: new ideas about avian reproduction. Oxford University Press, USA.

Spohr, S. M. 2001. Variables influencing nest success of eastern wild turkeys in Connecticut: nesting habitat, home range-scale fragmentation, and nest attentiveness. University of Maine, Electronic Theses and Dissertations.

Steven, C. T., and D. G. Raveling. 1987. Incubation behavior of emperor geese   compared with other geese: Interactions of predation, body size, and energetics. The Auk **104**:707-716.

Urbano, F., and F. Cagnacci. 2014. Spatial database for GPS wildlife tracking data. Springer.

Wall, J., G. Wittemyer, B. Klinkenberg, and I. Douglas-Hamilton. 2014. Novel opportunities for wildlife conservation and research with real-time monitoring. Ecological Applications **24**:593-601.

Wang, G. 2019. Machine learning for inferring animal behavior from location and movement data. Ecological Informatics **49**:69-76.

Wang, J. M., and S. R. Beissinger. 2011. Partial incubation in birds: Its occurrence, function, and quantification. The Auk **128**:454-466.

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.

Williams Jr, L. E., D. H. Austin, T. E. Peoples, and R. W. Phillips. 1971. Laying data and nesting

behavior of wild turkeys. Pages 90-106 *in* Proceedings of the Annual Conference of the

Southeastern Association of Game and Fish Commissioners.

Yeldell, N. A., B. S. Cohen, T. J. Prebyl, B. A. Collier, and M. J. Chamberlain. 2017. Prescribed

fire influences habitat selection of female eastern wild turkeys. The Journal of Wildlife

Management **81**:1287-1297.

CHAPTER 4: FACTORS INFLUENCING DAILY NEST SURVIVAL OF EASTERN WILD TURKEYS

ABSTRACT

During the reproductive season predation risk is high, particularly for ground-nesting bird species. Research suggests that birds can mediate this form of natural selection by selecting well-concealed nest sites and reducing trips to and from the nest location. However, for wild turkeys it remains unclear whether these forms of reproductive investment lead to increases in nest survival. I studied the influence of extrinsic (e.g., habitat, temperature, and landscape factors) and intrinsic (e.g., incubation recess behavior) factors on daily nest survival rate (DSR) among Eastern wild turkeys (*Meleagris gallopovo silvestris*) in Illinois (2015 – 2018). I monitored 50 Eastern wild turkey hens using backpack-type micro-GPS units and evaluated the DSR among 48 nest attempts. I observed 38 failures and 6 successes among the nest attempts included in this analysis, and apparent nest success was 14% across years. Among the final 12 candidate models of DSR that I evaluated, visual obstruction 51-100 cm above ground level was the top ranked model and was the only factor to improve predictions of DSR relative to the constant survival model. These results suggest that hens may exhibit a variety of incubation recess behavior that may not necessarily influence DSR. Moreover, hens may use sites with a range of visual obstruction conditions but are more likely to experience reduced DSR when nests are more concealed.

INTRODUCTION

Reproductive investment by breeding birds is the result of trade-offs between current and future fitness (Badyaev and Ghalambor 2001, Ghalambor and Martin 2001, Fontaine and Martin 2006). Nesting mortality can limit population growth and fitness by reducing nest success, immature bird survival, and adult survival (Newton 1998). To maximize the probability of raising young, incubating birds must maintain a favorable thermal environment for developing embryos, maintain their own energy reserves, and minimize predation risk to the nest and themselves (Flint and Grand 1999). Predation is the primary cause of nesting mortality among most bird species and is an important source of natural selection. Research indicates that birds can mediate predation risk by varying reproductive strategies, such as parental behavior and habitat selection (Martin 1993b, Merrill et al. 2016).

Habitat selection theory suggests that during the breeding season different habitats are available to birds, and fitness is maximized by selecting nest locations based on perceived habitat cues and the competitive ability of breeding individuals (Levin et al. 2009, Chalfoun and Martin 2010). Within a selected habitat, birds should select a nest location that provides concealment to the nest and incubating adult, while providing open views for the incubating adult to be able to detect and react to approaching predators (Götmark et al. 1995, Howlett and Stutchbury 1996, Wiebe and Martin 1998). Presumably, habitats with greater diversity in vegetation cover and structure can provide more potential nest sites and can increase the time spent by predators searching for prey (Martin 1993b). The habitat and nest site can also determine the predator community to which birds will be exposed, and the effectiveness of reproductive strategies, such as nest attentiveness and concealment (Martin 1993a, Rangen et al. 1999). For example, among ground-nesting species, selecting nest sites based on nest concealment is most beneficial for the

egg stage and is largely motivated by predators using visual cues (Latif et al. 2012). Among bird species that experience predation risk from predators using different cues (e.g., heat, scent), nest concealment may be less important as a factor in nest survival (Rangen et al. 1999).

Nest attentiveness during incubation is another behavioral form of reproductive investment that may influence nesting mortality (Bueno-Enciso et al. 2017, Lohr et al. 2020). Departures from the nest (i.e., incubation recesses) provide the attending adult opportunities to forage and defecate away from the nest (Lohr et al. 2020), but too much activity near the nest may increase predation risk (Allen Smith et al. 2007). The female of many bird species, without male assistance, relies primarily on internal reserves of energy and nutrients to form and incubate a clutch of eggs (Thompson and Raveling 1987, Deeming 2002). Energy reserves of incubating females influence how much time is spent between and during incubation recesses to forage (Aldrich and Raveling 1983, Thompson and Raveling 1987, Bueno-Enciso et al. 2017). Individuals that invest more time incubating generally have shorter incubation periods, and often have greater nest success, relative to less attentive individuals (Aldrich and Raveling 1983, Deeming 2002, Bueno-Enciso et al. 2017). However, the relationship between incubation behavior and nest survival remains unclear for many species.

