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DO MOVEMENT PATTERNS AND HABITAT USE DIFFER BETWEEN OPTIMAL- AND SUBOPTIMAL-SIZED NORTHERN BOBWHITE COVEYS?

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ABSTRACT

The group size of social animals and spatial structure of the environment can affect group behavior and movement decisions. Our objective was to investigate movement patterns and habitat use of northern bobwhite coveys (*Colinus virginianus*) of different size. Using radiotelemetry, we continuously monitored covey group size, daily movement, and habitat use on 12 independent 259-ha study areas in eastern Kansas, USA, during the winters between 1997 and 2000. We used correlated random walk models and fractal dimension models to determine if covey size affected movement characteristics or habitat selection. Intermediate-sized coveys (9–12 individuals, close to optimal covey size) exhibited daily movements that were substantially smaller and weekly home ranges that were more composed of woody escape cover than coveys of smaller or larger sizes. From the fractal dimension analyses, these coveys exhibited movement in between linear and a random walk at small spatial scales but very linear at large spatial scales. Large coveys had increased daily movement and tended to move in straighter lines (as indicated by the high proportion of turning angles [i.e., the angle between an initial direction and a new direction] around 0° and 180° and their multiscale fractal dimension) and they incorporated more cropland into their range, presumably to meet the feeding requirements of a larger group. In contrast, small coveys (1–4 individuals) tended to move more and increase the size of their home range, travel with a greater diversity of turning angles, and show movement patterns that were largely tortuous across a greater number of habitat patches at larger spatial scales (700 m). Small coveys have lower fitness and add new membership to increase fitness so it is possible that the movement behavior we observed represented a shift into a foray mode where bobwhites were searching for new membership. For areas with small populations and covey sizes, this information will help biologists better plan for habitat management to assist these coveys with their winter fitness.

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Key words: *Colinus virginianus*, correlated random walk, fractal dimension, habitat fragmentation, northern bobwhite, optimal group size

Population processes partially depend upon the spatial structure of the environment in which individuals occur (Turner and Gardner 1991, Tilman and Kareiva 1997, Turchin 1998) and individual behavior and movement decisions within a heterogeneous space can affect fitness (Okubo 1980, Kareiva 1990, Bell 1991, Levin 1992, Zollner and Lima 1999). Therefore, investigating the interplay between movement behavior and spatial structure provides a mechanistic link between ecological processes and the spatial landscape mosaic (Nathan 2008, Nathan et al. 2008). This relationship between behavioral ecology and landscape ecology is not only of growing ecological interest (Lima and Zollner

1996) but is of fundamental importance to understanding the population dynamics of mobile species (Merriam et al. 1991, Johnson et al. 1992).

To better understand the role of spatial structure in individual movement decisions, there has been increasing development and testing of individually based models (DeAngelis and Gross 1992, Judson 1994) in which movement is often the central component (Real et al. 1992; Johnson et al. 1992; Turner et al. 1993, 1994; Tischendorf 1997). Using individually based models has the advantage of taking into account the state of the animal and how that state changes according to the animal's actions and the environment. This can provide a greater degree of biological realism in assessing the relationship between an animal's behavior and surroundings (Houston et al. 1988).

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Several types of simple individually based models have been used successfully to test how individual behavior influences movement. First, correlated random walk (CRW) models summarize complex data on movement patterns, reducing movement paths into measures of movement distances over short time intervals and turning angles (e.g., daily). Correlated random walk models have been used to understand the search strategies behind specific behaviors (Kareiva and Shigesada 1983, Bovet and Benhamou 1988, Marsh and Jones 1988, McCulloch and Cain 1989, Olson et al. 2000). Turchin (1996) has recommended CRW models as the null hypothesis when analyzing paths of animal movement. Second, analyses of fractal dimension have been used to relate paths of animal movement to the spatial patterns of resource distribution (Crist et al. 1992; With 1994a,b; Etzenhouser et al. 1998; With et al. 1999; Marell et al. 2002). Rarely, however, have these 2 methods been used in conjunction to analyze animal behavior within the landscape (Crist et al. 1992, Marell et al. 2002).

To date, empirical studies that test individually based models of organismal movement patterns have primarily focused on the foraging patterns of insects (Kareiva and Shigesada 1983, Turchin 1991, Crist et al. 1992, With 1994a). Although research has investigated long-term movements of vertebrates (Benhamou 1990, Ward and Saltz 1994, Focardi et al. 1996), especially across large spatial scales (Koenig et al. 1996, Bergman et al. 2000, Cushman et al. 2005, Dai et al. 2007, Forester et al. 2007, Fryxell et al. 2008), there has been little work to consider how social rank within groups (e.g., Wittemyer et al. 2008) or how dynamics and/or maintenance of optimal and suboptimal group size affects movement decisions. Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite), is a nonmigratory bird species that often uses edge habitat and treeline corridors to travel and forms social groups of 2–22 individuals, called coveys, during the nonbreeding season (approx. Sep–Apr; Brennan 1999). Northern bobwhite maintain an average covey size of 11 individuals and, as covey size becomes smaller or larger, behaviors (e.g., distance moved, alert vs. feeding behavior) will change and survival will decline (Williams et al. 2003). Bobwhites experience high rates of winter mortality (Pollock et al. 1989, Burger et al. 1995) so covey size reduction occurs readily. Individuals in small coveys focus their behavior on finding new membership (often joining another small or intermediate-sized covey) to increase fitness (Bartholomew 1967, Yoho and Dimmick 1972, Williams et al. 2003). In contrast, individuals in large coveys show reduced feeding efficiency and necessarily spend more time foraging. However, it is not known whether group size can influence individual movement patterns via rapid linear paths to a required resource (e.g., food or new membership) or through longer explorations where animals drift into new territory or use forays into neighboring unknown areas followed by a return to their home range (Koenig et al. 2000, Conradt et al. 2003).

