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THE EFFECT OF AGGREGATED NESTING ON RED-WINGED BLACKBIRD NEST SUCCESS AND BROOD PARASITISM BY BROWN-HEADED COWBIRDS[1]

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Abstract. We examined temporal and spatial nesting aggregations in a prairie-nesting population of Red-winged Blackbirds (*Agelaius phoeniceus*). In particular, we were interested in the effects of aggregated nesting on blackbird nest success and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). Most cowbird parasitism occurred early in the breeding season during the peak in Red-winged Blackbird nesting. As a result, more parasitized nests were active simultaneously with other nests than were unparasitized nests, even when we controlled statistically for the effects of nest initiation date. The probability of parasitism across the entire study site did not decrease on days when many nests were initiated, suggesting no "swamping" effect of aggregated nesting on cowbirds. However, individual parasitized nests were less synchronous with their nearest neighbors and farther from the nearest simultaneously active nest than were unparasitized nests. These data are consistent with the hypothesis that brood parasitism by Brown-headed Cowbirds may select for aggregated nesting in Red-winged Blackbirds as a result of greater parasitism pressure on isolated nests. Nests that succeeded in producing at least one fledgling were initiated significantly earlier in the breeding season than were nests that failed. Nest aggregation had no effect on nest success; successful nests were no different from failed nests in the number of simultaneously active nests, their distance to nearest simultaneously active nests, the laying interval with their nearest neighbors, and the distance to their nearest neighbors. These data suggest that nest predation (the primary cause of nest failure), in contrast to nest parasitism, does not necessarily select for aggregated nesting, or that predation and nest aggregation are related only at high nest-densities.

Key words: Agelaius phoeniceus, *Brown-headed Cowbird,* Molothrus ater, *nearest neighbor, predation, Red-winged Blackbird, synchrony.*

INTRODUCTION

In many animal species, individuals reproduce in close proximity to their conspecifics, and within these spatial aggregations reproduction is often synchronized. The evolution of such colonial breeding has been studied thoroughly in birds, which offer diverse breeding ecologies in many closely-related species (Crook 1965, Wittenberger and Hunt 1985). Colonial nesting in birds might occur to exploit limited resources such as nesting sites or food (Ward and Zahavi 1973, Krebs 1974) and reduce the risk of predation (Hoogland and Sherman 1976, Picman et al. 1988). The mechanisms by which colonial nesting reduces predation have been subjects of considerable investigation. Neighboring birds may share vigilance responsibilities and/or cooperatively mob potential predators (Pulliam 1973, Curio 1978). Aggregations of nests may

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reduce the likelihood of predation as a result of predator satiation, dilution, or "selfish herd" effects (Hamilton 1971, Wilkinson and English-Loeb 1982). Alternatively, predation may select for dispersed nesting rather than aggregated nesting in cases where predators use area-restricted searches (Schieck and Hannon 1993, Hogstad 1995).

The relationship between nesting aggregations and patterns of brood parasitism has received less attention. Avian brood parasites such as cowbirds (*Molothrus* spp.) and cuckoos (*Cuculus* spp.) parasitize hundreds of host species worldwide (Johnsgard 1997, Ortega 1998). Females of many parasitic species remove host eggs from parasitized nests. In some cases, parasitic nestlings further reduce the reproductive success of their hosts by destroying host eggs or nestlings (Rothstein 1990, Ortega 1998). In cases where host offspring are not destroyed outright, they often suffer as a result of competition with parasitic nestlings. Therefore, brood parasitism represents a potentially strong selective pressure affecting temporal and spatial nesting patterns of their hosts. Several studies have investigated the relationship between host nesting aggregations and parasitism by cowbirds (Clark and Robertson 1979, Wiley and Wiley 1980, Freeman et al. 1990) or cuckoos (Lawes and Kirkman 1996, Martinez et al. 1996, Øien et al. 1996), but the mechanisms by which aggregated nesting reduces the risk of parasitism have not been investigated.