Ground nesting species are exposed to multiple predators that use different cues (i.e., visual, scent, heat) to locate nests, experience high amounts of nest predation, and may subsequently exhibit greater variation in life history traits, habitat use, and population patterns (Ellis-Felege et al. 2012, Melville et al. 2014). In Chapter 3 of this dissertation, I described the variation that Eastern wild turkeys (*Meleagris gallopovo silvestris*) exhibit in recess behavior, so here I sought to understand the relative role of incubation recess behavior and extrinsic factors on daily nest survival within a ground-nesting, precocial species. Reproductive success limits

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wild turkey population growth (Badyaev 1995, Paisley et al. 1998, Byrne and Chamberlain 2013), and nest mortality (here defined as complete failure of nests or death of hens while nesting) is primarily a function of predation (Vangilder et al. 1987, Vanderhaegen et al. 1988). Predation risk may influence where turkeys place nests (Porter 1992), and locations with greater visual concealment typically experience lower rates of nest predation (Badyaev 1995). Nest survival among turkeys may also be influenced by variation in recess activity during the incubation period, wherein hens depart from the nest to forage and defecate (Bakner et al. 2019, Lohr et al. 2020). From my own work on incubation behavior among Eastern wild turkeys, I detected variation in recess frequency and cumulative time spent in recess (see Chapter 3 of this dissertation). Here I examined the influence of recess behavior in addition to nest age, ambient temperature, visual obstruction, and landscape features on daily nest survival rates (hereafter "DSR") among Eastern wild turkeys in Illinois (Table 4.1). I expected that metrics of recess behavior would be better predictors of DSR relative to other effects - habitat, temporal, landscape, and temperature. More specifically, I predicted that DSR would decrease among nests when (a) total time and frequency of recesses increased, (b) visual obstruction was low, (c) ambient temperatures were very high or very low, (d) distance to road decreased, or (e) distance to water source decreased.

STUDY AREA

I studied nest survival among Eastern wild turkeys among three study areas across Illinois which included: Stephen A. Forbes State Recreation Area in Kinmundy, IL (herafter 'Forbes'; two sites); Lake Shelbyville area (hereafter 'Shelbyville'; three sites); and Western Illinois (three sites; hereafter 'W. IL.'; Fig. 4.1). Individual sites within each study area represent separate locations where we captured and monitored turkeys. Although all capture sites in Forbes

and Shelbyville were located on public lands, all capture sites in W. IL and many nest locations in all study areas occurred on private land. All study areas were comprised of a mix of agricultural row-crops (e.g., corn (*Zea mays*) and soy beans (*Glycine max*)), grassland/pasture, and oak-hickory (*Quercus* spp.-*Carya* spp.) forests.

Forbes is a 1256 ha multiuse recreation area that includes 465 ha of oak-hickory forest, open water (29 km of shoreline), grass-pasture, agricultural fields, and herbaceous wetlands (Parker et al. 2021). Land managers used prescribed fire and selective thinning to reduce invasive vegetation and to encourage regeneration of oak species.

Shelbyville is a vast patchwork of private, and public lands that include developed recreation sites, 276 kilometers of shoreline, and wildlife management areas amid ≥1000 ha of upland forest comprised of oak, hickory, and maples (*Acer* spp.). Land managers encouraged regeneration of oak species and manage invasive vegetation using selective tree thinning, prescribed fire, mechanical shrub removal, and aerial herbicide application.

W. IL. includes three private properties (i.e., Buckeye, McAllister, and Syrcle) located in Pike County. The capture site at Syrcle property is grazed by cattle, however, the surrounding landscape includes large, forested areas and agricultural cropland. The Buckeye property is an area managed for hunting and fishing recreation. Food plots (e.g., sunflowers (*Helianthus*) and radishes (*Raphanus raphanistrum*)) were part of the area and varied among years. The general landscape surrounding Buckeye included forest, grassland/pasture, and agricultural cropland. The McAllister property was also managed for hunting and fishing opportunities and included managed food plots (e.g., corn). The landscape surrounding McAllister included forest, grassland/pasture, and agricultural cropland.

METHODS

Turkey capture and tagging

During January – March of 2015 – 2018 I captured Eastern wild turkeys using drop nets and air cannons that were baited with cracked corn. I banded the leg of each captured turkey with an aluminum rivet band (National Band and Tag Company, Newport, Kentucky), and documented age as second year (i.e., in its second calendar year following hatch; hereafter "SY") or after second year (hereafter "ASY") based on the shape, wear, and barring of the 9th and 10th primaries (Leopold 1943). I determined sex using a combination of morphological features (e.g., caruncle coloration, beard presence/length, spur presence, and breast feather coloration; Pyle 2008), and fitted hens with a 100-g (~ 2% body weight) MiniTrack GPS unit (μGPS; Lotek Wireless Inc., Ontario, Canada). I programmed each μGPS to record a location (accurate to 20 m) every two hours during daylight hours, and once at midnight (Cohen et al. 2018). The μGPS accelerometer continuously measured hen movement and recorded the mean value within 5-minute intervals. Accelerometer values were reported for two axes: *x* (sideways/rotary motion) and *y* (forward/backward motion). The mean accelerometer values for each axis were aligned on a linear numeric scale ranging from 0 – 255 (unitless values; hereafter referred to as "activity data"). Once weekly until the μGPS no longer transmitted a signal, I relocated hens using a 3-element Yagi antenna and a receiver (R-1000, 148-160 MHz, Communications Specialists Inc.), and remotely downloaded all data using a Handheld Command Unit (Lotek Wireless Inc., Ontario, Canada). At distances up to 500 m, I was able to remotely download data, where I presumed my presence did not influence turkey movements. These methods were approved by the University of Illinois at Urbana-Champaign Institutional Animal Care and Use Protocol (#15010) and were described previously in Parker et al. (2021).

Virtual nest monitoring

To determine when nesting behaviors began and ended for each hen, I examined location and activity data following each weekly data download as described by Parker et al. (2021). When location data for an individual indicated smaller daily movements, I evaluated the activity data for that hen (Yeldell et al. 2017b). I inspected the activity data of each hen for periods of inactivity during daylight hours, as indicated by x and y values of < 15. I assumed incubation started when a hen remained inactive for at least 2.5 hours during daylight hours, and daily locations were generally within a radius of ≤ 50 m. I monitored the data for each incubating hen to detect signs of nest abandonment, predation, or a successful hatch. I assumed a continuous incubation period of 28 days was needed for successful hatching of eggs (Paisley et al. 1998), and that incubation ended when location and activity data signaled the hen moved away from the nest location without returning. I verified the location of each terminated nest in the field using a central GPS point from hen location data and searched the nest area for signs of abandonment, predation, or success. I determined nest status based on egg conditions (i.e., abandoned: intact and whole; predated: crushed and scattered; successful hatch: intact and in halves). I also located the female and flushed her twice within the two-week period immediately following nest termination to survey for poults. The nest was considered successful when at least one poult was present with the tagged hen. Some nests may have been predated soon following a successful hatch, so nests and respective hens were located as soon as possible post-hatch to reduce the probability of this source of bias (Yeldell et al. 2017a). I also estimated time of nest failure among predated nests using the location data to determine the first location away from the nest, and then examining activity data that were recorded before and after that location to define a

more precise time or time period of when the hen departed. I classified each nest as predated during night or day, as defined by daily sunrise and sunset times.