Spatio-temporal analyses of movement patterns in mobile species provide an approach for studying search-strategy behaviors associated with foraging, predator

avoidance, or group size maintenance (Benhamou 1990). Additionally, extrapolating individual decisions to the landscape scale is of interest to behavioral and landscape ecologists (Lima and Zollner 1996) and is critical to understanding population processes. The specific objective of our study was to use random walk and fractal dimension models to quantify how movement patterns differ between small or large (suboptimal) and intermediate (optimal) covey sizes and how these patterns may be influenced by habitat structure at different spatial scales.

STUDY AREAS

We conducted our research on 12 259-ha parcels of private and public land in eastern Lyon, western Osage, and western Coffey counties, Kansas, USA. Each study area was separated by a minimum of 1.6 km (range = 1.6–18.4 km). Winter bobwhite covey ranges are between 4 and 20 ha (Roseberry 1964, Bartholomew 1967, Yoho and Dimmick 1972, Williams 1996); therefore, we assumed distances between study areas were large enough to prohibit interchange of bobwhites among study areas.

Habitat types on study areas comprised on average 35% cropland (e.g., grain sorghum [*Sorghum bicolor*], soybean [*Glycine max*], wheat [*Triticum* spp.]), 27% native tallgrass rangeland (e.g., big bluestem [*Andropogon gerardii*], little bluestem [*Schizachyrium scoparium*], indiangrass [*Sorghastrum nutans*], switchgrass [*Panicum virgatum*]), 11% native grass under Conservation Reserve Program guidelines, 12% idleland (e.g., treelines, hedgerows, farmsteads, and old fields), 6% woodland, 5% water or marshland, and 4% hayland. All study areas consisted of habitat that was representative of east-central Kansas (Byram 1996) and no recreational hunting occurred.

METHODS

We captured bobwhites between 1 October and 31 January from 1997 to 2000 using bait-traps (Stoddard 1931) and nightlighting (Labisky 1968). Upon capture, we determined sex and age of birds (Rosene 1969), and weighed them to the nearest gram. From each covey we randomly selected (i.e., regardless of sex or age of other birds radioed in the covey) ≥ 3 birds weighing ≥ 150 g and fitted each with a necklace-type radiotransmitter weighing < 6 g (Burger et al. 1995). We did not radiomark birds weighing < 150 g to prevent stress from radiocollars (i.e., radiocollars $< 5\%$ of body mass; Samuel and Fuller 1994). We leg-banded all other captured birds in the covey. We immediately released all birds at the capture location. We located radiotagged individuals approximately 5 times/week by homing (White and Garrott 1990) between 9 November until death, radio failure, or 31 January 1997–2000. We systematically varied location times over all diurnal hours to capture a full range of behavioral variation. We recorded individual locations as Universal Transverse Mercator coordinates (Exum et al. 1982). We attempted to estimate size of the covey containing radiocollared individuals every week between 9 Novem-

ber and 31 January via flush counts. Reliance on flush counts to estimate covey size can be biased (Janvrin et al. 1991); therefore, we created a “diary” of covey membership and size over time by supplementing weekly flush counts with information gathered from continuous trapping of banded and radiocollared birds as well as from known live and dead birds identified via radiolocations. Anecdotally, these complimentary data sets tended to provide a consistent and predictable estimate of covey membership.

To determine whether covey size influenced covey movement patterns, we examined only coveys that had both 1) an estimated covey size for the week (covey only flushed once per week) and 2) 5 consecutive radiolocations within a week. If a covey was radiolocated <5 times or the covey size was unknown during the same time interval, we removed the covey from analysis. To avoid pseudoreplication, if a covey size remained the same over multiple weeks, we only included the first week of data. Each covey-week was considered as an independent sampling unit and would contain 5 locations, 4 daily path distances, 3 turning angles, and an estimated covey size. We measured effect of covey size on distance the covey moved per day using linear regression ($\alpha \leq 0.05$) and Mallow's C_p statistic (Draper and Smith 1981) to find the best-fit trend.