Red-winged Blackbirds (*Agelaius phoeniceus*) nest in loose aggregations; these assemblages reach greater densities in marshes than in uplands (Robertson 1973, Orians 1980). They are frequent hosts of Brown-headed Cowbirds (*Molothrus ater*), especially in upland habitats (Freeman et al. 1990). Differences in parasitism rates between marsh and upland populations of Red-winged Blackbirds presumably result from increased cowbird deterrence at high host-density (Robertson and Norman 1977, Freeman et al. 1990). Red-winged Blackbirds respond aggressively to cowbirds (Neudorf and Sealy 1992, Gill et al. 1997, Clotfelter 1998), and the intensity of these responses increases with increasing host nest-density (Robertson and Norman 1977). It is not known how host defensive behavior affects cowbird egg laying. Although parasitism by cowbirds rarely causes complete reproductive failure for Red-winged Blackbirds, it often results in nest abandonment or clutch size reduction (Røskaft et al. 1990, Clotfelter and Yasukawa 1999). The current study examines the effects of spatial and temporal nest aggregations in a prairie-nesting population of Red-winged Blackbirds on redwing nest success and brood parasitism by Brown-headed Cowbirds.

METHODS

STUDY AREA AND POPULATIONS

We conducted this study in southern Wisconsin (42°32′N, 89°08′W) on two grass and sedge meadows. Newark Road Prairie (NRP) is a 13-ha wet-mesic prairie that supports 25–30 territorial male Red-winged Blackbirds each year. Diehls Prairie (DP) is a 12-ha oldfield/prairie that supports 30–35 males each year. The two sites share a common boundary and are separated by a paved, two-lane road. Although we make reference to NRP and DP in this paper, we consider the Red-winged Blackbirds nesting on them to be from a single population. Several observations support this conclusion. First, Red-winged Blackbirds regularly emigrated from one site to the other. Second, some males had territories that straddled the road and mated with females nesting on both sites. Third, there were no significant differences in nest success, parasitism rates, nest density, or nesting phenology between NRP and DP. We studied the Red-winged Blackbirds of NRP and DP from 1984–1997 and 1995–1997, respectively.

Red-winged Blackbirds are polygynous; territorial males usually attract 2–3 females to their territories at NRP and DP. We located nests by searching the vegetation and by observing female behavior. The majority of nests were found during the construction or egg-laying stages (Yasukawa et al. 1990). For nests located after clutch completion, we estimated nest initiation date based on an incubation period of 13 days (Yasukawa and Searcy 1995). We marked nests with flagging tape and revisited them daily to determine their fate. We allowed cowbird eggs laid in Red-winged Blackbird nests on DP to hatch. Cowbird eggs found in nests on NRP were removed for reasons unrelated to the current study. Beginning in 1995, we placed these eggs in redwing nests on DP 2–24 hr after laying. Nests on DP that were experimentally parasitized in this manner (17 in 1995, 8 in 1996, and 9 in 1997) were excluded from comparisons of parasitized and unparasitized nests, but we included these nests in calculations of nest success, nearest neighbor distances, and number of simultaneously active nests (see below). A further explanation of experimentally parasitized nests can be found in Clotfelter and Yasukawa (1999). We counted nests containing multiple cowbird eggs only once for all analyses.

We recorded the fates of almost all nests in the study. We considered a nest successful if any nestlings, including cowbirds, survived to fledging age (10 days after hatching). A nest failed if no fledglings were produced. Failures resulted from many factors, including predation, abandonment, starvation of the entire brood, and inclement weather. Approximately 70% of nest failures were attributed to predation (Yasukawa et al. 1990).

