SPATIAL ASPECTS OF ROOST-SITE SELECTION IN BREEDING MALE DARK-EYED JUNCOS¹

C. RAY CHANDLER Department of Biology, Ball State University, Munice, IN 47306

ELLEN D. KETTERSON AND VAL NOLAN JR. Department of Biology, Indiana University, Bloomington, IN 47405

Key words: Dark-eyed Junco; habitat use; Junco hyemalis; roost sites; spatial activity.

With the exception of a few species that roost communally or in cavities (e.g., Kluyver 1957, Meanley 1965, Kilham 1971, Pitts 1976, Swingland 1977, Lyon and Caccamise 1981, Morrison and Caccamise 1985, Stouffer and Caccamise 1991), roost-site selection is one of the more poorly known aspects of habitat use in passerine birds (Cody 1985). Available studies indicate that roost sites are chosen with respect to energetic considerations (Kendeigh 1961; Buttemer 1985; Walsberg 1986, 1990; Buttemer et al. 1987) or predator avoidance (Lack 1968, Walsberg and King 1980). Although it is also recognized that roosts (particularly communal ones) may be positioned with respect to local resource availability (e.g., Morrison and Caccamise 1985. Caccamise and Morrison 1988), roost-site selection may play a broader role in the spatial activity of birds. Choice of a particular roost might determine not only access to feeding sites, but also a variety of other behavioral options open to an individual at dawn (e.g., territory defense, intrusion onto neighboring territories). Conversely, behavioral demands at dawn might constrain roost-site selection (Chandler and Tolson 1990 provide an example for male lizards).

In this note we describe spatial aspects of roost-site selection in breeding male Dark-eyed Juncos (*Junco hyemalis*). The purpose of our analysis was to explore the possible role that roost sites might play in the overall spatial activity of a male passerine bird during the breeding season. Specifically, our objectives were to quantify (1) the spatial distribution of roost sites relative to the diurnal activity of male juncos, (2) the short-term (3–5 days) stability of these sites, and (3) the physical characteristics of summer roost sites.

METHODS

We studied juncos (*J. h. carolinensis*) at Mountain Lake Biological Station, Giles County, Virginia (37°22'N, 80°32'W) during the summers (May–July) of 1990 and 1991. Juncos are abundant summer residents at this montane site in southwestern Virginia (see Chandler et al. 1994 for a complete description). Males establish territories in March or April, pair socially with a single female (polygyny is very rare), and feed nestlings at rates equal to those of the female (Ketterson et al. 1992). Since 1983, almost all of the 150–200 juncos occurring in the vicinity of Mountain Lake each summer have been banded with U.S. Fish and Wildlife Service bands and marked with a unique combination of color bands.

We quantified the roost sites of 13 individuals as part of a broader study of the effects of testosterone on spatial activity in male juncos (Chandler et al. 1994). All birds involved in this study had received small, subcutaneous silastic implants earlier in the spring (April). Control males received empty implants and testosterone males received implants filled with crystalline testosterone (which maintained their testosterone levels at spring maxima throughout the summer; Ketterson and Nolan 1992). Although we identify the treatment status of all birds used in the analysis of roost sites, the effects of testosterone were not the focus of this study (for details of this work see Ketterson et al. 1991, 1992; Ketterson and Nolan 1992; Chandler et al. 1994). The majority (n = 9) of birds used in this analysis were control males (no hormone manipulation), and there were no apparent differences in roost sites between the two treatment groups (see below).

Roosts were found by placing a small radiotransmitter (from Wildlife Materials, Inc., Carbondale, IL in 1990; AVM Corp., Livermore, CA in 1991) on each male. Males were captured near their nests in mist nets or traps, equipped with a transmitter, and returned to their territories within 30 min. The transmitters were no more than 5% of the body mass of any individual and were attached with eyelash glue and cyanoacrylate to the birds' upper back (Chandler et al. 1994 provide details of the attachment procedure). Individuals were located using a hand-held Yagi antenna and a Wildlife Materials Merlin 24 receiver. Transmitters had no detectable effect on male activity.