Incubation behavior classification

To accommodate the large volume of data produced by µGPS units, activity and location data were stored and managed in a PostgreSQL 13 database (The PostgreSQL Global Development Group 2018), and then classified into four behavioral states using hidden Markov models created in R (R Core Team 2016). The data selected for each nest attempt occurred only between the start and end dates of continuous incubation. Variation in definitions of 'nest attempt' is a source of bias that can lead to incorrect conclusions and inappropriate comparisons of success and relative site quality among analyses of daily nest survival (Garcia and Conway 2009). Therefore, in the following analyses 'nest attempts' refers only to nests that experienced continuous incubation behavior. Described in complete detail in Chapter 3 of this dissertation, I used hidden Markov models to classify activity data from the continuous incubation period into four behavioral states (McClintock and Michelot 2018, McClintock et al. 2020), and grouped all records into bouts of behavior (states 1-2: inactive; states 3-4: active). I calculated daily values of recess frequency and total time in recess, and mean recess duration for each nest attempt. On the last day a nest was incubated, the value of each behavior was set as the covariate mean for a given nest attempt to avoid inflating recess values with data that instead represented post-hatch or fail movement.

Vegetation Surveys

Although wild turkey hens do not usually construct nests beyond scraping a shallow depression in the ground, they appear to select nest sites that provide concealment (i.e., visual obstruction) for the incubating hen and for the eggs when the hen is away from the nest

(Badyaev et al. 1996, Little et al. 2016). To determine the influence of visual obstruction at nest sites on DSR, I surveyed nest-site vegetation within two weeks of incubation termination, with some exceptions due to logistical issues. I did not survey vegetation at five nests because I was unable to obtain land access permission (n = 2), or the nests were detected virtually after the field season (n = 3). I measured visual obstruction at 15 m from the nest bowl, in each cardinal direction, using a density board (Nudds 1977). In each direction from a nest, I recorded an index of vegetation cover for each height level represented on the density board, including 0-50 cm, 51-100 cm, and 101-200 cm above ground level. Cover index values indicating the percent of the cover board range covered by vegetation were: [1] < 2.5%, [2] 2.5 – 25%, [3] 26 – 50%, [4] 51 – 75%, [5] 76 – 95%, and [6] > 95%. For each nest, I calculated the mean index value of vegetation cover for each height level.

Landscape Data

Previous research indicates that wild turkeys often nest along linear corridors (e.g., roads, trails) where nest predation is high relative to sites farther from habitat edges (Cobb and Doerr 1997, Thogmartin 1999, Byrne and Chamberlain 2013). Proximity to a water source is valuable for incubating hens but is also important for other wildlife, including nest predators. Therefore, I expected proximity to roads and water would negatively influence wild turkey nest survival. To determine the distance to nearest road and water body, I obtained Illinois road data for 2018 from the US Census Bureau TIGER Geodatabase (Bureau 2018), and I obtained Illinois hydrography data for 2018 from the US Geological Survey National Hydrography Dataset (Survey 2020). In ArcGIS Pro, I used the 'Near' tool to measure the distance between each nest and the nearest road and waterbody feature (ArcGIS Pro v.2.7.3, Redlands, CA: Environmental Systems Research Institute).

Temperature Data

Many studies have documented the influence of ambient temperature conditions on DSR and indicate that extreme temperatures are likely to disrupt development of embryos, which may lead to nest failure (Conway and Martin 2000, Brown and Downs 2003, Deeming and Reynolds 2015). Therefore, I expected to observe a decrease in DSR with an increase in the daily maximum temperature difference and with increasing ambient temperature. To understand how daytime ambient temperature influenced DSR among Eastern wild turkey nests, I collected temperature data from each µGPS unit and used daily sunrise and sunset times to limit the data to daytime temperature readings. I summarized the temperature readings for each day of incubation for each nest attempt to produce a daily mean temperature value (C°), and the maximum difference in extreme temperatures (i.e., max. temp. – min. temp.). The value of temperature covariates on the last day a nest was incubated was set as the covariate mean for that nest attempt to exclude temperature data that were recorded post-hatch or fail.

Statistical analyses

I calculated all data summaries and conducted all statistical modeling in program R (v4.0.5; R Core Team, 2016). I created generalized linear mixed models to evaluate the influence of 13 individual predictor variables on daily nest survival (Table 4.1). Including hen age as a random effect, models of daily nest survival were fit with a binomial distribution and logit link. To model daily nest survival as a binary response, I coded the status for each day of an incubation period a nest was active as '1', and as '1' on the day a nest successful hatched or '0' on the day a nest failed. Nests categorized as "unknown" status were censored to the day prior to when the nest became inactive. I excluded the five nests with missing vegetation survey data from model comparisons to permit comparisons among all models of nest survival. One nest was

abandoned due to presumed observer influence, and I decided to retain this nest in the analysis because by censoring it I would lose potentially valuable information about hens that abandon nests, which is not uncommon (Vangilder et al. 1987, Haegen et al. 1988, Crawford et al. 2021). To evaluate support for models of DSR I ranked models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) and calculated model weights ('AICcmodavg'; Mazerolle 2020). I considered models with $\Delta AICc \leq 2$ and to be competing models. Since my primary objective was to evaluate the ability of recess behavior to predict DSR, and metrics of recess were highly correlated, I created univariate models of DSR that included each behavior metric. I also sought to examine the influence of behavior on DSR relative to habitat, landscape, temporal, and temperature effects, which I expected would also influence recess behavior among incubating hens. Therefore, I selected top-ranking effects from each category of models (Table 4.2) and included only effects with low correlation coefficients ($r \leq |0.7|$) in models that were included in the final set of candidate models of DSR. The final set of candidate models includes univariate incubation recess models, univariate models of top-ranking covariates from other model categories (i.e., landscape, visual obstruction, temperature, and temporal effects), and interactions between incubation recess metrics and top-ranking covariates. I reported 85% confidence limits for model parameters because they provide inferences that closely align with results from AIC_c analyses. (Arnold 2010, Powell and Gale 2015).