NEAREST NEIGHBOR DISTANCES

Prior to the 1996 breeding season, we used a surveyor's instrument (theodolite) and divided DP into a grid of 20 × 20 m squares. In 1996 and 1997, we determined exact locations of Red-winged Blackbird nests on DP by measuring the distances from each nest to the two nearest grid markers using a 30-m tape measure. From the resulting triangle, we calculated precise x and y coordinates using trigonometric laws (e.g., law of cosines). We entered the coordinates of each nest into a TurboPascal (v. 1.5) program to determine the nearest neighbor. In addition to distances between nearest neighbors, we calculated laying intervals between nearest neighbors. We defined the laying interval as the number of days between the laying of the first egg in each of a given pair of nests. Some nests on DP (21 in 1996 and 34 in 1997) were located outside of the surveyed area. We included these nests in other analyses but not in the analysis of nearest neighbor distances.

SIMULTANEOUSLY ACTIVE NESTS

In addition to nearest neighbor distances, we calculated the distance to the nearest simultaneously active nest and the number of simultaneously active nests for each nest. We defined simultaneously active nests as those with a laying interval of ≤ 2 days (this is equivalent to Westneat's [1992] "temporal neighbor," but we chose not to use this term to avoid confusion). Although a 2-day time window may seem conservative, it represents a biologically meaningful period for a female brood parasite, which must lay during the host's egg-laying period (3–4 days for Red-winged Blackbirds) to be successful. Distances to nearest simultaneously active nests were calculated using a modified version of the TurboPascal program. We excluded from the analysis any nests for which no others were simultaneously active (i.e., "temporally isolated"). To ensure that excluding these nests did not bias our results, we conducted the same analysis using an unusually large, but theoretically possible, value (300 m) for the distance to the nearest simultaneously active nest. We obtained similar results from this analysis, so excluding temporally isolated nests did not appear to be a source of bias.

We calculated the distance to the nearest simultaneously active nest only for nests on DP in 1996 and 1997 (when accurate nest locations were available). We calculated the total number of simultaneously active nests for all nests on both DP (1995–1997) and NRP (1984–1997). Because we had reason to believe *a priori* that cowbird parasitism and nest success varied with nest initiation date, we controlled nest initiation date statistically in our calculations of the number of simultaneously active nests for each nest. We ran a linear regression of the ($\log_{10}$) number of simultaneously active nests for all nests in all years with Julian date as the independent variable. We then calculated the expected number of simultaneously active nests for each nest given the date the nest was initiated using the equation: N simultaneously active nests = $10^{3.52-(0.017)(\text{Julian date})}$. We subtracted the expected number of simultaneously active nests from the observed number of simultaneously active nests. We compared the resulting values for parasitized vs. unparasitized nests and for successful vs. failed nests.

STATISTICAL ANALYSES

We performed statistical tests using SYSTAT 6.0 (Wilkinson 1996). Means are presented ± SE. When the data were not normally distributed, we used the nonparametric Spearman rank correlation coefficient. We used independent t-tests. All tests were two-tailed and we considered differences significant at $P < 0.05$.

RESULTS

NESTING PHENOLOGY

We found a combined total of 1,320 Red-winged Blackbird nests on NRP (1984–1997) and DP

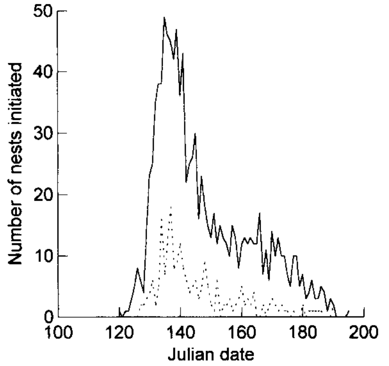

FIGURE 1. The number of Red-winged Blackbird nests initiated per day that were parasitized (dashed line) or unparasitized (solid line). These data are for 1,286 nests (34 experimentally parasitized nests excluded) initiated on Newark Road Prairie (1984–1997) and Diehls Prairie (1995–1997).

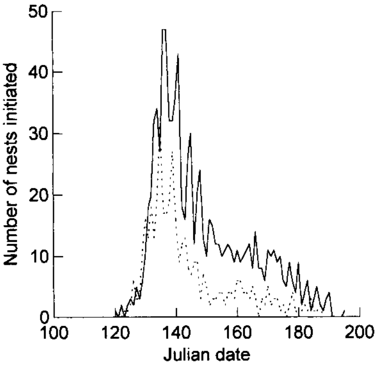

FIGURE 2. The number of Red-winged Blackbird nests initiated per day that subsequently succeeded (dashed line) or failed (solid line). These data are for 1,315 nests initiated on Newark Road Prairie (1984–1997) and Diehls Prairie (1995–1997).