Roosting juncos were located between 22:00 and 24: 00 for 3-5 consecutive nights during the time when they had active nests containing eggs or nestlings. We followed transmitter signals to their source, approached to within approximately 10-20 m of the roost (being careful not to disturb the bird), and determined the tree being used as a roost site. In dense forest we carefully circled the site to identify the source of the signal with precision. Each site was then flagged and we returned later to identify the species of tree used for roosting, to estimate the height of the tree (to the

¹ Received 8 June 1994. Accepted 23 August 1994.

	Number of nights tracked	Number of roost sites	Number of sites off ter- ritory	Number of nights spent off ter- ritory	Mean distance (m) between sites (±SE)
Contro	l males				
1	4	4	0	0	62.9 (19.1)
2	3	2	1	1	216.3
3	3	2	1	1	195.9
· 4	5	4	0	0	98.4 (31.1)
5	4	1	0	0	
6	4	1	1	4	_
7	3	2	0	0	46.0
8	4	1	0	0	—
9	5	3	2	3	158.3 (46.3)
Testost	erone m	ales			
10	4	4	2	2	176.1 (39.1)
11	3	2	0	0	81.2
12	4	1	0	0	_
13	3	2	1	1	325.1
Mean	3.8	2.2	0.6	0.9	

TABLE 1. Summary of roost-site selection by male Dark-eyed Juncos.

nearest meter), and to map the location (Chandler et al. 1994).

RESULTS

We located 49 roost sites of 13 individual juncos (Table 1). Nine of these individuals (69%) used multiple sites, with three individuals using as many as four different sites over 4-5 nights. Male juncos averaged slightly more than two roost sites per individual over an average of about four nights (Table 1). In those individuals with multiple roosts, the mean distance between sites ranged from 46-325 m (Table 1).

Not only was the use of multiple sites common, but some individuals roosted beyond the apparent boundaries of their territory. These off-territory roosts were identified conservatively as sites (1) located beyond the daily activity range of an individual (as indicated by diurnal radiotelemetry during the same time period; Chandler et al. 1994) and (2) known to be in areas defended by another male. Using these criteria, 46% (6/13) of males had at least one site located off their territory. In one case, a male failed to roost on his territory on any of four consecutive nights (male #6; Table 1).

Off-territory sites (n = 8) were often considerable distances from a male's own nest $(x = 243.2 \text{ m} \pm 34.9 \text{ SE}; \text{ range } 110-427 \text{ m})$. However, the exact spatial significance of these sites was not always clear. The offterritory roost of male #6 was located within 10 m of a frequent song perch of a neighboring male. Male #10 roosted for a single night within 20 m of a nest where a neighboring female was in the process of laying a clutch. Male #13 roosted for a single night directly above a favored feeding site of a neighboring pair of birds.

All junco roosts were located in coniferous trees (33

in hemlocks, *Tsuga canadensis*; 11 in pines, *Pinus* spp.; and 5 in ornamental spruce, *Picea* spp.), despite the fact that deciduous trees outnumbered conifers on the territories of all juncos involved in this study. Height of roost trees ranged from 2 m (ornamental spruce) to about 25 m (mature hemlock) ($\bar{x} = 10.6 \text{ m} \pm 1.3 \text{ SE}$). We could not determine precise heights of the actual perch, but if the height of the tree permitted most juncos roosted several meters above the ground.

DISCUSSION

Our results demonstrate that male juncos during the breeding season show considerable short-term variability in choice of a roost site, that these sites are occasionally located off an individual male's territory, and that coniferous trees are used for roosting.

