ABSTRACT Recent advances in animal tracking technology have increased interest in the field of animal movement ecology. Numerous methods have been developed to extract information from animal movement paths that can be used to link movement behavior to external stimuli such as habitat and climatic conditions. Given the recent development of Global Positioning System (GPS) technology suitable for use on wild turkeys (\textit{Meleagris gallopavo}), we advocate the adoption of new methodologies to design novel research on wild turkey ecology. Here we provide a worked example using first-passage time on male Rio Grande wild turkeys (\textit{M. g. intermedia}) tracked via GPS in South Texas, USA, during April 2009 to illustrate one methodological option on which research can be based. From our example, we infer behavioral decisions in response to habitat variables that varied during the diurnal cycle; turkeys were more likely to exhibit localized movements during midday in open areas near food and water resources. We contend that by taking advantage of GPS technology and focusing research questions on movement behavior, wild turkey research can progress toward answering mechanistic questions regarding turkey habitat use. This shift in research focus will provide much-needed information to managers that is currently lacking at both local and regional scales. © 2014 The Wildlife Society.

KEY WORDS animal movement, first-passage time, GPS, habitat use, \textit{Meleagris gallopavo}, Rio Grande wild turkey, telemetry.

Recently, Collier and Chamberlain (2010) argued that wild turkey (\textit{Meleagris gallopavo}) research had begun to stagnate, and emphasized the need for refocusing research nationally. The application of very-high frequency (VHF) radiotelemetry has contributed greatly to our present understanding of many aspects of wild turkey ecology, including survival (Godwin et al. 1991, Miller et al. 1998, Pack et al. 1999, Humberg et al. 2009), nesting ecology (Lazarus and Porter 1985, Still and Baumann 1990, Chamberlain and Leopold 1998, Lehman et al. 2008), and habitat use (Phalen et al. 1986, Bidwell et al. 1989, Thommartin 2001, Miller and Conner 2007). However, after several decades, the argument can be made that the limits of what this technology can teach us have been reached. Presently, it appears unlikely that continued studies relying solely on VHF telemetry will add much novel information to our collective knowledge of wild turkey ecology, or serve to notably advance management strategies. The recent development of Global Positioning System (GPS) tracking technology suitable for use on wild turkeys represents a substantial addition to the toolbox of turkey researchers, allowing for the collection of positional data at very high spatial and temporal resolutions (Guthrie et al. 2010). Collier and Chamberlain (2010) provided a list of potential testable hypotheses and avenues of research that could be pursued using GPS technology, as well as several brief examples of turkey behaviors collected via GPS telemetry that had not been previously observed.

Technological advances that allow for the remote tracking of highly mobile vertebrate species have increased interest in animal movement ecology. This interest has, in turn, facilitated the rapid development of analytical methods to analyze animal movement data, and relate observed behaviors to various external stimuli at multiple spatial and temporal scales (Giuggioli and Bartumeus 2010). We believe that the application of contemporary methodologies for the analysis of animal tracking data to GPS-derived wild turkey movements can serve to shed light on new aspects of wild turkey ecology and answer questions in the spirit of those posited by Collier and Chamberlain (2010). Our objective was to provide a brief worked example of the

Received: 4 April 2013; Accepted: 6 September 2013

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Wildlife Society Bulletin; DOI: 10.1002/wsb.404
applications of one such method to GPS data collected from wild turkeys to demonstrate how the quantitative analysis of movement paths can provide understanding of turkey behavior and ecology beyond the limits of what is feasible with traditional VHF telemetry.

We applied first-passage time analysis (Fauchald and Tveraa 2003) to the daily movement paths of 3 adult male Rio Grande turkeys (M. g. intermedia) in South Texas, USA, to explore how local habitat features, climatic conditions, and time of day influence turkey behavior. One would expect turkeys to structure daily movements in such a way as to maximize time in the vicinity of reliable food resources, and to avoid extensive activity during the warmest portions of the day in order conserve energy and maintain thermoregulatory homeostasis. As such, we chose to investigate behavior in relation to variables associated with food resources, cover, and daily temperature fluctuations.

