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Recommended Citation
Badyaev, A. V.; Etges, W. J.; and Martin, Thomas E., "Age-Biased Spring Dispersal in Male Wild Turkeys" (1996). Wildlife Biology Faculty Publications. 35.  
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Age-biased Spring Dispersal in Male Wild Turkeys

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In polygamous animal species, the reproductive component of male fitness largely is determined by the number of females to which they can gain access (e.g. Wright 1946). Access to females often is strongly influenced by the possession of high-quality breeding or display grounds by males (Weatherhead and Robertson 1977). For animals that move between winter and breeding areas, access to high-quality breeding or display grounds can be determined by timing and distance of such movements, but ability to hold high-quality sites could be determined by local familiarity, as well as social and physiological status (Greenwood 1980, Johnson 1986, Johnson and Gaines 1990, Pärt 1994, Tsuji et al. 1994).

Early dispersal and short-distance movements should allow access to best sites and dominant individuals should be expected to exhibit such movement behaviors. Moreover, shorter dispersal can enhance the survival component of fitness because it often reduces potential costs of increased mortality risk with dispersal distance (e.g. Johnson and Gaines 1990). Subordinates, however, may be expected to disperse longer distances and move more within display areas because it takes them longer and more movement to find suitable areas from which a dominant individual will not exclude them. Here we examine this dominance hypothesis.

Wild Turkeys (Meleagris gallopavo) are especially suitable for study of potential effects of dominance status on dispersal and movement patterns. They are polygynous and, in females, nest-site selection precedes mate selection (Healy 1992, Badyaev 1994). The social status in this species is largely set by age; young males are subordinate to older males and can be prevented from breeding by these older males (Healy 1992). In addition, the use of radiotelemetry allowed us to quantify female movements during spring dispersal and distribution of nesting areas (Badyaev et al. 1996).

We predicted that: (1) older males should disperse the shortest distance; (2) movements of older males should concentrate around suitable display grounds (i.e. around limited nesting areas; Badyaev et al. 1996) once they reach their display grounds, and should encompass a smaller area than subordinates; and (3) if movements of males in spring are influenced by displaying activity, males are expected to move more and farther in later parts of the breeding season when female renesting and breeding receptiveness causes changes in distribution of females.

Methods.—Our study was conducted during 1992-1993 in the Ozark National Forest in northern Arkansas. The study site was flat-topped hills (elevation to 746 m) with narrow valleys. Dominant canopy species included white oak (Quercus alba), northern red oak (Q. rubra), post oak (Q. stellata), shagbark hickory (Carya ovata), and shortleaf pine (Pinus echinata). For a detailed description of the study site, see Badyaev (1995). All birds were captured using cannon nets on pre-baited sites distributed throughout the study area. All captured birds were fitted with 120 g backpack-style radio transmitters and released at capture sites. Most of the 35 radio-tagged males were located once every four to five days, although more frequent locations and visual observations also were recorded. Only birds with 15 or more recorded locations were used to calculate home ranges (for details of telemetry protocol, see Badyaev et al. 1996).

Females initiated 80% of first nests by 1 May in both years. Thus, the period prior to 2 May is referred as "early" as opposed to "late," which extends from 2 May to 2 June. Successive locations separated by more than 2 days but less than 10 days were statistically independent (Swihart and Slade [1985] test for two-day intervals; F/r² > 1.85, P < 0.05) regardless of time lags between them. Observations separated by five days were used for interlocation distance analyses. The display range was defined as the home range occupied from 1 April through 15 June. This time interval was based on female nest-initiation phenology (Badyaev 1994). Dispersal distance was defined as the distance from harmonic mean of home range used in February to harmonic mean of display range. Partial area was calculated as sum of areas of all polygons drawn around centers of activity divided by the total area of single polygon of range occupied by an animal (Kenward 1990). Home-range estimates, interlocation distances, and associated statistics were computed using RANGES IV software (Kenward 1990; for details, see Badyaev et al. 1996). Neither morphological measurements nor dispersal parameters differed between study sites or years (ANOVA, all P > 0.3). We used the criteria of Kelly (1975) and Steffen et al. (1990) to classify males into SY (second year since hatching), TY (third year after hatching), and ATY (after third year since hatching) age groups.

Results.—ATY males dispersed shorter distances than either SY or TY males (Kruskal-Wallis test, X² = 7.45, df = 2, P < 0.05; Table 1). Dispersal distances of SY and TY males were not significantly different (X² = 3.42, P = 0.12). Heavier SY males dispersed shorter distances than SY and TY males (X² = 10.57, P < 0.001). Heavier males dispersed shorter distances than heavier SY males (X² = 4.37, P < 0.05), and SY males were not significantly different from heavier SY males (X² = 2.66, P > 0.05).
Table 1. Descriptive statistics ($\bar{x} \pm$ SE, with $n$ and range in parentheses) of spring-dispersal and home-range estimates of male Wild Turkeys in the Arkansas Ozarks, 1992-1993.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>SY</th>
<th>TY</th>
<th>ATY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring dispersal (km)</td>
<td>$5.1 \pm 1.0$ (12, 1.1-12.6)</td>
<td>$6.8 \pm 1.4$ (17, 0.5-22.2)</td>
<td>$2.6 \pm 0.7$ (6, 0.4-4.7)</td>
</tr>
<tr>
<td>Harmonic-mean range (km$^2$)</td>
<td>$18.9 \pm 7.9$ (5, 2.5-36.7)</td>
<td>$1.7 \pm 0.5$ (9, 0.4-4.2)</td>
<td>$0.38$ (1)</td>
</tr>
<tr>
<td>Multinuclear polygon (km$^2$)</td>
<td>$6.9 \pm 1.6$ (7, 2.1-12.7)</td>
<td>$3.3 \pm 0.9$ (11, 0.9-10.8)</td>
<td>$0.5 \pm 0.3$ (3, 0.2-0.8)</td>
</tr>
<tr>
<td>Convex polygon (km$^2$)</td>
<td>$10.7 \pm 2.8$ (7, 2.1-18.9)</td>
<td>$4.9 \pm 1.4$ (11, 0.7-14.3)</td>
<td>$0.9 \pm 0.05$ (3, 0.92-1.0)</td>
</tr>
</tbody>
</table>

