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NEST DISPERSION IN THE RED-WINGED BLACKBIRD[1]

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Observations and experiments have demonstrated that female Red-winged Blackbirds (*Agelaius phoeniceus*) are aggressive toward one another. This female-female aggression is most common early in the breeding season (Nero and Emlen 1951, Nero 1956, Orians and Christman 1968, Lenington 1980, Hurly and Robertson 1984, Roberts and Searcy 1988, Langston et al. 1990), and can be elicited by presenting stuffed females near active nests (LaPrade and Graves 1982, Yasukawa and Searcy 1982, Searcy 1988, Langston et al. 1990) or by playback of female vocalizations (Beletsky 1983).

The aggressiveness of female Red-winged Blackbirds and the similarity of their displays and other behavior to those of males have led many authors to conclude that females defend "sub-territories" within the territories of males (Nero 1956, Orians and Christman 1968, Beletsky 1983, Hurly and Robertson 1984). Recent considerations of polygyny, however, have led some authors (Altmann et al. 1977, Picman et al. 1988, Searcy and Yasukawa 1989) to conclude that females with simultaneously active and closely spaced nests might benefit, or at least might not pay a cost, from their clumped nesting distribution.

Female territoriality, however, is inconsistent with a mutual benefit because territorial behavior would reduce the density of females and cause their nests to be over-dispersed (Yasukawa and Searcy 1981; Searcy 1986, 1988), thus reducing any mutual benefit. We conducted a preliminary test of these alternative hypotheses by examining the dispersion of Red-winged Blackbird nests. An over-dispersed distribution of nests would be consistent with female territoriality, while a clumped distribution would be consistent with mutual benefit. A random distribution would be consistent with the hypothesis that females neither benefit nor pay a cost when they nest in proximity to one another.

Territoriality and over-dispersion. We measured nearest-neighbor distances for Red-winged Blackbird nests constructed at Newark Road Prairie, a 13-ha prairie habitat in southern Rock County, Wisconsin, in 1984-1986. Using the method of Sinclair (1985), we compared the mean nearest-neighbor distances with those expected if nests were distributed randomly. This method, which calculates expected nearest-neighbor distances based on nest density and total area available, has the advantage of correcting for edge effects, which would otherwise bias the test in favor of over-dispersion.

In a homogeneous habitat, territoriality would produce an over-dispersed distribution of nests. In a heterogeneous habitat such as our study area, however, the distribution of nests will also be affected by the distribution of suitable nesting habitat and preferred nest sites. To test our assumption that territoriality produces over-dispersion, we first measured nearest-neighbor distances among primary nests. A primary nest was defined as the first nest on a male's territory to receive an egg. Limiting analysis to these nests allowed us to determine whether the territorial behavior of males produced over-dispersion in the nesting attempts of their first mates, who usually nest first within each male's territory (Lenington 1980, Teather et al. 1988, Langston et al. 1990).

As shown in Table 1, primary nests were significantly over-dispersed. This result is not surprising because male Red-winged Blackbirds are known to be territorial (Nero 1956, Orians and Christman 1968), but it is important because it demonstrates that (male) territory defense produces over-dispersion on our study area.

Nest dispersion and the alternative hypotheses. Having confirmed our assumption that territoriality produces over-dispersion, we next measured nearest-neighbor distances for all simultaneously active nests on our study area. Limiting analysis to simultaneously active nests avoids bias produced by re-nesting attempts of females whose earlier nests failed or were abandoned. As shown in Table 2, there was no evidence that simultaneously active nests were over-dispersed on our study area. In 1984 and 1985, simultaneously active nests were randomly dispersed, and in 1986 they were significantly clumped. These results are not consistent with territorial behavior by female Red-winged Blackbirds.

It is possible to argue that the females within a male's territory are not equal in their ability or motivation to defend territories. Agonistic interactions among females are most common early in the breeding season, and primary females are most aggressive (Nero 1956, Lenington 1980, Hurly and Robertson 1984, Roberts and Searcy 1988, Langston et al. 1990). Primary females are also the most likely beneficiaries of benefits that could reduce or compensate the cost of sharing a male and his territory (Yasukawa and Searcy 1982, Roberts and Searcy 1988, Langston et al. 1990). Primary females, therefore, are the most likely candidates for territoriality, and including later-nesting females may bias the analysis against the female territoriality hypothesis. To control for this possible bias, we also analyzed distances between primary nests and their nearest, simultaneously active neighbors. As shown in

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TABLE 1. Observed mean (±SE) and expected (Sinclair 1985) nearest-neighbor distances (m) of primary Red-winged Blackbird nests at Newark Road Prairie.