STUDY AREA

We conducted our research on the Temple Ranch (hereafter, study site) northwest of San Diego, Texas, located in the eastern portion of the Central Rio Grande plains eco-region in southern Texas. Our study site covered 5,261 ha, was bisected by a broad riparian corridor (San Diego Creek), and was intensively managed for white-tailed deer (Odocoileus virginianus) and northern bobwhite (Colinus virginianus) hunting, with limited turkey hunting occurring on site. Timer-controlled wildlife feeders that provided corn and protein feed were scattered across the study site, typically paired with pumped surface-water troughs; we designate these areas hereafter as “feeders.” Vegetation consisted of thornscrub parklands with well-defined mosaic patterns of shrub clusters scattered throughout low-succession grasslands (Northup et al. 2005). Closed-canopy woodlands were limited to riparian corridors and were intermittently present in the clay loam drainages along San Diego Creek. Woodlands consisted primarily of honey mesquite (Prosopis glandulosa), hackberry (Celtis occidentalis), and Texas persimmon (Diospyros texana; Archer 1990). Grassland herbaceous species included thin paspalum (Paspalum setaceum), fringed signal grass (Urochloa ciliatissima), red grama (Bouteloua trifida), and coastal sandbur (Cenchrus incertus; Archer 1990). The climate was subtropical, with cool winters and hot summers. Cool-season prescribed fire and brush management was used to maintain an early successional grassland–brush land habitat matrix, with approximately 800 ha burned annually on a 2- to 3-year rotation given adequate rainfall.

METHODS

We captured 8 adult male Rio Grande wild turkeys in March 2009 using drop nets baited with milo and cracked corn. All turkeys were banded with an aluminum Texas Parks and Wildlife Department leg band, fitted with a store-on-board μGPS unit (Guthrie et al. 2010), and released at the capture site. Units were programmed with variable daily collection schedules for the period 1 March–30 March designed to intensively sample movements during scheduled hunts on our study site. Starting on 30 March, these units defaulted to collect a single location at 20-minute intervals during the day and 3 locations at night while turkeys were roosted. We successfully recaptured 5 males during May 2009 using walk-in traps, which allowed us to retrieve data stored in the μGPS units. Three of these units successfully collected data as programmed. We used the data from these 3 individuals for our example. All capture and handling procedures were covered under Texas A&M Institutional Animal Care and Use Protocol number 2010-287.

We limit our analysis to the time period 31 March–21 April for several reasons. First, first-passage time analysis is most effective when relocations are collected at evenly spaced time intervals (Fauchald and Tveraa 2003), a condition met when the μGPS unit on each individual was collecting locations at 20-minute intervals. Additionally, the 20-minute collection schedule provided relatively fine-scale data on behavior. Finally, after 21 April, the μGPS units began to vary in their collection schedules.

We performed first-passage time analysis for daily paths of each turkey individually following the methods of Fauchald and Tveraa (2003). First passage time is defined as the time it takes an animal to move through a circle of a given radius r (Johnson et al. 1992). Inferences about animal behavior can be made based on first-passage time values measured at evenly spaced points along a movement trajectory (Fauchald and Tveraa 2003). High first-passage time values are generally associated with slower and more sinuous movements, possibly representing an encamped state or area-restricted searching. Conversely, low first-passage time values are generally associated with faster, more straight-line movements. We interpolated times and locations at 1 m intervals along each path, and calculated first-passage time centered on these locations for circles with radius r ranging from 10 m to 400 m in 10-m increments. For each path, the variance of log-transformed first-passage time values (trans-formed to make variance independent of magnitude) for each value of r can be plotted, with the resulting peak in variance indicating the scale at which the organism is concentrating its activities (Fauchald and Tveraa 2003). This scale may vary for individual paths, and finding a common scale for analysis purposes is recommended so that comparisons of first-passage time values across paths are scaled similarly (Fauchald and Tveraa 2006). We defined the common scale as that associated with the largest mean variance when averaged across all paths, which was found to occur at r = 110 m (Fig. 1). Because this is the scale at which the variance is most pronounced, it follows that it is the scale at which first-passage time values should best be able to differentiate movement behaviors and where the largest effect sizes should be found. As such, we extracted the interpolated times, locations, and first-passage time values every 110 m along each path, and used these locations for analysis.