Correlated Random Walk Models

To test statistically whether animal movement is nonrandom, a CRW model should be considered as a null hypothesis. Correlated random walk models assume independent distributions of move lengths and turning angles that describe an animal's movement path. Although each move consists of random draws from each of these 2 distributions, the moves are considered correlated because the turning angles are not distributed uniformly around a circle but rather movement occurs in a preferred direction around which there is random variation. Correlated random walk models assume there are no long-term movement strategies—specifically, that movement in one day depends only on movement in the preceding day. The expected displacement of coveys over time is given by

$$R_n^2 = n \times (l_1) + 2 \times (l_2^2) \times \left(\frac{c}{1-c} \right) \times \left(n - \frac{1-c^n}{1-c} \right) \quad (\text{Eq. 1})$$

where R_n^2 is the net squared displacement from the first location (m^2), n is the number of subsequent moves from the first location, l_1 is the mean squared move distance (m^2), l_2 is the mean move distance (m), and c is the mean of the cosines of the turning angles (Bovet and Benhamou 1988). Observed movement can be tested against the null model of the CRW model to identify long-term strategies. For example, if the turning angle in one day is negatively correlated with the turning angle in the preceding day (in violation of the assumption of the CRW model), coveys will tend to move in a straight line and movement displacement after several days will be greater than that

predicted under the null CRW model. If the log-predicted displacement divided by observed displacement were equal to zero (one-sample t -tests, $P \leq 0.05$), we would conclude that the covey moved in a correlated random walk. If the model overpredicted displacement, then the tested covey size would show preference for a region. Lastly, if the model underpredicted displacement, then the tested covey size would show greater directional movement that could be inferred as avoidance of a region (Bergman et al. 2000). First we tested for uniformity of turning angles by a Rayleigh's test of Uniformity ($P \leq 0.01$) and Chi-square analysis of turning angles distributions using Program ORIANA 3.13 (Rockware, Inc., Golden, CO, USA). Second, we examined a correlated random walk model as a descriptor of movement of small, intermediate, and large-sized coveys. For these tests, we combined data from pathways recorded for different coveys within the same size categories; preliminary analyses found no consistent differences among covey-weeks.

Fractal Dimension Analysis

We examined the fractal dimension of movement patterns shown by small (<9 individuals), medium (9–12 individuals), and large (>12 individuals) coveys. Fractal dimension analysis of animal movement provides a method for assessing species' behavioral responses to landscape heterogeneity at multiple scales (Milne 1991, With 1994b). The fractal dimension D indexes overall tortuosity (complexity) of an animal's movement pattern. Tortuosity of animal paths represents their reaction to landscape heterogeneity in which they translate environmental stimuli into movements (Dicke and Burroughs 1988, Crist et al. 1992, With 1994b). Theoretically, in two-dimensional space, tortuosity can range from 1—indicating a straight line—to 2—indicating a Brownian diffusion or random walk that essentially fills a plane. Linear movement patterns ($D = 1$) typically indicate directed movements that offer little resistance and where the landscape is viewed as homogeneous by the organism, while $D = 2$ indicates convoluted movement patterns typical of animals using a structurally complex environment (Wiens and Milne 1989; Crist et al. 1992; With 1994a, b). We calculated fractal dimensions for average weekly movement of coveys across multiple spatial scales using the VFRACTAL program implemented with the modified dividers method to account for truncation error (Nams 1996, Nams 2006).

Habitat Use

To determine whether covey size affected habitat selection differently, we compared average study-area habitat availability to average habitat used per covey-week. We digitized land cover in the 12 study areas from aerial photographs using ArcView and we ground-truthed all land-use maps to assure accuracy. We divided major land-use categories across all study areas into pasture ($23.3 \pm 6.0\%$ SE), hayland ($2.6 \pm 1.3\%$ SE), cropland ($33.0 \pm 6.3\%$ SE), idle grassland (including roadsides,

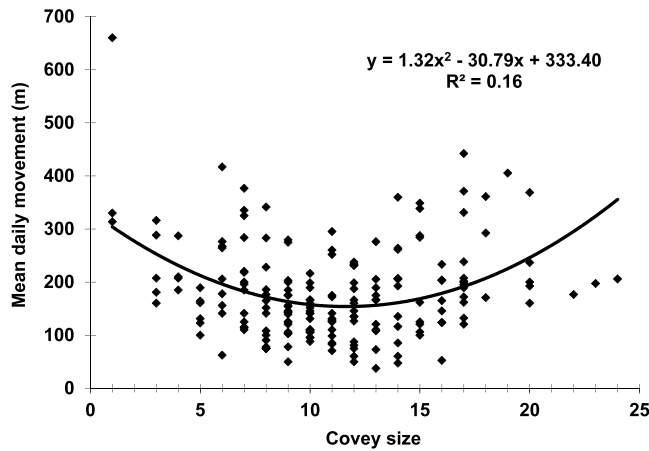


Fig. 1. The effect of covey size on mean daily movement (m) of northern bobwhite coveys in East-central Kansas, USA, 1997–2000. Solid line indicates quadratic relationship ($F_{2,192} = 17.79$, $P < 0.01$) estimated by regression.

Conservation Reserve Program and native grassland, grassy waterways, and old fields: $22.8 \pm 5.9\%$ SE), and woody vegetation (mainly corridors, $33.0 \pm 6.3\%$ SE). We considered a covey's habitat use as the average percentage of cover types observed within the independent covey-week. We used multivariate analysis of variance with Tukey's *post hoc* test with Bonferroni adjustments ($P \leq 0.05$) to determine overall variability in habitat use among different covey sizes and with average study area habitat availability.