(1995–1997). Excluding 34 experimentally parasitized nests on DP, Brown-headed Cowbirds parasitized 222 (17.3%) nests. Of the total number of nests, 899 (68.1%) failed, 416 (31.5%) succeeded in producing at least one fledgling, and 5 (0.4%) had unknown fates. Of the 416 successful nests, 2 (0.5%) produced only cowbird fledglings.

Mean initiation dates of parasitized nests (145.7 ± 0.9 days, n = 222; Julian date, where 140 = 20 May) were approximately 2 days earlier than mean initiation dates of unparasitized nests (147.6 ± 0.5 days, n = 1,064), but this difference was not significant (t_{1284} = 1.73, P = 0.08; Fig. 1). Successful nests were initiated significantly earlier in the season (143.9 ± 0.7 days, n = 416) than failed nests (148.6 ± 0.5 days, n = 899; $t_{1,313}$ = 5.39, $P < 0.001$; Fig. 2).

To determine whether nesting synchrony was related to cowbird parasitism, we correlated the number of nests initiated per day with the proportion of nests parasitized each day. Each day on which ≥ 1 nest was initiated in the NRP 1984–1997 and DP 1995–1997 study periods constituted a data point. We found a weak but significant positive relationship between the number of nests initiated per day and the proportion of nests parasitized (r_s = 0.23, n = 575, $P < 0.001$), suggesting that parasitism across the study area was not reduced when nests were aggregated in time.

NEAREST NEIGHBORS AND NEAREST SIMULTANEOUSLY ACTIVE NESTS

The nearest neighbor data for the 161 nests on the DP grid in 1996 and 1997 are summarized in Table 1. Distances between nearest neighbors in the same year ranged from 4.1 to 38.4 m. There was no difference in the distances to nearest neighbors of parasitized nests and unparasitized nests (t_{159} = 0.77, P = 0.44). However, parasitized nests were more temporally separated (had longer laying intervals) from their nearest neighbors than were unparasitized nests (t_{159} = 2.4, P = 0.019).

TABLE 1. Mean (± SE) nearest neighbor distances for Red-winged Blackbird nests on Diehls Prairie in 1996 and 1997. Sample sizes in parentheses are for analyses of simultaneously active nests.

Nest fate	n	Distance to nearest neighbor (m)	Laying interval to nearest neighbor (days)	Distance to nearest simultaneously active nest (m)
Parasitized	40 (39)	19.8 ± 1.5	19.6 ± 2.2	79.3 ± 8.8
Unparasitized	121 (119)	18.6 ± 0.8	14.1 ± 1.2	54.2 ± 3.7
Successful	53 (52)	16.5 ± 2.0	20.0 ± 1.2	56.4 ± 4.6
Failed	125 (123)	14.6 ± 1.1	18.5 ± 0.8	57.1 ± 4.2

Simultaneously active nests were farther apart than nearest neighbors. The distances between nearest simultaneously active nests ranged from 8.5 to 267.9 m. Three nests (two unparasitized, one parasitized) were excluded from the analysis because no nests were simultaneously active with them (see Methods above). Parasitized nests were farther from their nearest simultaneously active nests (79.3 ± 8.8 m, $n = 39$) than were unparasitized nests (54.2 ± 3.7 m, $n = 119$; $t_{156} = 3.08$, $P = 0.002$).

The analysis of nest success on DP 1996–1997 included 17 experimentally parasitized nests ($n = 178$ nests total; Table 1). Successful nests and failed nests did not differ in the distance to the nearest simultaneously active nest ($t_{173} = 0.11$, $P = 0.92$), the distance to the nearest neighbor ($t_{176} = 0.94$, $P = 0.35$), or the laying interval to the nearest neighbor ($t_{176} = 1.06$, $P = 0.29$).