For our example, we were interested in determining how movements were influenced by time of day, temperature, and habitat variables including habitat type, distance to a
We fitted cox proportional hazard models as suggested by Freitas et al. (2008), where first-passage time values were treated as survival times, and time, temperature, and habitat variables were treated as explanatory variables. Because first-passage times are continuous event–time measures, they are well-suited to the proportional hazard modeling approach. Essentially, we were attempting to discern how the various explanatory variables influenced the risk (probability) of a turkey leaving a circle with a radius of 110 m. We created a suite of 32 biologically plausible models (see Supplementary Appendix 1, available online at www.onlinelibrary.wiley.com) using various combinations of explanatory variables. We found high negative correlation between the percentage of open–herbaceous and woody riparian cover ($r^2 = 0.8$), and as such included only the open–herbaceous cover type as a variable in model creation. Additionally, thorn scrub was rarely present in buffered areas ($\leq 10\%$), and consequently we did not consider it when constructing models. In several models we included various interactions of other variables with period of the day (morning, midday, and afternoon), because it seemed plausible that turkey behavior in respect to other variables may change over the course of a day. We calculated Akaike’s Information Criterion adjusted for small sample sizes ($\text{AIC}_c$) for each model and used $\Delta\text{AIC}_c$, and Akaike weights ($w_i$) to evaluate model performance (Burnham and Anderson 2002). We calculated hazard ratios (HR) from the exponential of each coefficient ($e^{\beta}$) in the highest ranked model and used HR to make inferences on variable effects (Collet 2003, Murray 2006). For continuous variables, a HR $>1$ indicates that the risk of the turkey leaving the circle increases as the variable in question increases, while a HR $<1$ indicates the risk of leaving decreases as the variable increases. For categorical variables with $\geq 2$ levels, the first level is considered the base level and for all other levels a HR $>1$ indicates that risk of the turkey leaving the circle is increased relative to the base level, while a HR $<1$ indicates a reduced risk relative to the base level. Given this, we based our interpretations of turkey behavior only on the variables in the best performing model in which the 95% confidence interval around the associated HR did not bound 1. All analysis was performed in the R statistical computing environment (R Core Team 2013). First-passage time analysis was performed using custom code developed by D. Pinaud of the Centre National de la Recherche Scientifique (CNRS), France. Models were fit using the survival package (Therneau 2013), and AIC values were derived using the AICcmodavg package (Mazerolle 2013).

RESULTS

We used 66 daily movement paths from 3 adult males representing 2,385 GPS locations. The most supported model included interaction terms between time of day and all other variables considered (parameters $= 14$, $w_i > 0.99$). The next best model had no support ($\Delta\text{AIC}_c = 13$). Two variables in the model had HR confidence intervals that did not bound 1 (Table 1); these were the interaction between the middle portion of the day and distance to the nearest feeder, and the

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Figure 1. Mean variance ($\pm$SE) of log-transformed first-passage time values for 66 daily paths as a function of circle radius (m) for 3 adult male Rio Grande wild turkeys from 31 March to 21 April 2009 in South Texas, USA. The peak in variance occurs at a radius of 110 m.
interaction between the middle portion of the day and the percentage of open–herbaceous cover within a 25-m buffer around the turkey’s position. During midday, the risk of a turkey leaving a circle with a radius of 110 m increased approximately 1.0007% for each 1-m increase in distance from a feeder relative to morning. For each percentage increase in open–herbaceous cover habitat within 25 m during midday, the risk of leaving decreased approximately 0.9939% compared to the morning hours (Table 1).

Turkeys were more likely to remain in the same 110-m-radius area for a given amount of time during midday, and moved through localized areas most quickly during the afternoon (Fig. 2). These turkeys were generally located nearest to feeders during midday, and appeared to show a preference for open areas during morning and midday (Fig. 3). Plotting locations used in the analysis revealed an affinity for clusters of wildlife feeders located in openings south and west of the primary roost area, respectively (Fig. 4). Taken collectively, we concluded that during the study period these individual turkeys tended to move to openings associated with feeders during midday, during which time they restricted their movements to relatively localized areas, until late afternoon when they engaged in more rapid and directed movements toward the roost site.

**DISCUSSION**

Our objective was to provide an example of how new technology can be used to improve our understanding of turkey ecology beyond the limits of what was possible with traditional VHF telemetry, and to demonstrate how using movement paths can extend inferences about animal behavior. We found that turkeys altered their movements in relation to particular habitat features dependent on time of day. Our work generally coincided with mating season on our study area, and perhaps males congregated in openings during midday to display to females. Another, but not mutually exclusive, possibility is that turkeys used openings near clusters of feeders as loafing areas during the warmest part of the day because of the proximity to water resources. Feeders likely provide a consistent food source and open areas near feeders may provide protection from ambush predators. Although woody vegetation was used for roosting, our observations show these birds tended to avoid woody cover during most of the day. Rather, males were more likely to make use of woody cover during the end of the day as they moved toward the roosting area; this occurred at the same time they exhibited their fastest and most directed movements.

We feel it is important to point out that first-passage time analysis is scale-dependent and based on the shape and characteristics of the movement path, and the methodology we employ here requires the researcher to

<table>
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<th>CI ($e^\beta$)</th>
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<td>0.9939</td>
<td>0.9903–0.9975</td>
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<td>1.3036</td>
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</tbody>
</table>

**Figure 2.** Survival curves with 95% confidence intervals representing the probability of a Rio Grande wild turkey remaining in a specific circle with a radius of 110 m for a given amount of time during 3 different parts of the day. Data collected during April 2009 in South Texas, USA.