RESULTS

Across all 3 years, 195 covey-weeks were available for analysis (i.e., were followed for 5 consecutive days within a week, the covey size was estimated, and any subsequent covey-weeks with the same covey size were excluded to avoid pseudoreplication). Covey size was related to mean daily movement in a convex manner ($F_{2,192} = 17.79$, $P < 0.01$), where both small and large coveys traveled greater distances than intermediate-sized coveys (Fig. 1). For further analysis, covey sizes were combined into categorical groups 1–4, 5–8, 9–12, 13–16, and ≥ 17 individuals (Table 1).

All covey size categories, except the smallest group (Rayleigh's test for uniformity $P = 0.11$), exhibited a

Table 2. Chi-square value ($df = 17$) of turning angles of different categories of northern bobwhite covey size in East-central Kansas, USA, 1997–2000. Analyses test the probability associated with the null hypothesis that samples are drawn from the same population.

Covey size	1–4	5–8	9–12	13–16	≥ 17
1–4	—				
5–8	18.24	—			
9–12	32.89**	24.20	—		
13–16	28.99*	34.26**	11.92	—	
≥ 17	24.49	24.17	23.98	26.71	—

* $P < 0.05$.

** $P < 0.01$.

nonuniform distribution of turning angles (Rayleigh's test for uniformity, $P < 0.01$) with prevalence toward turning angles of approximately 180° , especially for small and large coveys (Table 1). Coveys of intermediate size also tended to have a greater proportion of turning angles at 0° (Fig. 2). Additionally, small coveys (1–4 and 5–8) showed a broader distribution of turning angles (Fig. 2) than medium and large coveys (9–12, 13–16, ≥ 17 individuals; Chi-square analysis; Table 2). Using the correlated random walk model, we found weekly displacement showed preference for a region ($t > -4.40$, $P < 0.01$), with statistically indistinguishable differences among covey size categories ($F_{4,190} = 1.98$, $P = 0.10$; Fig. 3). Additionally, examining the autocorrelation of successive turning angles for different covey sizes showed consistent negative first-order and second-order correlations for all covey sizes. For example, if a covey moved in the same direction for 2 successive days, then it was less likely to continue moving in the same direction in the third day. This made the weekly displacement of coveys less than predicted by the CRW model.

Analyzing the fractal dimension of movement patterns, we found that the movement of small coveys (1–4 individuals) increased toward 2—the fractal dimension of a random walk—with increased scale. This observation indicates that the searching behavior of small coveys was more directed at small scales (100 m: $D = 1.34$) but became more tortuous at larger scales (700 m: $D = 2.00$). Because habitat patches are typically several hundred meters in diameter, this result suggests that movement of small coveys within habitat types (small scales) is directed, whereas movement among types (large

Table 1. Descriptive statistics of daily path distances and turning angles of northern bobwhite covey sizes in East-central Kansas, USA, 1997–2000.

Covey size	Sample size			Mean daily move distance (m) (SE)	Mean angle of successive move ($^\circ$) (SE)	Angular concentration ^a	Rayleigh's test of uniformity, P
	Covey-weeks	Daily path distances	Turning angles				
1–4	12	48	36	278.9 (38.8)	182.7 (15.6)	0.54	0.11
5–8	44	176	132	183.2 (13.2)	239.0 (15.2)	0.47	<0.01
9–12	74	296	222	147.0 (6.5)	168.3 (45.4)	0.12	<0.01
13–16	40	160	120	172.4 (13.2)	127.7 (27.3)	0.27	<0.01
≥ 17	25	100	75	237.3 (18.0)	185.7 (9.2)	1.08	<0.01

^a The angular concentration is a parameter that measures the departure of the distribution from a perfect circle (or a uniform distribution).