*Harmonic-mean estimate, multinuclear polygon by clustering, and convex polygon methods based on 90%-probability polygons.*

Distances, and body mass in spring explained 59% of the variation in spring dispersal distance in this age class (linear regression, $F_{1,12} = 14.2, P < 0.005$). Dispersal distances of TY and ATY males did not correlate with body mass (both $P > 0.2$).

Display ranges of TY and ATY males were significantly smaller than those of SY males (Kruskal-Wallis test, $X^2 = 8.35, P = 0.01$; Table 1). This difference was most apparent when harmonic-mean estimates of display range were used ($P < 0.001$; Table 1). Males of different ages used display ranges differently (Fig. 1). Partial-area estimate differed between age classes (Kruskal-Wallis test, $X^2 = 3.61, P = 0.06$) and averaged $0.49 \pm$ SE of $0.13$ ($n = 10$, range $0.11-1.0$) for adults (TY and ATY males combined) and $0.79 \pm 0.13$ ($n = 7$, range $0.37-1.00$) for SY males. Adult-male use of range was concentrated around several centers of activity ($\bar{x} = 1.8 \pm 0.2$), but SY male range use was less restricted to particular areas. Range estimates for subadults increased with almost every additional observation because birds frequently ventured into previously unvisited areas (Fig. 1).

For SY males, distances between successive locations averaged $4.1 \pm 0.3$ km late in the season and were significantly longer than $2.2 \pm 0.1$ km distances early in the season (pairwise t-test, $t = 3.89, P = 0.02$). However, there were no differences between early ($4.6 \pm 1.3$ km$^2$) and late ($9.0 \pm 3.5$ km$^2$) home ranges in this age class ($t = 0.67, P = 0.53$). For adult males, distances between successive locations averaged $1.4 \pm 0.4$ km late in the season and $1.3 \pm 0.2$ km early in the season, and were not significantly different ($t = 0.26, P = 0.79$). Adult male home ranges used late in the season ($2.4 \pm 1.3$ km$^2$) were significantly larger than home ranges used early in the season ($0.6 \pm 0.1$ km$^2$; $t = 3.56, P = 0.01$).

Discussion. —Our findings were consistent with predictions of the dominance hypothesis: late-winter home ranges of ATY males were closer to spring display grounds than were ranges of younger males. In addition, larger SY males, which presumably are dominant over smaller SY males, also dispersed shorter distances within this age group. Because suitable habitats for nesting are limited in our study area and prenesting dispersal of females is influenced by nest-habitat searching (Badyaev 1994, 1995), males benefit from being closer to such areas by assuring frequent encounters with females (see also Bradbury and Gibson 1983, Schroeder and White 1993). In the population under study, early nest initiation was the most important factor contributing to nest survival (Badyaev 1994). Thus, males that reach spring display grounds earliest profit by mating with early-nesting females.

Adult males occupied smaller display home ranges than did SY males (see also Hoffman 1991). Adult-male home-range use was more heterogeneous, which possibly reflects an uneven distribution of suitable nesting areas of females (Badyaev 1994, 1995, Badyaev et al. 1996). Adult-male movements within their display ranges were more restricted than those of SY males, potentially because nondisplaying SY males experience reduced aggression from older conspecifics when moving among display grounds (e.g. Healy 1992). Adult males showed considerable fidelity to display sites within the breeding season (Fig. 1). Bergerud (1988) and Phillips (1990) also speculated that female forest grouses preferred males showing the

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Fig. 1. Patterns of display range use in SY ($n = 6$) and adult (TY and older; $n = 8$) male Wild Turkeys. SE shown for every [20 + 10n] percentage of observation for SY males, and for every [25 + 10n] percentage of observation for adult males.
most predictability in display behavior when near nesting grounds. Male fidelity to displaying sites contributes to maintaining safe distances between female nests and male display sites, ensuring that males will not follow females to their nesting areas, thereby making them more conspicuous to predators (Bergerud 1988).

Wild Turkey males of all examined age groups increased their movements later in the season. The observed pattern is consistent with our prediction and could result from a decline in availability of receptive females and changes in the previously established hierarchy in breeding areas as a result of human disturbance (e.g. hunting). In addition, more areas became suitable for nesting later in the season (Badyaev 1995) and, therefore, female distribution was not so restricted as it was early in the season.

Acknowledgments.—We are grateful to D. Frick, D. Hasenbeck, A. Hodgson, T. Lane, and K. Teter for help with the fieldwork. We thank F. C. James and J. E. Johnson for helpful discussion. This paper was significantly improved by comments from A. T. Bergerud, G. D. Schnell, M. A. Schroeder, and an anonymous reviewer. The support of the Arkansas Game and Fish Commission and the University of Arkansas is gratefully acknowledged.

LITERATURE CITED


Received 5 December 1994, accepted 26 June 1995.