**Figure 3.** (A) Distance to feeders, and (B) the % of habitat type within 25 m of Rio Grande wild turkey locations interpolated at 110-m intervals along daily movement paths for 3 parts of the day. Data collected during April 2009 in South Texas, USA.
sample from the path accordingly. As such, the scale of inference in such a study is necessarily dictated by the scale of data in space and time. Based on the relatively fine temporal scale (20 min) of data acquisition and the scale of displacements between raw locations, we are confident that the 110-m scale at which we made behavioral inferences was valid. However we note that it is possible that behavior could be characterized at finer scales given greater temporal resolutions.

We offer that it would be practically impossible to detect these temporally fine-scale variations in behavior using VHF telemetry. Considering the practicalities of VHF monitoring, it is likely that even in the best-case scenario, no more than 1 or 2 locations/day would be recorded for each location.

Figure 4. First-passage time values for locations interpolated at 110-m intervals along daily Rio Grande wild turkey paths. Data collected during April 2009 in South Texas, USA. Panels indicate locations with first-passage time values <1 hour (A), between 1 hour and 2 hours (B), between 2 hours and 3 hours (C), between 3 hours and 4 hours (D), between 4 hours and 5 hours (E), and >5 hours (F). Habitat types are woody riparian (dark green), thorn scrub (medium green), and open–herbaceous (light green). Open circles indicate feeder locations. Blue star indicates the location of the primary roost site.
individual. Additionally, the spatial accuracy of these locations would be considerably less than those collected via GPS. The average spatial error associated with GPS locations in this habitat type has been calculated at approximately 11 m, and even in heavily forested habitats only averaged approximately 22 m (Guthrie et al. 2010). This error is significantly improved over triangulation-error estimates of VHF telemetry, where error ellipses have been reported to range from 3.3 ha (Chamberlain and Leopold 2000) to 73.9 ha (Thogmartin 2001). These temporal and spatial constraints limit the analysis options of data collected by VHF telemetry to relatively coarse use-availability measurements. By capitalizing on the increased precision and sampling rate of GPS, and focusing analyses on movement paths as opposed to independent locations, we have demonstrated that biologists and land managers can move beyond questions of “where are turkeys found?” to more mechanistic questions regarding “how?” and “in what context” do turkeys make use of specific habitats. As pointed out by Collier and Chamberlain (2010), the information derived from pursuing these lines of questions would have important implications for wild turkey habitat management.

We chose to use first-passage time for this example because it was relatively simple to implement and interpret, was suitable for the data we collected, and because it has been previously used to successfully link habitat and behavior in terrestrial vertebrates (Frair et al. 2005, Byrne and Chamberlain 2012). It should be noted, however, that the field of animal movement is rapidly developing and there are a wide variety of methods available for extracting behavioral information from animal movement data; these include, but are not limited to, state-space modeling (Jonsen et al. 1992, Burnham and Anderson 2002), residence time analysis (Barraquand and Benhamou 2008), behavioral change-point analysis (Guararie et al. 2010), impulse response signal-filtering (Boettiger et al. 2011), the use of Brownian bridges (Horne et al. 2007, Kranstauber et al. 2012), and velocity-based movement modeling (Hanks et al. 2011). Even the relatively common practice of identifying home ranges and estimating space use can be improved through the incorporation of movement behavior (Benhamou and Cornelis 2010, Kranstauber et al. 2012). Movements of individuals can provide important insights into population-level characteristics (Johnson et al. 1992, Turchin 1998); therefore, population-level inferences can be scaled up to make regional predictions of population connectivity and dispersal based on landscape features such as habitat fragmentation and urbanization (Tracey et al. 2011, 2013), and would have powerful management implications for wild turkey management on a regional level that is sorely lacking.

ACKNOWLEDGMENTS

Our research was funded by the Texas Parks and Wildlife Upland Game Bird Stamp Fund, the Texas State Chapter of the National Wild Turkey Federation, and the National Wild Turkey Federation. Additional funding and support were provided by the Warnell School of Forestry and Natural Resources at the University of Georgia. We are grateful to A. “Buddy” and E. Temple from the Temple Ranch for providing access and support for our ongoing research activities. We thank R. and J. Sanders, Temple Ranch managers, for their assistance with field operations. Additionally, we greatly appreciate spatial modeling assistance from K. L. Skow.

LITERATURE CITED


Associate Editor: Sands.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher’s web-site.

Appendix 1. Variables and model ranking results for all Cox proportional hazard models fit to first-passage time data.