RESULTS

From 2015 – 2018, I detected 62 Eastern wild turkey nest attempts and had complete data for 48 nests to model nest survival (Table 4.3). I was unable to include five nests that were missing vegetation data, eight nests that were missing behavior data, and one nest that never entered continuous incubation. Of the 48 nests for which I modeled nest survival, 38 failed and 6

succeeded (Table 4.4). Apparent nest success was 14% across years. Among the nests that failed, I documented probable causes of failure as abandonment (n = 4), predation (n = 22), and I was unable to determine cause of failure for 12 nests. Nests that failed due to predation occurred both during day (n = 9) and night hours (n = 13).

The overall daily nest survival rate was 0.95 (85% CI: 0.93, 0.96). One model predicting DSR received strong support (ΔAICc ≤ 2) and ranked higher than the constant survival model (Table 4.5). The top-ranked model of DSR was visual obstruction between 51 – 100 cm at the nest; as values of visual obstruction increased, DSR decreased (β = -0.19, 85 % CI's: -0.34, -0.04; Fig. 4.2). All other candidate models ranked below the constant survival model, including those containing incubation recess behavior (Table 4.5).

DISCUSSION

Overall, apparent nest success and DSR in this study was similar to nest success rates observed in previous studies of Eastern wild turkeys in other locations (Paisley et al. 1998, Pittman and Krementz 2016, Bakner et al. 2019). Recess behavior was not among top ranked models of DSR in this analysis. Instead, the analysis revealed that visual obstruction between 51 – 100 cm at the nest best predicted DSR, given the models compared and the data.

With advances in remote monitoring technology (e.g., *i*Buttons®, GPS tags), automated remote observation of nesting behavior has become more common and permits researchers to examine behavioral variation and the influence those behaviors may have on individual and population-level reproductive metrics (Smith et al. 2015). Among and within species across the altricial-precocial spectrum there is a large amount of variation in reproductive behavioral strategies (e.g., uni- and bi-parental incubation) and incubation rhythms (i.e., nest attentiveness; Marasco and Spencer 2015). The purpose that this variation serves requires further study for

most species. Recent work in the southeastern United States revealed that when incubating hens took longer recess bouts they experienced higher individual survival, but nest survival decreased (Lohr et al. 2020). While results from Lohr et al. (2020) suggest that a trade-off between hen and nest survival is an important factor driving variation in nest attendance, recess behavior did not appear to influence DSR among Eastern wild turkeys in Illinois. Although sample size in this study may have influenced my ability to detect an effect of recess behavior on DSR, an alternative explanation for why I was unable to detect a relationship between recess behavior and DSR may be due to the types of cues that nest predators in our study areas used to detect nests. For example, if most predators are using scent to detect nests, then hen movement and time spent off the nest may be less likely to influence DSR. While I was unable to assign specific predators to most nest failures, limited evidence suggests that coyotes (*Canis latrans*) and raccoons (*Procyon lotor*) are likely suspects (unpublished data). Further investigation of wild turkey nest attendance as a function of exposure to known predator species would be a fascinating avenue for additional research.

This analysis demonstrated that wild turkey hens may use a range of nest concealment conditions and that daily nest survival rates decreased as nest concealment increased. The association between greater visual obstruction and reduced DSR suggests that visual obstruction, across a horizontal plane, may not provide effective camouflage against detection by nest predators. Other studies among Galliformes also detected a decrease in DSR in response to greater vegetation density (Wiebe and Martin 1998, Fuller et al. 2013), whereas no relationship was found between visual obstruction and DSR among turkey nests in the southeastern United States (Lohr et al. 2020). Based on estimated "time of failure" among nests included in this analysis, both nocturnal and diurnal predation events occurred. Due to the different predator

species that are active nocturnally vs. diurnally, nests may be detected using different cues. For example, coyote (*Canis latrans*), raccoon (*Procyon lotor*), and red fox (*Vulpes vulpes*) are primarily nocturnal, rely on olfactory cues, and are well-documented predators of turkey nests (Melville et al. 2014). Other nest predators, such as bobcats (*Lynx rufus*) and American crows (*Corvus brachyrhynchos*) also prey on turkey nests but rely on visual cues to detect nests (Melville et al. 2014). As suggested by Conover et al. (2010), nesting birds may select sites that reduce detection by a particular cue (e.g., visual) or provide an optimal thermal location for a nest, but nests may be exposed to increased detection by predators through alternative cues (e.g., olfactory) as a result.