Year	n	Observed	Expected
1984	10	56.1 ± 3.38	37.4[a]
1985	18	54.3 ± 3.23	36.1[b]
1986	18	45.9 ± 4.94	36.0[a]

[a] $P < 0.05$.
[b] $P < 0.01$.

Table 3, the results of this analysis were similar to the previous analysis. In 1984 and 1985 these nests were again randomly dispersed, and in 1986 they were again significantly clumped. We thus found no support for female territory defense.

DISCUSSION

Our results demonstrate that nests of Red-winged Blackbirds were not over-dispersed in a prairie habitat. Yasukawa and Searcy (1981) also failed to demonstrate over-dispersion of nests in marsh-nesting populations of this species. In addition, Searcy (1986) found that female Red-winged Blackbird "defended areas" overlapped considerably, much more than did the territories of males, and Picman et al. (1988) suggested that clumped nesting can reduce predation through mutual nest protection (see also Picman 1980, Ritschel 1985). Thus, female Red-winged Blackbird aggression does not appear to space nesting, but it might enable females to acquire superior breeding situations or primary status (Yasukawa and Searcy 1982, Roberts and Searcy 1988, Langston et al. 1990).

We should stress that our focus on primary nests in our analyses was an attempt to investigate indirectly the choices made by later-nesting (secondary) females. One difficulty facing the first female to settle on a male's territory is the uncertainty of subsequent female settlement. For a later-arriving female, however, the presence of the primary female is guaranteed by definition, so nearest-neighbor distances from the primary nest can provide information about nest-site choices made by later-arriving females.

We should also point out that, although restricting analysis of nearest-neighbor distances to nests within the territory of each male might be a better test of some cost-compensation hypotheses (e.g., reduced male provisioning and anti-predator behavior; see Searcy and Yasukawa 1989), many forms of cost (e.g., increased predation, brood parasitism and disease transmission) should accrue to females regardless of whether the nearest nest is within the male's territory or a neighboring male's territory.

TABLE 2. Observed mean (±SE) and expected (Sinclair 1985) nearest-neighbor distances (m) of simultaneously active Red-winged Blackbird nests at Newark Road Prairie.

Year	n	Observed	Expected
1984	14	29.2 ± 5.24	29.2[a]
1985	26	30.8 ± 4.37	29.4[a]
1986	37	19.1 ± 1.32	24.3[b]

[a] $P > 0.10$.
[b] $P < 0.05$.

TABLE 3. Observed mean (±SE) and expected (Sinclair 1985) nearest-neighbor distances (m) of primary and simultaneously active Red-winged Blackbird nests at Newark Road Prairie.

Year	n	Observed	Expected
1984	8	32.7 ± 4.29	33.2[a]
1985	18	34.2 ± 3.34	36.1[a]
1986	18	21.4 ± 2.13	36.0[b]

[a] $P > 0.10$.
[b] $P < 0.05$.

Our results are consistent with both the mutual benefit and the random settlement hypotheses, but offer no information to separate them. Nests were significantly clumped in one year and randomly dispersed in two, but the mechanisms that produced these distributions are unknown. Clumping could occur in response to a heterogeneous nest site distribution, rather than as a functional strategy, but this is unlikely to explain our results for several reasons. First, the distribution of potential nest sites changed little among years, yet the distribution of nests varied among years. Second, nest sites did not appear to be limited on any territory, and breeding density was relatively low, thus female choice of site did not seem constrained. Finally, the prairie nesting habitat within each territory was neither highly patchy nor highly stratified vertically. Nests were often closely placed despite the presence of very many, more distant, potential nest sites.

Ritschel (1985) found that the nests of Red-winged Blackbirds in a marsh-nesting population were also clumped, and she provided strong evidence that clumping was an adaptive strategy to reduce predation by Marsh Wrens (*Cistothorus palustris*) (see also Picman 1980, Picmann et al. 1988). We found no evidence of wren predation on our study area, although two or three Sedge Wrens (*C. platensis*) were present on our study area in 1986. We cannot evaluate whether the presence of a few Sedge Wrens in 1986 was a real or spurious correlate of the significant clumping we found in that year.

Further tests of the mutual benefit hypothesis must determine whether later-arriving females actively seek or avoid occupied territories and nest sites near active nests. For example, Langston et al. (1990) found that female Red-winged Blackbirds avoided territories of already-mated males until primary females began to nest, but Searcy (1988) found that removal of primary females did not affect the timing of nesting by secondary females. Even if secondary females delay settling, however, they might still place their nests near those of primary females. Yasukawa and Searcy (1981) found that nesting attempts within a territory could be over-dispersed in time, but randomly dispersed in space, and Searcy (1988) found a negative, though nonsignificant, correlation between female aggressiveness and distance to the closest simultaneously active nest. In addition, the direct effects of nest site quality, the distribution of preferred nest sites, and the potential benefits of sharing a male's territory or nesting in proximity to another female must be investigated.