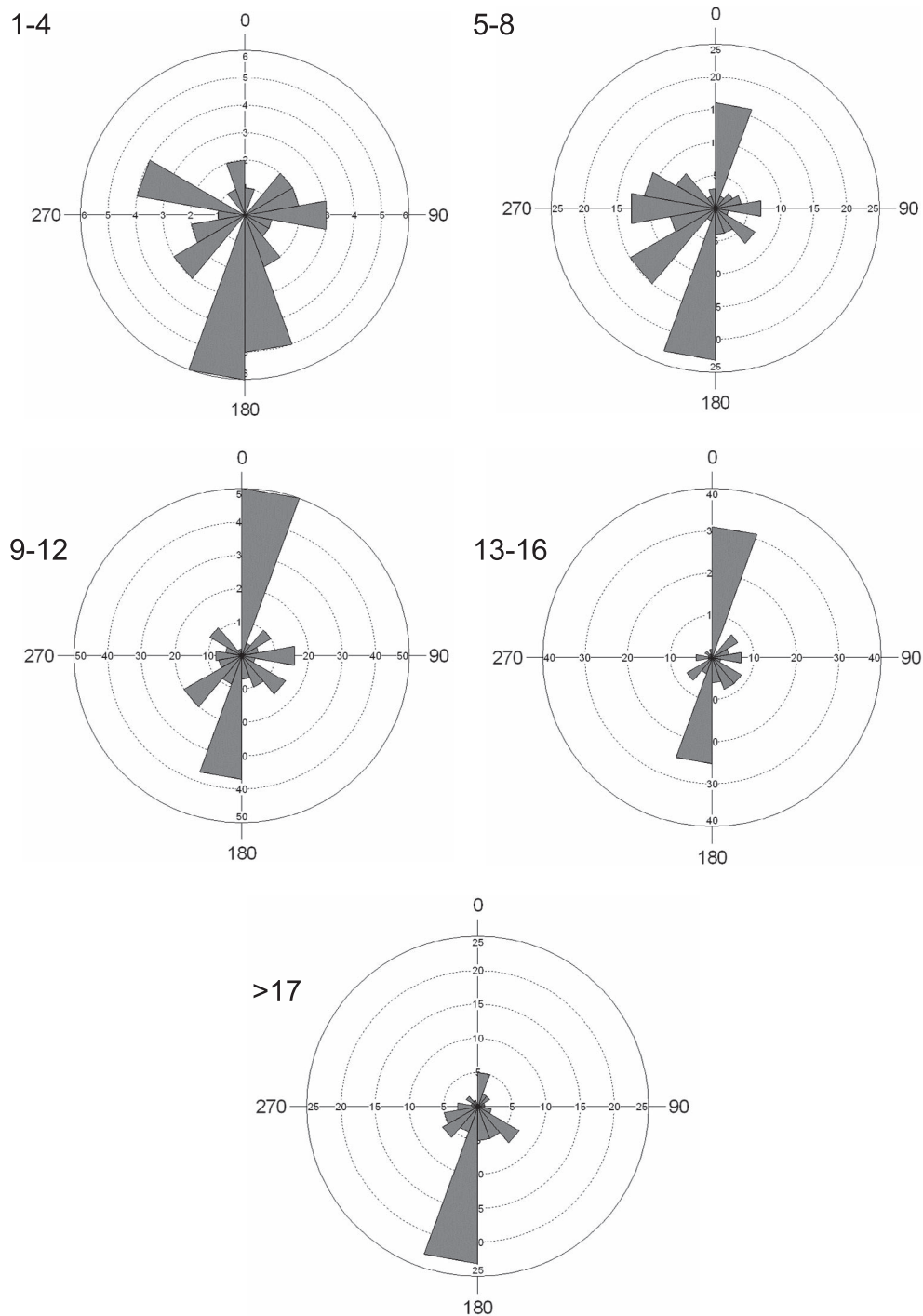


Fig. 2. Angular distributions of successive turning angles for northern bobwhite covey sizes in East-central Kansas, USA, 1997–2000. The length of the bars indicate the number of data points that fit the specific angular concentration.

scales) is more complex. Intermediate (9–12 individuals) and moderately large coveys (13–16) show the opposite search behavior. Although their small-scale (100 m) movement patterns are moderately directed ($D = 1.56$ – 1.62), at larger scales their movement patterns become strongly linear ($D = 1.00$ for both; Fig. 4). This suggests that coveys of intermediate size (9–16 individuals) make a thorough search of habitats (perhaps for food resources) at smaller scales. Yet at larger scales they tend to move

linearly among habitat types (such as through linear corridors of woody cover). The largest coveys (≥ 17 individuals), who tended to have increased daily movement, showed an interesting oscillation in fractal dimension, producing an average $D = 1.37$.

Pasture was used in relatively equal percentage to its availability and across coveys of all sizes, although small coveys (1–4 individuals) tended to use it slightly less than coveys of all other sizes (Fig. 5). Hayland was also used

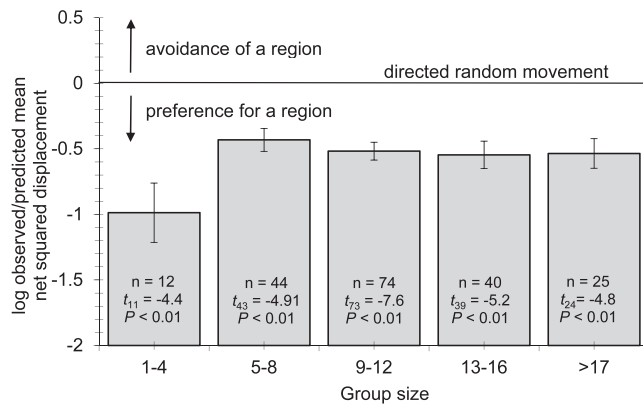


Fig. 3. Observed/predicted weekly displacement (R^2 , eq. 1) of northern bobwhite coveys from a correlated random walk model (± 2 SE) in East-central Kansas, USA, 1997–2000. Values >0 indicate observed weekly displacement was more directive than estimated from a correlated random walk (CRW), values $=0$ indicate correspondence to a CRW, and values <0 indicate fidelity for an area. One sample t -test ($P < 0.05$) measures significant departure from CRW.

in relatively equal percentage to its availability and across coveys of all other sizes. Idleland (such as Conservation Reserve Program grasslands and grassy waterways) was used differently across coveys and small coveys (1–4 individuals) used idleland more than average (9–12 individuals) and large (>17 individuals) coveys. Woody cover (primarily linear corridors of treelines and woodlots) was used differently across groups and average-sized coveys (9–12 individuals) used woodland more than large (>17 individuals) coveys. Woody cover (often associated with edge habitat) is generally preferred by northern bobwhite for daytime escape cover; therefore, this result seems to indicate coveys of intermediate size have ranges that allow them to take advantage of higher quality habitat. Last, cropland was used differently across groups and coveys of 5–8 individuals used it less than the largest coveys (≥ 17 individuals).