In this analysis, predictive models of DSR among Eastern wild turkey nests in Illinois were not improved by the addition of recess behavior metrics. While I did not detect a relationship between recess behavior and DSR, it is possible that the cues with which nest predators used to detect nests in Illinois are unrelated to recess behavior, or that our sample size was not large enough for differences in behavior to elicit detectable changes in DSR. These results do confirm that visual obstruction is a nest site characteristic that influences DSR. Daily nest survival rates remained above 90% across most of the range of obstruction values I observed, which indicates that wild turkey hens in Illinois can use nest sites with minimal to heavy visual obstruction (i.e., values of 0 – 5) and experience a somewhat lower risk of nest failure. However, sites with the greatest visual obstruction (i.e., value = 6) may experience a greater risk of failure.
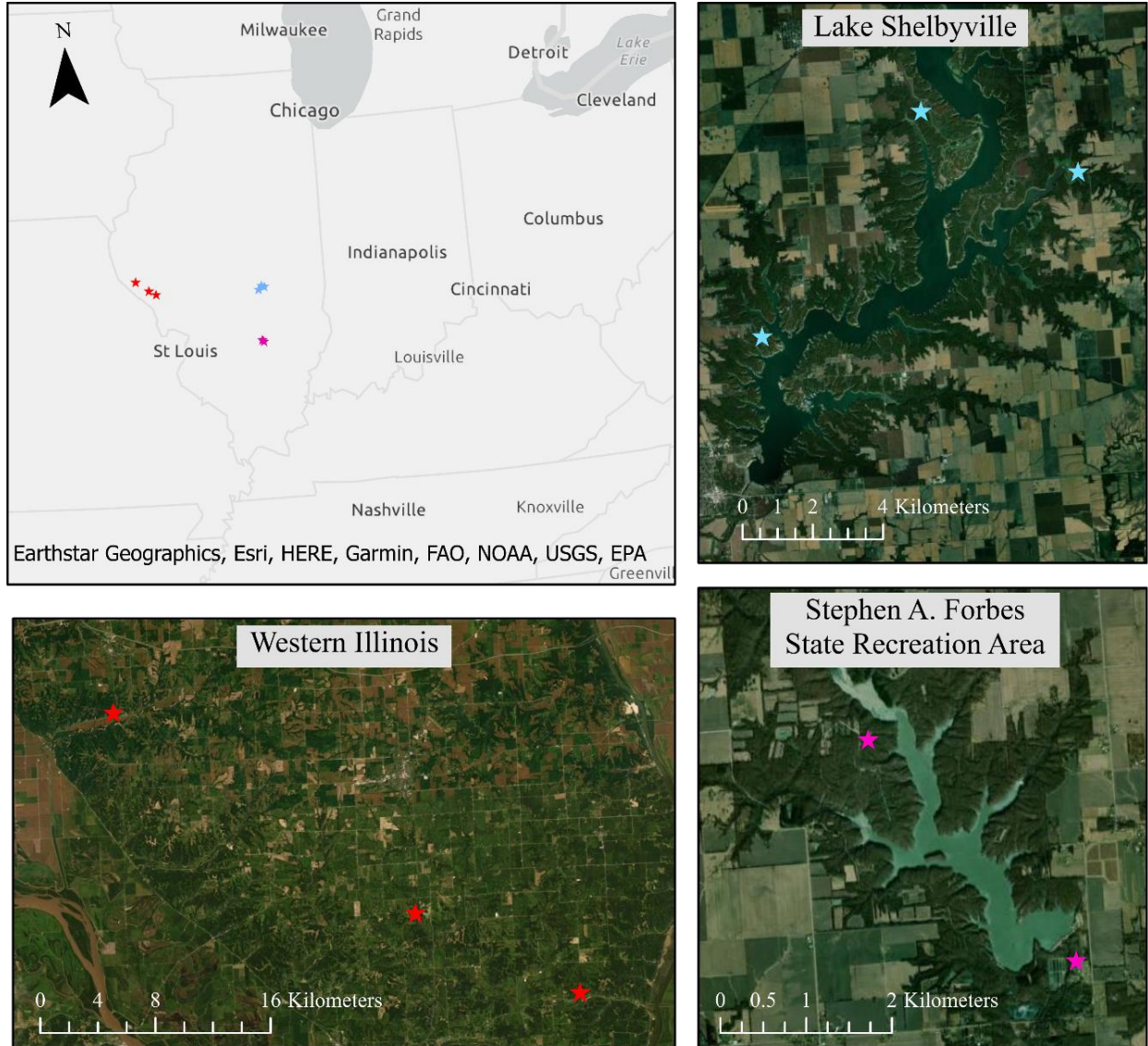
Figure 4.1. Map of study areas in Illinois, USA where Eastern wild turkey hens were captured and monitored during 2015 - 2018.
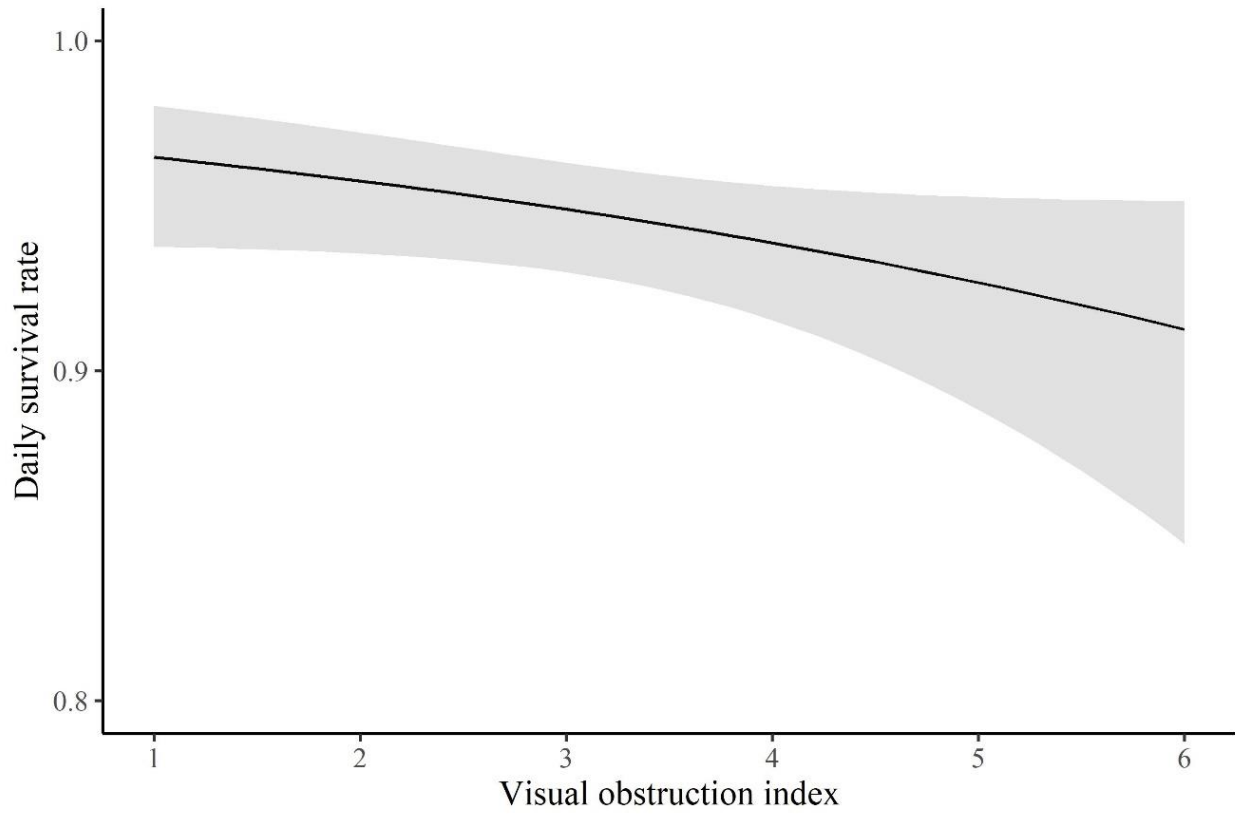
Figure 4.2. Predicted daily survival rate of Eastern wild turkey nests in Illinois as a function of visual obstruction between 51 – 100 cm at the nest, during 2015-2018.