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LITERATURE CITED

ALTMANN, S. A., S. S. WAGNER, AND S. LENINGTON. 1977. Two models for the evolution of polygyny. Behav. Ecol. Sociobiol. 2:397–410.

BELETSKY, L. D. 1983. Aggressive and pair-bond maintenance songs of female Red-winged Blackbirds (*Agelaius phoeniceus*). Z. Tierpsychol. 62: 47–54.

HURLEY, T. A., AND R. J. ROBERTSON. 1984. Aggressive and territorial behaviour in female Red-winged Blackbirds. Can. J. Zool. 62:148–153.

LANGSTON, N. E., S. FREEMAN, S. ROHWER, AND D. GORI. 1990. The evolution of female body size in Red-winged Blackbirds: the effects of timing of breeding, social competition, and reproductive energetics. Evolution 44:1764–1779.

LAPRADE, H. R., AND H. B. GRAVES. 1982. Polygyny and female-female aggression in Red-winged Blackbirds. Am. Nat. 120:135–138.

LENINGTON, S. A. 1980. Female choice and polygyny in Redwinged Blackbirds. Anim. Behav. 28:347–361.

NERO, R. W. 1956. A behavior study of the Red-winged Blackbird. I. Mating and nesting activities. II. Territoriality. Wilson Bull. 68:5–37, 129–150.

NERO, R. W., AND J. T. EMLEN. 1951. An experimental study of territorial behavior in Red-winged Blackbirds. Condor 53:105–116.

ORIANS, G. H., AND G. M. CHRISTMAN. 1968. A comparative study of the behavior of Red-winged, Tri-colored, and Yellow-headed Blackbirds. Univ. Calif. Publ. Zool. 84:1–85.

PICMAN, J. 1980. Impact of Marsh Wrens on reproductive strategy of Red-winged Blackbirds. Can. J. Zool. 58:337–350.

PICMAN, J., M. LEONARD, AND A. HORN. 1988. Antipredation role of clumped nesting by marsh-nesting Red-winged Blackbirds. Behav. Ecol. Sociobiol. 22:9–16.

RITSCHEL, S. E. 1985. Breeding ecology of the Red-winged Blackbird (*Agelaius phoeniceus*): tests of models of polygyny. Unpubl. Ph.D.thesis, Univ. of California, Irvine, CA.

ROBERTS, L. B., AND W. A. SEARCY. 1988. Dominance relationships in harems of female Red-winged Blackbirds. Auk 105:89–96.

SEARCY, W. A. 1986. Are female Red-winged Blackbirds territorial? Anim. Behav. 34:1381–1391.

SEARCY, W. A. 1988. Do female Red-winged Blackbirds limit their own breeding densities? Ecology 69:85–95.

SEARCY, W. A., AND K. YASUKAWA. 1989. Alternative models of territorial polygyny in birds. Am. Nat. 134:323–343.

SINCLAIR, D. F. 1985. On tests of spatial randomness using nearest neighbor distances. Ecology 66:1084–1085.

TEATHER, K. L., K. E. MUMA, AND P. J. WEATHERHEAD. 1988. Estimating female settlement from nesting data. Auk 105:196–200.

YASUKAWA, K., AND W. A. SEARCY. 1981. Nesting synchrony and dispersion in Red-winged Blackbirds: is the harem competitive or cooperative? Auk 98:659–668.

YASUKAWA, K., AND W. A. SEARCY. 1982. Aggression in female Red-winged Blackbirds: a strategy to ensure male parental investment. Behav. Ecol. Sociobiol. 11:13–17.

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NESTING FAILURE OF THE WOOD STORK IN A NEOTROPICAL WETLAND[1]

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Key words: Wood Stork; breeding phenology; nesting failure; México.

The Wood Stork (*Mycteria americana*) is one of the three New World Ciconiidae, that ranges from the southern United States to Northern Argentina. During recent decades frequent nesting failures have been associated with a pronounced population decline in southern Florida and a northward shift in the location of colony sites in the United States population (Ogden and Nesbitt 1979, Ogden and Patty 1991, Kushlan and Frohring 1986, Ogden et al. 1987). Although some colonies failed due to high winds or cold weather (Kahl 1964, Clark 1978), the main cause of nesting failure appears to be related to changes in hydropattern caused by management programs. Here we report a case of generalized nesting failure in an almost pristine tropical

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