DISCUSSION

In the growing effort to establish a movement ecology paradigm, it is critical that ecologists not only understand the interplay between movement behavior and spatial structure (Nathan 2008, Nathan et al. 2008) but also how social structuring of animals could add complexity to this paradigm (Wittemyer et al. 2008). Williams et al. (2003) demonstrated in the same area that northern bobwhite coveys of roughly 11 individuals were optimal, corresponding to the greatest fitness achieved by their members. Small coveys (1–7 individuals) had lower group persistence and individual survival and used increased movement to create or join larger coveys where survival was higher, while large coveys (15–22 individuals) had lower individual survival, increased group movement, and individual mass loss (Williams et al. 2003). Density-dependent feedbacks (e.g., lower survival and increased competition) may have reduced larger

coveys to a stable size. Williams et al. (2003) results suggested the regulation of an optimal group was promoted by high group persistence, low group movement, improved feeding efficiency, improved individual predator detection, and improved individual survival. On account of these complex optimal group size dynamics, we hypothesized that coveys could have the potential to respond to their environment in different ways depending on their size and deviance from optimal covey size.

Movement patterns of different-sized coveys depended on the scale at which they were measured. With (1994a) suggested departure from random search patterns reflects encounters with the physical structure of the vegetation or responses to correlates of patch structure. Consequently, routine daily movements within a covey's home range will largely dictate bobwhite habitat use and landscape perception. This movement was based on remembered characteristics of the landscape, forage quantity and quality, and escape cover quantity and quality. Indeed, increased knowledge of the landscape around these coveys probably allowed them the ability to make strategic 'decisions' regarding their movements and needs (Lima and Zollner 1996, Marell et al. 2002). We initially questioned whether covey size could affect movement rates and patterns via either directed-and-quick movements or through longer forays where animals drift into new territory and/or then return to the initial home range. From our coarse daily analysis, the way different covey sizes departed from random movement indicated that different behavioral states (associated with covey size) could influence perception and use of the landscape. We encourage future researchers to replicate our efforts using the recent technological advancements of Global Positioning System radiocollars with data loggers with very short temporal resolutions because this should strengthen our understanding of these movement processes.

In this study, coveys of intermediate size (9–12 individuals, close to optimal group size) exhibited daily movements that were substantially smaller and weekly home ranges that consisted of more woody escape cover than was exhibited by coveys of smaller or larger sizes. From the fractal dimension analyses, these coveys exhibited movement in between linear and a random walk at small spatial scales but very linear at large spatial scales. Thus, at larger spatial scales, habitat use became largely homogeneous as would be expected by increased selection for woody cover. Woody cover generally acts as escape cover and a mode for travel (Williams et al. 2000); therefore, increased linear movement within these corridors by coveys of intermediate size would enhance their observed increased fitness (Williams et al. 2003).

However, the relationships observed by large and small coveys showed a different result. Large coveys (≥ 17 individuals) are known to have lower feeding efficiency and fitness (Williams et al. 2003) yet low probabilities of breaking apart into smaller coveys. Williams et al. (2003) hypothesized behavioral patterns of large coveys reflected more concern with feeding than with adjusting membership to create a more intermediate-sized group. In the present study, large coveys had increased daily movement relative to smaller coveys and