Table 4.1 Descriptions of covariates included in generalized mixed models of daily nest survival among Eastern wild turkeys in Illinois, during 2015 - 2018.

Variable category	Variable	Description
Behavior	Recess frequency	The mean daily number of recess bouts for the incubation period.
Behavior	Recess duration	The mean recess bout duration for the incubation period. Measured in minutes.
Behavior	Sum of daily recess bouts	The mean total time spent in recess during the incubation period. Measured in minutes.
Landscape	Distance to road	Distance between a nest and the nearest road.
Landscape	Distance to water	Distance between a nest and the nearest water body (stream, river, pond, lake, etc…).
Habitat	Visual obstruction 0-50 cm	Mean index value of vegetation cover at the nest site from 0-50 cm.
Habitat	Visual obstruction 51-100 cm	Mean index value of vegetation cover at the nest site from 51-100 cm.
Habitat	Visual obstruction 101-200 cm	Mean index value of vegetation cover at the nest site from 101-200 cm.
Temperature	Ambient temp (C)	Daily mean temperature collected from hen gps units.
Temperature	Max diff in ambient temp	Daily difference in temperature extremes collected from hen gps units.
Temporal	Day of year	Numerical day of the year (e.g., 1- 365).
Temporal	Day of reproductive season	Numerical day within a given reproductive season. The reproductive season for each year was defined by the first day of incubation of the first nest detected and the last day of incubation of the last surviving nest.
Temporal	Day of incubation period	Numerical day within individual incubation periods that started on the first day of continuous incubation and ended following termination of incubation.

Table 4.2. Model comparison results from all candidate models of daily survival rate among Eastern wild turkey nests (n = 48) in response to landscape, visual obstruction, temporal, temperature, and behavior variables in Illinois, 2015 - 2018.

Models by category	K	AICc	ΔAICc	w_i	LL
Landscape					
Dist. to road	3	302.63	0.00	0.44	-148.30
Dist. to water	3	302.89	0.25	0.39	-148.43
Road + Water	4	304.51	1.87	0.17	-148.23
Visual Obstruction					
51 - 100 cm	3	299.99	0.00	0.52	-146.98
0 - 50 cm	3	301.17	1.18	0.29	-147.57
101 - 200 cm	3	302.93	2.95	0.12	-148.45
50 + 100 + 200	5	303.88	3.89	0.07	-146.90
Temporal					
Day of incubation	3	302.30	0.00	0.41	-148.13
Day of year	3	302.97	0.67	0.30	-148.47
Season day	3	303.00	0.70	0.29	-148.48
Temperature					
Daily Mean Temp (C)	3	302.74	0.00	0.53	-148.35
Daily Max Temp Diff	3	303.01	0.27	0.47	-148.49
Daily recess behavior					
Recess duration	3	302.36	0.00	0.39	-148.16
Total recess time	3	302.67	0.30	0.33	-148.32
Recess frequency	3	303.00	0.64	0.28	-148.48

Table 4.3. Summary statistics of covariates included in models of daily nest survival among Eastern wild turkeys in Illinois, 2015 - 2018.

Covariate	Mean	SD	Min	Max
Landscape				
Dist. to road	286.4	239.4	8.5	894.2
Dist. to water	143.3	99.2	7.6	412.1
Visual obstruction				
0 - 50 cm	3.0	2.1	1.0	6.0
51 - 100 cm	3.0	1.5	1.0	6.0
101 - 200 cm	3.3	1.3	1.3	6.0
Temporal				
Day of incubation	11.2	8.0	1.0	37.0
Day of year	137.8	15.4	107.0	183.0
Season day	29.0	16.0	1.0	77.0
Temperature				
Daily Mean Temp (C)	29.0	4.4	15.8	44.6
Daily Max Temp Diff	15.9	9.4	1.0	56.0
Daily recess behavior				
Recess duration (min)	34.2	33.7	0.0	275.0
Recess frequency	0.8	0.8	0.0	5.0
Total recess time (min)	41.6	46.1	0.0	535.0

Table 4.4. Comparison of Eastern wild turkey nest attempts among years and study areas in Illinois during 2015 – 2018.

Study Area	Year	All hens	ASY[1]	SY[2]	Start[3]	End[4]	Numb. nests by attempt		Success by attempt		Failure
							First	Second	First	Second	
Forbes	2015	9	5	4	20-Apr	10-Jun	8	1	0	0	8
Forbes	2016	11	8	3	23-Apr	12-Jun	10	1	2	0	8
Forbes	2017	1	1	0	23-Apr	26-Apr	1	0	0	0	1
Lake Shelbyville	2015	1	0	1	3-May	30-May	1	0	0	0	1
Lake Shelbyville	2016	13	9	4	16-Apr	1-Jul	11	2	3	0	9
Lake Shelbyville	2017	3	3	0	21-Apr	18-May	3	0	0	0	3
W. Illinois	2017	3	3	0	25-Apr	16-Jun	2	1	0	0	3
W. Illinois	2018	7	6	1	29-Apr	12-Jun	6	1	1	0	5

[1] After second year hens

[2] Second year hens

[3] Represents the first day of continuous incubation of the first nest detected in the study area

[4] Represents the last day of continuous incubation of the last nest detected in the study area

Table 4.5. Model comparison results from final candidate models of daily survival rate among Eastern wild turkey nests (n = 48) in Illinois, 2015 - 2018.