Some other passerines are known to change roost sites nightly (Pitts 1976) or over other short time periods (Nolan 1978, Morrison and Caccamise 1985, Atkinson 1993). In the case of juncos, at least for withinterritory shifts of roost site, the most likely explanation for this frequent movement is predator avoidance. Frequent changes in the location of a roost would minimize visual (droppings) and olfactory cues that might attract predators (Pitts 1976). There are other passerines that use the same roost for extended periods of time, but these tend to be nest, cavity, or communal roosters (e.g., Kilham 1971, Balda et al. 1977). The need for predator avoidance through frequent changes of roost site may be greater in species (like juncos) that roost solitarily in foliage. Another possibility is that some male juncos simply roost wherever nightfall overtakes them. However, several juncos, including some of those individuals with multiple sites, were observed to fly considerable distances to a roost site at dusk.

Predator avoidance is unlikely to explain the offterritory roosts of some male juncos. Shortage of appropriate roost sites is probably not a factor either. Although deciduous trees outnumber conifers on almost all junco territories at Mountain Lake, all males involved in this study had many coniferous trees available as potential roost sites on their territories (trees that appeared identical to those used as off-territory roosts). We cannot eliminate the possibility that appropriate roosts are limiting on some junco territories, but we believe it is unlikely.

It seems more likely that off-territory roosts are an active part of territorial intrusions by male juncos. Male passerines frequently intrude onto neighboring territories (e.g., Nolan 1978, Leary and Sullivan 1991) and might facilitate successful intrusion by moving onto those territories in the poor light of dusk and being present, unseen, at dawn. These males may gain extrapair fertilizations (Birkhead and Møller 1992; P. Parker, E. D. Ketterson, V. Nolan, Jr., unpubl. data for this population of juncos), useful information about their neighbors' activities or territory quality, or temporary use of a high-quality feeding site before returning to their own territory shortly after dawn. The possible role of roost sites in the more general spatial activity of breeding male birds deserves further study.

During the breeding season, male juncos roosted exclusively in coniferous trees. Wintering juncos also favor coniferous trees as roost sites (Gottfried and Franks 1975, Webb and Rogers 1988). The use of conifers by wintering juncos has been interpreted as an energysaving strategy, but the evidence for energy savings is equivocal (Webb and Rogers 1988, Walsberg and King 1980) and the preference for conifers persists in the breeding season when energetic concerns are like to be minimal (nighttime temperature during the study did not drop below approximately 10° C). The dense foliage of conifers probably makes a more important contribution to reducing predation (e.g., Walsberg and King 1980).

In summary, the roost sites used by male Dark-eyed Juncos are variable in both space (occurring both on and off territory) and time (often shifting from night to night). We suggest that this variability may reduce predation rates (for shifts within the territory) and may affect male diurnal spatial activity by facilitating intrusions onto neighboring territories. The possible use of roost sites to facilitate territorial intrusions by male birds adds another factor to those known to influence selection of a roost site. More generally, the spatial distribution of roosts in breeding birds that traditionally have been thought to restrict all activities to an all-purpose Type-A territory (Hinde 1956) deserves greater attention.

Larry Callahan, Michelle Cawthorn, Dan Cullen, Kevin Kimber, Sanam Radjy, Lise Rowe, and Charles Ziegenfus provided skillful assistance in the field. This work would not have been possible without the cooperation of Mountain Lake Biological Station and the Mountain Lake Resort Hotel. This research was supported by the Frank M. Chapman Memorial Fund, Indiana University, and the National Science Foundation (BSR 87-18358 and BSR 91-11498).