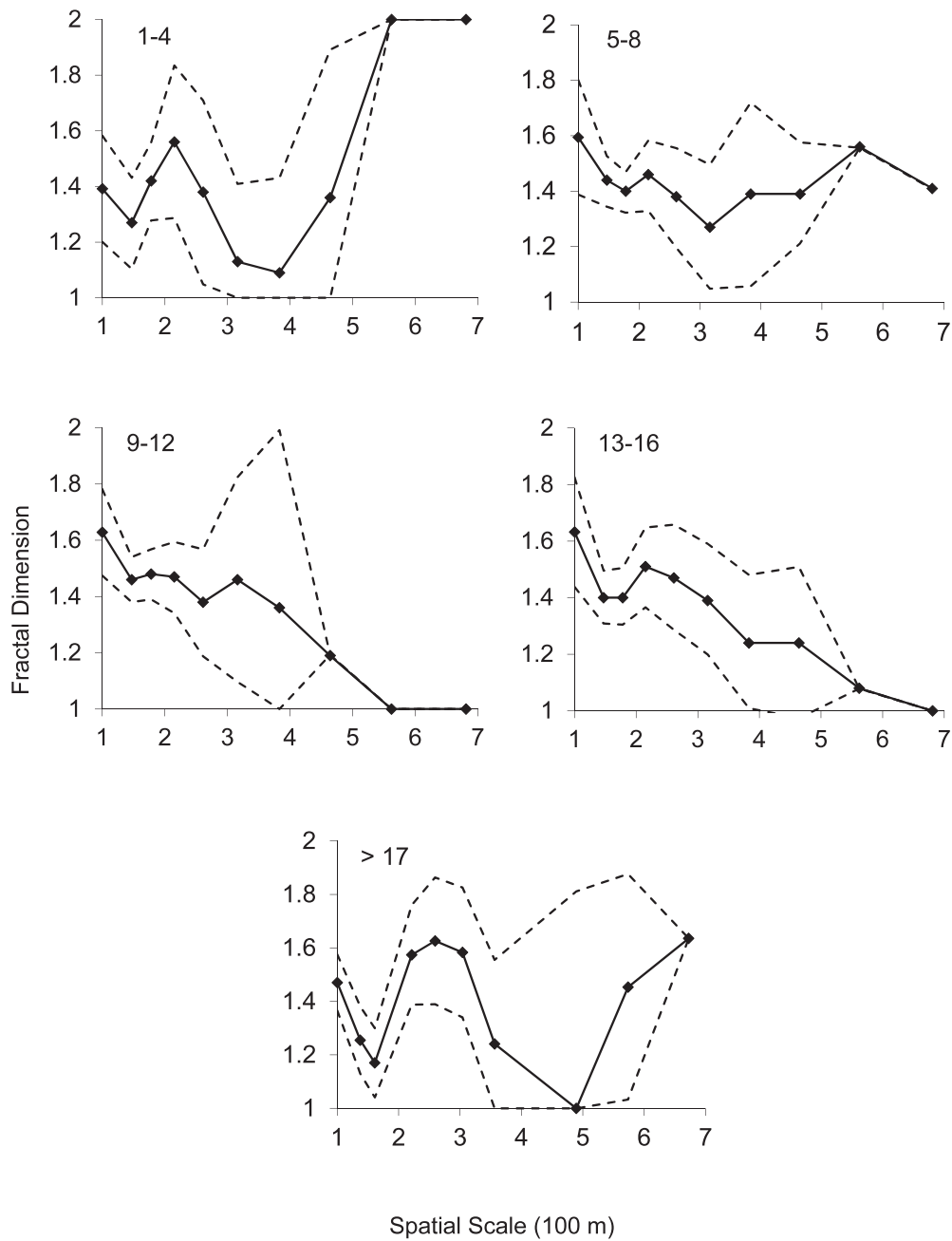


Fig. 4. Fractal dimensions D ($\pm 95\%$ CI indicated by dashed lines) across scales for different covey sizes of northern bobwhite coveys in East-central Kansas, USA, 1997–2000.

tended to move in straighter lines (as indicated by the high proportion of turning angles around 0° and 180° , and their multiscale fractal dimension) and they incorporated more cropland into their range, presumably to meet the feeding requirements of a larger covey. These results support the idea that large coveys are using complex searching behavior within larger home ranges containing more complex habitat structure as a response to increased nutritional demands.

In contrast, small coveys (1–4 individuals) tended to move more and increase the size of their home range, travel with a greater diversity of turning angles, and show movement patterns that were largely tortuous across a

greater number of habitat patches at larger spatial scales (700 m). Small coveys have lower fitness and add new membership to increase fitness (Williams et al. 2003) so it is possible that the movement behavior we observed represented a shift into a foray mode where they were searching for new membership (Conradt et al. 2003) by making themselves known through morning epideictic displays (Stokes 1967). Indeed, the difference in movement patterns in small coveys (that are searching for new membership) as compared with movement patterns of large coveys (that are presumably dominated by feeding) supports Fletcher's (2006) argument that incorporating