Model	K	AICc	ΔAICc	w_i	LL
51 - 100 cm	3	299.99	0.00	0.30	-146.98
Constant survival	2	301.00	1.01	0.18	-148.49
Recess duration	3	302.36	2.38	0.09	-148.16
Dist. to road	3	302.63	2.65	0.08	-148.30
Total recess time	3	302.67	2.68	0.08	-148.32
Daily mean temp (C)	3	302.74	2.75	0.08	-148.35
Recess frequency	3	303.00	3.01	0.07	-148.48
51 - 100 cm x Total recess time	5	303.69	3.71	0.05	-146.80
51 - 100 cm x Recess frequency	5	303.90	3.91	0.04	-146.91
Dist. to road x Recess frequency	5	306.60	6.61	0.01	-148.26
Daily mean temp (C) x Recess frequency	5	306.76	6.77	0.01	-148.34
Global	8	309.54	9.55	0.00	-146.67

REFERENCES

R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/; 2013.

Aldrich, T. W., and D. G. Raveling. 1983. Effects of experience and body-weight on incubation behavior of Canada geese. Auk **100**:670-679.

Allen Smith, P., H. Grant Gilchrist, and J. N. M. Smith. 2007. Effects of nest habitat, food, and parental behavior on shorebird nest success. The Condor **109**:15.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management **74**:1175-1178.

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

Badyaev, A. V., and C. K. Ghalambor. 2001. Evolution of life histories along elevational gradients: Trade-off between parental care and fecundity. Ecology **82**:2948-2960.

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

Bakner, N. W., L. R. Schofield, C. Cedotal, M. J. Chamberlain, and B. A. Collier. 2019. Incubation recess behaviors influence nest survival of wild turkeys. Ecology and Evolution **9**:14053-14065.

Brown, M., and C. T. Downs. 2003. The role of shading behaviour in the thermoregulation of breeding crowned plovers (*Vanellus coronatus*). Journal of Thermal Biology **28**:51-58.

Bueno-Enciso, J., R. Barrientos, E. S. Ferrer, and J. J. Sanz. 2017. Do extended incubation

    recesses carry fitness costs in two cavity-nesting birds? Journal of Field Ornithology

    88:146-155.

Bureau, U. S. C. 2018. TIGER/line shapefiles - primary & secondary roads - Illinois.

Byrne, M. E., and M. J. Chamberlain. 2013. Nesting ecology of wild turkeys in a bottomland

    hardwood forest. The American Midland Naturalist **170**:95-110.

Chalfoun, A., and T. Martin. 2010. Facultative nest patch shifts in response to nest predation risk

    in the Brewer's sparrow: a "win-stay, lose-switch" strategy? Oecologia **163**:885-892.

Cobb, D. T., and P. D. Doerr. 1997. Eastern wild turkey reproduction in an area subjected to

    flooding. Journal of Wildlife Management **61**:313-317.

Cohen, B. S., T. J. Prebyl, B. A. Collier, and M. J. Chamberlain. 2018. Home range estimator

    method and GPS sampling schedule affect habitat selection inferences for wild turkeys.

    Wildlife Society Bulletin **42**:150-159.

Conover, M. R., J. S. Borgo, R. E. Dritz, J. B. Dinkins, and D. K. Dahlgren. 2010. Greater sage-

    grouse select nest sites to avoid visual predators but not olfactory predators. The Condor

    112:331-336.

Conway, C. J., and T. E. Martin. 2000. Evolution of passerine incubation behavior: influence of

    food, temperature, and nest predation. Evolution **54**:670-685.

Crawford, J. C., W. F. Porter, M. J. Chamberlain, and B. A. Collier. 2021. Wild turkey nest

    success in pine-dominated forests of the Southeastern United States. The Journal of

    Wildlife Management **85**:498-507.

Deeming, C. 2002. Avian incubation: behaviour, environment and evolution. Oxford University

    Press, Oxford.

Deeming, D. C., and S. J. Reynolds. 2015. Nests, eggs, and incubation: new ideas about avian reproduction. Oxford University Press, USA.

Ellis-Felege, S. N., M. J. Conroy, W. E. Palmer, and J. P. Carroll. 2012. Predator reduction results in compensatory shifts in losses of avian ground nests. Journal of Applied Ecology **49**:661-669.

Flint, P. L., and J. B. Grand. 1999. Incubation behavior of spectacled eiders on the Yukon-Kuskokwim Delta, Alaska. Condor **101**:413-416.

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.

Garcia, V., and C. J. Conway. 2009. What constitutes a nesting attempt? Variation in criteria causes bias and hinders comparisons across studies. The Auk **126**:31-40.

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

Group, T. P. G. D. 2018. Documentation PostgreSQL 10.3.

Götmark, F., D. Blomqvist, O. C. Johansson, and J. Bergkvist. 1995. Nest site selection: A trade-off between concealment and view of the surroundings? Journal of Avian Biology **26**:305-312.

Haegen, W. M. V., W. E. Dodge, and M. W. Sayre. 1988. Factors affecting productivity in a northern wild turkey population. The Journal of Wildlife Management **52**:127-133.

Howlett, J. S., and B. J. Stutchbury. 1996. Nest concealment and predation in hooded warblers: Experimental removal of nest cover. The Auk **113**:1-9.

Latif, Q. S., S. K. Heath, and J. T. Rotenberry. 2012. How avian nest site selection responds to predation risk: testing an 'adaptive peak hypothesis'. Journal of Animal Ecology **81**:127-138.

Leopold, A. S. 1943. The molts of young wild and domestic turkeys. The Condor **45**:133-145.

Levin, S. A., S. R. Carpenter, H. C. J. Godfray, A. P. Kinzig, M. Loreau, J. B. Losos, B. Walker, and D. S. Wilcove. 2009. The Princeton guide to ecology. Princeton University Press.

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**:4.

Lohr, A. K., J. A. Martin, G. T. Wann, B. S. Cohen, B. A. Collier, and M. J. Chamberlain. 2020. Behavioral strategies during incubation influence nest and female survival of wild turkeys. Ecology and Evolution **10**:11752-11765.

Marasco, V., and K. Spencer. 2015. Improvements in our understanding of behaviour during incubation. Nests, Eggs and Incubation: New Ideas about Avian Incubation (DC Deeming and SJ Reynolds, Editors). Oxford University Press, New York, NY, USA:142-151.