NUMBER OF SIMULTANEOUSLY ACTIVE NESTS

For all NRP 1984–1997 and DP 1995–1997 nests, the number of simultaneously active nests was calculated while controlling for nest initiation date. For each parasitized nest, there were significantly more simultaneously active nests than predicted by the regression equation when compared with unparasitized nests (parasitized: 2.4 ± 0.6 nests, $n = 222$; unparasitized: 0.3 ± 0.3 nests, $n = 1{,}064$; $t_{1284} = 3.42$, $P < 0.001$). However, successful and failed nests were similar in the accuracy with which the regression equation predicted the number of simultaneously active nests for each nest. There were no differences in the residuals between successful and failed nests (successful: 0.4 ± 0.5 nests; failed: 1.1 ± 0.3 nests; $t_{1313} = 1.33$, $P = 0.18$).

DISCUSSION

PARASITISM AND NEST SUCCESS

Approximately 17% of Red-winged Blackbird nests in this study were parasitized by cowbirds. This parasitism rate is consistent with other studies of upland populations of redwings (Freeman et al. 1990, Searcy and Yasukawa 1995). As has been reported elsewhere (Ortega and Cruz 1988, Weatherhead 1989, Røskaft et al. 1990), cowbirds in our study area reduced redwing reproductive success primarily through host egg removal, which decreased the number of fledglings produced per successful nest (Clotfelter and Yasukawa 1999). The nest success rate we observed (31.5%) was comparable to other studies of redwings (Searcy and Yasukawa 1995, Beletsky and Orians 1996). We found that the majority of nesting attempts were initiated early in the season, although nest initiation in our population was less normally-distributed than in some studies (Robertson 1973, Westneat 1992, Beletsky and Orians 1996). The seasonal decline in nest success we observed is typical of many birds (Cooke et al. 1984, Price et al. 1988) including Red-winged Blackbirds (Langston et al. 1990, Beletsky and Orians 1996).

NESTING PHENOLOGY

Our results show that parasitized nests were initiated earlier in the breeding season than unparasitized nests. In some hosts of the Common Cuckoo (*Cuculus canorus*), early nesting attempts suffer greater risks of parasitism than later attempts (Wyllie 1981, Palomino et al. 1998). Two studies of Brown-headed Cowbird parasitism of Red-winged Blackbirds in Washington, however, found that cowbird parasitism increased after the peak in redwing nesting (Freeman et al. 1990, Røskaft et al. 1990). The discrepancy between those studies and ours is likely the result of earlier nesting by redwings in Washington than in Wisconsin, rather than differences in parasitism strategies among cowbird populations. Studies of several other host-parasite systems have reported late-season increases in the risk of parasitism (Clark and Robertson 1979, Smith and Arcese 1994, Øien et al. 1996). Differences among studies may also be due to site-specific differences in host species diversity or the availability of alternate hosts at different stages of the nesting season.

We found no evidence of a decreased probability of parasitism during the peak of nesting. Thus, there was no swamping effect of synchronized nesting on cowbird parasitism over the entire study area as reported by Clark and Robertson (1979) for Yellow Warblers (*Dendroica petechia*).

NEAREST NEIGHBORS

We found that parasitized nests were active simultaneously with more nests over the entire study area than expected when nest initiation date was controlled statistically. In a study of Yellow-hooded Blackbirds (*A. icterocephalus*) parasitized by Shiny Cowbirds (*M. bonariensis*), Wiley and Wiley (1980) found the opposite result: parasitized nests were more isolated in time than were unparasitized nests. Similarly, Martinez et al. (1996) found that Magpies (*Pica pica*) whose nests were simultaneously active with their neighbors were less likely to be parasitized by Great Spotted Cuckoos (*Clamator glandarius*) than were Magpies that were less synchronized.