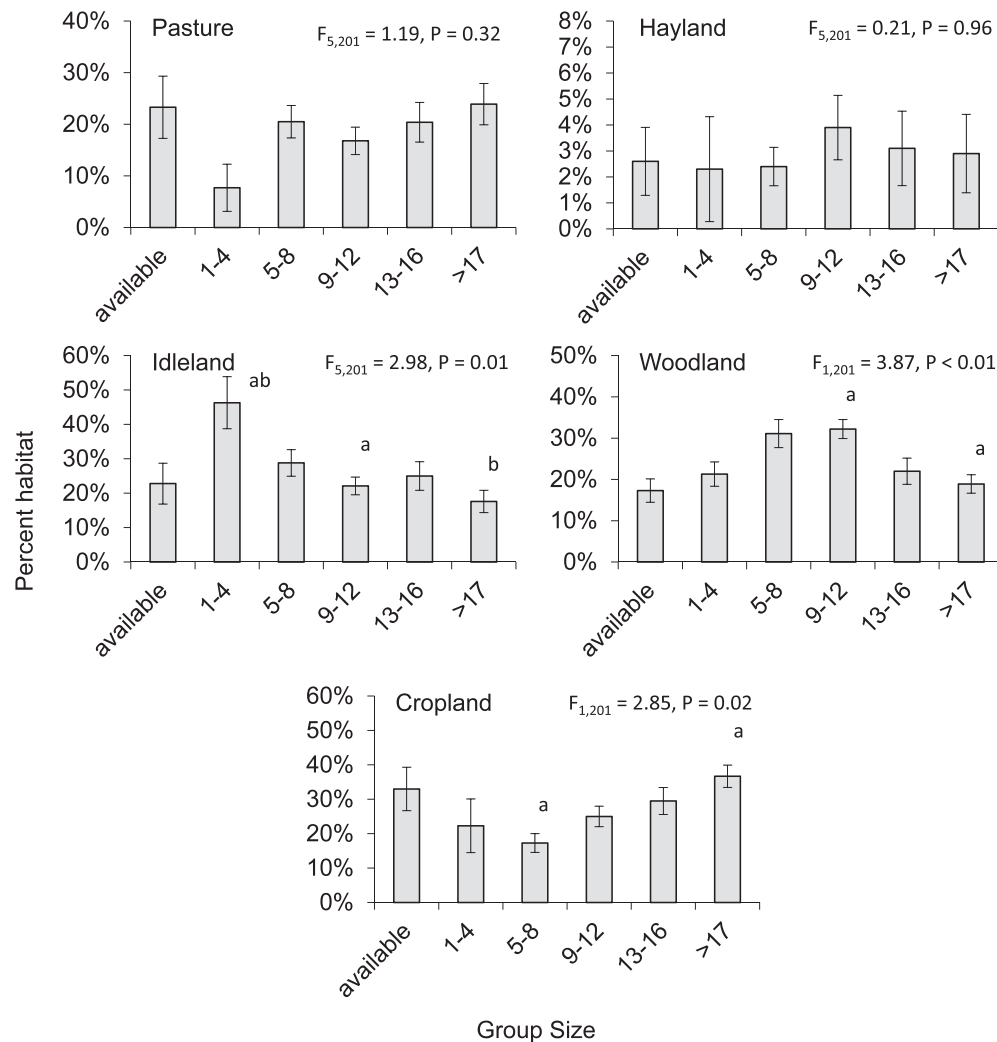


Fig. 5. Average percent habitat availability across all 12 study areas and average percent habitat use ($\pm$ SE) by different covey sizes of northern bobwhite in East-central Kansas, USA, 1997–2000. Multivariate analysis of variance ($P < 0.05$) was tested for differences among groups. Like letters indicate differences between pairs of groups using Bonferroni adjusted Tukey's *post hoc* test ($P < 0.05$).

conspecific attraction into movement decisions greatly alters habitat selection and population dynamics.

Use of corridors to aid animal movement from one habitat patch to another for improving resource acquisition has generated substantial recent interest (e.g., Henein and Merriam 1990, Saunders and Hobbs 1991, Rosenberg et al. 1997, Gilliam and Fraser 2001, Mabry and Barrett 2002, Berggren et al. 2002). Within this context, Lima and Zollner (1996) argued that an important unanswered behavioral question is whether corridors are perceived (i.e., sought out) as travel routes to other patches or whether they are simply landscape elements into which animals passively enter. During the nonbreeding season, northern bobwhites use a variety of habitat types but nonetheless rely heavily on edge corridors (treelines, hedgerows, etc.), not only for escape cover but also for daytime travel between grassland and agricultural fields for feeding and roosting (Williams et al. 2000). In this study, we found this to be especially true for coveys of intermediate size. Immigration and emigration are critical to group-size maintenance via covey fission and fusion;

therefore, distribution and spatial arrangement of woody corridors might influence the maintenance of optimal covey size. This type of relationship has been seen in Florida scrub jay (*Aphelocoma coerulescens*) groups where habitat fragmentation can inhibit movement between groups and disrupt the maintenance of a stable group size (Stith et al. 1996). However, in the case of small coveys, corridors may not be as crucial a mechanism to finding new membership. Small coveys appear to travel with a greater diversity of turning angles and have movement paths with high tortuosity at larger spatial scales; therefore, they appear willing to move outside of habitat corridors as a means of travel from one patch to another when maintenance of group size is important. Fletcher (2006) further hypothesized that conspecific attraction (e.g., the epideictic displays produced by bobwhite; Stokes 1967) would become increasingly important in fragmented landscapes where travel corridors may not always exist. Although we found linear woody corridors were important for covey size maintenance, small coveys appeared to move via forays across

other types of fragmented habitat supporting Conradt et al.'s (2003) and Fletcher's (2006) hypotheses.

Northern bobwhites are primarily short-distance ground-travelers that make occasional short flights (we observed average daily movement = 183 m and the farthest 1-day distance = 1,100 m); therefore, we suspect they have relatively limited perceptual ranges. Consequently, any barrier approximately >1 km in width is unlikely to be crossed despite the presence of conspecific attraction. Management plans designed to enhance northern bobwhite populations should include recommendations for developing corridors or patches juxtaposed between useable habitat to avoid long-distance barriers. Our results also suggest that if population expansion is of priority, there is a need to examine further whether habitat management should be focused on expansion of the number of optimum covey ranges (with smaller, less complex areas) or on promoting ideal conditions for large coveys (with larger, more complex areas).

MANAGEMENT IMPLICATIONS

Comparisons of northern bobwhite movement patterns suggest that bobwhites respond to their environment differently depending on covey size. Additionally, covey movements may have the potential to affect habitat use, foraging success, and group fission and fusion dynamics. All of these factors have the potential to affect overwinter survival, which is critical for increasing bobwhite numbers (Sandercock et al. 2008). Of particular importance, in portions of the bobwhite range where populations are small with the possibility of smaller and isolated coveys, managers should be aware that bobwhites potentially will take larger forays across habitat types, thus increasing the likelihood of daily mortality risk. Thus we believe it is important that habitat management goals include the development of as many corridors with escape cover as possible to decrease predation risk or to enhance contiguity of habitat components, such as development of old field habitats where all components are in close juxtaposition.

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