Martin, T. E. 1993a. Nest predation among vegetation layers and habitat types: Revising the dogmas. The American Naturalist **141**:897-913.

Martin, T. E. 1993b. Nest predation and nest sites. Bioscience **43**:523.

McClintock, B. T., R. Langrock, O. Gimenez, E. Cam, D. L. Borchers, R. Glennie, and T. A.

   Patterson. 2020. Uncovering ecological state dynamics with hidden Markov models.

   Ecology Letters **23**:1878-1903.

McClintock, B. T., and T. Michelot. 2018. momentuHMM: R package for generalized hidden

   Markov models of animal movement. Methods in Ecology and Evolution **9**:1518-1530.

Melville, H. I. A. S., W. C. Conway, M. L. Morrison, C. E. Comer, and J. B. Hardin. 2014.

   Artificial nests identify possible nest predators of Eastern wild turkeys. Southeastern

   Naturalist **13**:80-91.

Merrill, L., E. M. Baehl, K. E. Ripple, and T. J. Benson. 2016. Do birds alter levels of parental

   investment based on nest-site habitat features? Ethology **122**:859-868.

Newton, I. 1998. Population limitation in birds. Academic press.

Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Society

   Bulletin (1973-2006) **5**:113-117.

Paisley, R. N., R. G. Wright, J. F. Kubisiak, and R. E. Rolley. 1998. Reproductive ecology of

   eastern wild turkeys in southwestern Wisconsin. The Journal of Wildlife Management

   62:911-916.

Parker, C., W. M. Schelsky, L. Garver, and J. P. Hoover. 2021. Pyrodiversity matters: wild

   turkey habitat selection in a fire managed landscape. Forest Ecology and Management.

Pittman, H. T., and D. G. Krementz. 2016. Impacts of short-rotation early-growing season

   prescribed fire on a ground nesting bird in the Central Hardwoods region of North

   America. PloS one **11**:e0147317.

Porter, W. 1992. Habitat requirements. Pages 202-213 The wild turkey: biology and

   management. Stackpole, Harrisburg, Pennsylvania, USA.

Powell, L., and G. Gale. 2015. Parameter Estimation for Animal Populations. Caught Napping
    Publications, Lincoln, Nebraska, USA.

Pyle, P. H., Steve N.G.; Ruck, Siobhan; Desante, David F. 2008. Identification Guide to North
    American birds, Part II Anatidae to Alcidae. Slate Creek Press, Point Reyes Station,
    California.

Rangen, S. A., R. G. Clark, and K. A. Hobson. 1999. Influence of nest-site vegetation and
    predator community on the success of artificial songbird nests. Canadian Journal of
    Zoology **77**:1676-1681.

Smith, J., C. Cooper, S. Reynolds, D. Deeming, and S. Reynolds. 2015. Advances in techniques
    to study incubation. Pages 179-195. Nests, eggs, and incubation: new ideas about avian
    reproduction. Oxford University Press, USA.

Survey, U. S. G. 2020. National Geospatial Program, 20200615, NHD 20200615 for Illinois
    State or Territory shapefile model version 2.2.1: U.S. Geological Survey.

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

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

Thompson, S. C., and D. G. Raveling. 1987. Incubation behavior of emperor geese compared
    with other geese: Interactions of predation, body size, and energetics. The Auk **104**:707-
    716.

Vanderhaegen, W. M., W. E. Dodge, and M. W. Sayre. 1988. Factors affecting productivity in a
    northern wild turkey population. Journal of Wildlife Management **52**:127-133.

Vangilder, L. D., E. W. Kurzejeski, V. L. Kimmeltruitt, and J. B. Lewis. 1987. Reproductive

    parameters of wild turkey hens in north Missouri. The Journal of Wildlife Management

    51:535-540.

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.

Yeldell, N. A., B. S. Cohen, A. R. Little, B. A. Collier, and M. J. Chamberlain. 2017a. Nest site

    selection and nest survival of eastern wild turkeys in a pyric landscape. The Journal of

    Wildlife Management **81**:1073-1083.

Yeldell, N. A., B. S. Cohen, T. J. Prebyl, B. A. Collier, and M. J. Chamberlain. 2017b.

    Prescribed fire influences habitat selection of female eastern wild turkeys. The Journal of

    Wildlife Management **81**:1287-1297.

CHAPTER 5: SUMMARY

An understanding of wildlife behavior is key to the ability to predict how a species will respond to any number of extrinsic and intrinsic factors. Moreover, how wildlife behave during the reproductive season has important survival and fitness consequences. I remotely monitored 50 Eastern wild turkeys (*Meleagris gallopovo silvestris*) using micro-GPS units and analyzed data from the reproductive season to complete three primary objectives: 1) Examine the influence of prescribed fire on habitat selection among hens; 2) Describe recess behavior among incubating hens and 3) Compare the influence of recess behavior and additional factors on daily nest survival. Analyses of habitat selection in response to prescribed fire revealed that nesting hens did not exhibit any general preference for burned vs. non-burned forest areas, but hens did use a mosaic of burned areas during different periods of the reproductive season and preferred areas that had experienced at least one growing season since burning. These results highlighted the importance of pyrodiversity when managing forests with fire, including leaving some areas not burned. Results from my analysis of incubation behavior revealed that partial incubation appears to be a common behavioral strategy among nesting turkeys, and in this study hens exhibited partial incubation between 1 – 6 days prior to beginning continuous incubation. On average, continuously incubating hens took 1.3 recesses per day which lasted 45.3 min, and hens took recesses more frequently in the afternoon than in the morning. Analysis of nest survival among Eastern wild turkeys in Illinois indicated apparent nest success was low but comparable to other studies. I did not detect a relationship between DSR and recess behavior, however, increasing values of visual obstruction of the nest between 51 – 100 cm resulted in a slight decline in DSR. Overall, these results demonstrate that remotely monitoring wildlife can provide researchers with the means to detect and examine behaviors that may otherwise be unobservable.

By analyzing the movements of wild turkeys remotely, my results provide information that improves our understanding of the natural history, ecology, behavior, and conservation of wild turkeys. In particular, the approach used to detect incubation behavior (Chapter 3) can be used to study many types of unobservable behavior in other species, with minimal or no influence on the behavior itself.