Despite the fact that parasitized redwing nests were simultaneously active with more nests overall, we found that individual parasitized nests were less synchronized with their nearest neighbors and farther from the nearest simultaneously active nest than were unparasitized nests. This suggests that aggregated nesting provides some benefit in terms of reduced cowbird parasitism. Our data show that the potential importance of aggregated nesting as a cowbird deterrent varies at different spatial scales; there was no evidence of cowbird swamping at the population level, but inter-nest distance was significantly related to parasitism of individual nests.

Our results are consistent with the hypothesis that marsh-nesting populations of Red-winged Blackbirds are less vulnerable to parasitism than their upland-nesting counterparts because high nest density facilitates cooperative vigilance and deterrence (Robertson and Norman 1977). Other studies, including several on related host species, have examined the relationship between aggregated nesting and brood parasitism. Freeman et al. (1990) reported that nesting densities of Red-winged Blackbirds on several marshes were negatively correlated with the proportion of nests parasitized by cowbirds. Small colonies of Yellow-hooded Blackbirds were more susceptible to parasitism by Shiny Cowbirds than large colonies (Wiley and Wiley 1980). Robinson (1988) and Webster (1994) found that dense colonies of oropendolas (*Psarocolius* [= *Gymnostinops*] *montezuma* and *P. angustifrons*) and caciques (*Cacicus cela*) were more effective at deterring groups of Giant Cowbirds (*Scaphidura oryzivora*) than were single pairs or isolated colonies. Martinez et al. (1996) found that Magpie nesting density was negatively related to parasitism by Great Spotted Cuckoos. Parasitism of Red Bishops (*Euplectes orix*) by Diederik Cuckoos (*Chrysococcyx caprius*) also occurred at higher rates in smaller, less dense colonies (Ferguson 1994, Lawes and Kirkman 1996). Finally, Øien et al. (1996) reported that Reed Warblers (*Acrocephalus scirpaceus*) were more susceptible to parasitism by Common Cuckoos if they were isolated from their nearest neighbors.

NEST SUCCESS

Our results show no effect of spatial or temporal nesting aggregations on nest success in Red-winged Blackbirds. This is surprising because predation caused the majority of nest failures. Therefore, our results are inconsistent with many studies (Wittenberger and Hunt 1985), including several on redwings, which show that predation is negatively related to nest density. Westneat (1992) found that the probability of nest predation in Red-winged Blackbirds was negatively related to the number of simultaneously active nests. Robertson (1973) also showed that predator swamping occurred as a consequence of synchronized nesting by Red-winged Blackbirds. Using artificial nests, Ritschel (1985) and Picman et al. (1988) found that proximity to active neighbors reduced the likelihood that Red-winged Blackbird nests were depredated by Marsh Wrens (*Cistothorus palustris*). However, Caccamise (1976) reported that the probability of predation in a marsh-nesting population of Red-winged Blackbirds was constant regardless of the spatial arrangement of nests within the colony. One explanation for the absence of a relationship between nest aggregation and nest success in our study is that predators may only be deterred at very high nest-densities, densities that rarely occur in prairie-nesting populations such as the one we studied. Differences between our study and previous studies of nest success in redwings also may be the result of differences in predator species or abundance (Searcy and Yasukawa 1995, Beletsky and Orians 1996).

In summary, we found that most parasitism occurred during the peak of the breeding season and that the proportion of nests parasitized per day increased slightly with the number of nests available over the entire study area. However, individual nests that were isolated from their nearest neighbors or were far from the nearest simultaneously active nest were more likely to be parasitized. Although there appears to be strong selection for early breeding in Red-winged Blackbirds (Beletsky and Orians 1996), the temporal and spatial aggregation of nests between and within territories may be subject to a variety of selection pressures (Yasukawa and

Searcy 1981, Yasukawa et al. 1992). Our results suggest that cowbird parasitism may be a contributing factor in the selection for increased aggregation of Red-winged Blackbird nests. Our results also suggest that temporal and spatial nesting aggregations were not related to nest predation in our population of Red-winged Blackbirds, contrary to results from other studies.

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