LITERATURE CITED

- ATKINSON, E. C. 1993. Winter territories and night roosts of Northern Shrikes in Idaho. Condor 95: 515-527.
- BALDA, R. P., M. L. MORRISON, AND T. R. BEMENT. 1977. Roosting behavior of the Piñon Jay in autumn and winter. Auk 94:494–504.
- BIRKHEAD, T. R., AND A. P. Møller. 1992. Sperm competition in birds: evolutionary causes and consequences. Academic Press, New York.
- BUTTEMER, W. A. 1985. Energy relations of winter roost-site selection by American Goldfinches (*Carduelis tristis*). Oecologia 68:126–132.
- BUTTEMER, W. A., L. B. ASTHEIMER, W. W. WEATHERS, AND A. M. HAYWORTH. 1987. Energy savings attending winter-nest use by Verdins (*Auriparus flaviceps*). Auk 104:531-535.
- CACCAMISE, D. F., AND D. W. MORRISON. 1988. Avian communal roosting: a test of the "patch-sitting" hypothesis. Condor 90:453–458.
- CHANDLER, C. R., AND P. J. TOLSON. 1990. Habitat relationships between a boid snake, *Epicrates monensis*, and its anoline prey, *Anolis cristatellus*. J. Herpetology 24:151-157.
- CHANDLER, C. R., E. D. KETTERSON, V. NOLAN JR., AND C. ZIEGENFUS. 1994. Effects of testosterone on spatial activity in free-ranging male Dark-eyed

Juncos, Junco hyemalis. Anim. Behav. 47:1445-1455.

- CODY, M. L. [ED.] 1985. Habitat selection in birds. Academic Press, Orlando, FL.
- GOTTFRIED, B. M., AND E. C. FRANKS. 1975. Habitat use and flock activity of Dark-eyed Juncos in winter. Wilson Bull. 87:374–383.
- HINDE, R. A. 1956. The biological significance of the territories of birds. Ibis 98:340-369.
- KENDEIGH, S. C. 1961. Energy of birds conserved by roosting in cavities. Wilson Bull. 73:140–147.
- KETTERSON, E. D., AND V. NOLAN JR. 1992. Hormones and life histories: an integrated approach. Am. Nat. 140:S33–S62.
- KETTERSON, E. D., V. NOLAN JR., L. WOLF, AND C. ZIEGENFUS. 1992. Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the Dark-eyed Junco (Junco hyemalis). Am. Nat. 140:980-999.
- KETTERSON, E. D., V. NOLAN JR., L. WOLF, C. ZIE-GENFUS, A. M. DUFTY, JR., G. F. BALL, AND T. S. JOHNSEN. 1991. Testosterone and avian life histories: the effect of experimentally elevated testosterone on corticosterone and body mass in Darkeyed Juncos. Horm. Behav. 25:489-503.
- KILHAM, L. 1971. Roosting habits of White-breasted Nuthatches. Condor 73:113–114.
- KLUYVER, H. N. 1957. Roosting habits, sexual dimorphism and survival in the Great Tit. Cold Spring Harbor Symp. Quant. Biol. 22:281-285.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- LEARY, J., AND K. A. SULLIVAN. 1991. Intruders on Yellow-eyed Junco territories. Wilson Bull. 103: 292–295.
- LYON, L. A., AND D. F. CACCAMISE. 1981. Habitat selection by roosting blackbirds and starlings: management implications. J. Wildl. Manage. 45: 435-443.
- MEANLEY, B. 1965. The roosting behavior of the Redwinged Blackbird in the southern United States. Wilson Bull. 77:217-228.
- MORRISON, D. W., AND D. F. CACCAMISE. 1985. Ephemeral roosts and stable patches? A radiotelemetry study of communally roosting starlings. Auk 102:793–804.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler, *Dendroica discolor*. Ornithol. Monogr., No. 26.
- PITTS, T. D. 1976. Fall and winter roosting habits of Carolina Chickadees. Wilson Bull. 88:603-610.
- STOUFFER, P. C., AND D. F. CACCAMISE. 1991. Roosting and diurnal movements of radio-tagged American Crows. Wilson Bull. 103:387–400.
- SWINGLAND, I. R. 1977. The social and spatial organization of winter communal roosting in Rooks (Corvus frugilegus). J. Zool. Lond. 182:509–528.
- WALSBERG, G. E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. Auk 103:1–7.
- WALSBERG, G. E. 1990. Communal roosting in a very small bird: consequences for the thermal and respiratory gas environments. Condor 92:795–798.

WALSBERG, G. E., AND J. R. KING. 1980. The thermoregulatory significance of the winter roost-sites selected by robins in eastern Washington. Wilson Bull. 92:33–39. WEBB, D. R., AND C. M. ROGERS. 1988. Nocturnal energy expenditure of Dark-eyed Juncos roosting in Indiana during winter. Condor 90:107-112.

The Condor 97:282–283 © The Cooper Ornithological Society 1995

GENETIC VARIATION AND NESTING BALD EAGLES¹

RICHARD L. KNIGHT

Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523

GERALD R. CRAIG Colorado Division of Wildlife, 317 W. Prospect Ave, Fort Collins, CO 80526

MICHAEL H. SMITH Savannah River Ecology Laboratory, Drawer E., Aiken, SC 29802

JAMES W. GRIER Department of Zoology, North Dakota State University, Fargo, ND 58105

ROBERT G. MCLEAN Division of Vector-Borne Infectious Diseases, Centers for Disease Control and Prevention, P.O. Box 2087, Fort Collins, CO 80523

As habitats become fragmented, once-contiguous populations may be spatially isolated and reduced in size. In addition, new populations may arise through dispersal and colonization. When this occurs, the founding population is often small and there is a reduced chance that the founding individuals represent the full genetic compliment found in the parent population. Resulting populations may be characterized by reduced heterozygosity and allelic diversity. We assessed genetic variation in two nesting populations of Bald Eagles (*Haliaeetus leucocephalus*): a small isolated one in Colorado and a large contiguous one in Ontario, Canada. We predicted that the Colorado population would have reduced heterozygosity and allelic diversity when compared with the Ontario population.

STUDY AREA AND METHODS

The Colorado Bald Eagle population is apparently recent in origin and, at the time of our study, consisted of 14 breeding pairs and was at least 300 km away from any other nesting population (i.e., Arizona and Yellowstone, in Montana and Wyoming). The northwestern Ontario population is part of a large contiguous population of nesting eagles which stretches from the Atlantic seaboard to the Pacific Ocean and numbers close to 10,000 nesting pairs (Stalmaster 1987). The study populations and sites are described in detail elsewhere (Grier 1974, Grier 1982, Kralovec et al. 1993).

During the breeding seasons of 1988-1991, we collected tissue samples from 72 nestlings (Colorado = 20 birds; Ontario = 52 birds) when young were 6-10

weeks old. Tissues included mature pin feathers, blood cells and serum and were analyzed using starch-gel electrophoresis (Stangel et al. 1992). Electrophoretic conditions and general staining procedures were those of Selander et al. (1971) and Harris and Hopkinson (1976). Each sample was scored at 32 presumptive genetic loci (Appendix 1). Buffer codes are identified as follows: A = amino propylmorpholine citrate - pH6.0 (Clayton and Tretiak 1972); B = lithium hydroxide-pH 8.1 (Selander et al. 1971); C = tris citratepH 8.0 (Selander et al. 1971); D = tris maleate - pH7.4 (Selander et al. 1971). Stain recipes were taken from Selander et al. (1971), Siciliano and Shaw (1976), Harris and Hopkinson (1977), and Lydeard et al. (1989). The following systems were not adequately resolved in our analyses: enolase, glyoxalase 1; guanylate kinase, inosine trophosphate, pyruvate kinase and triosephosphate isomerase.

RESULTS AND DISCUSSION

All loci were monomorphic except peptidase 2. There were eight heterozygotes and no homozygotes for the rare allele observed among the 52 birds from Canada (frequency of 8% [8/104]). Peptidase 2 was monomorphic among the birds from Colorado. The probability of not detecting this rare allele in Colorado from a sample of 20 birds is quite low (0.036 $[0.92^{40}]$).

Although the two eagle populations we studied differed dramatically in spatial isolation and population size, we found virtually no allozymic genetic variation between and within them. This study is one of very few cases where an apparent lack of variation was reported for a bird species in which a relatively large number of individuals and loci were screened (Bar-

Received 29 June 1994. Accepted 24 August 1994.