WITHIN-SEASON BREEDING DISPERSAL IN PRAIRIE WARBLERS AND OTHER PASSERINES[1]

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Abstract. We examine the hypothesis that avoidance of predation on the nest can select for within-season breeding dispersal, as it does for between-season breeding dispersal. Only five studies have adequately tested this hypothesis against a null hypothesis, e.g., that dispersal is more likely to occur following a failure than following a successful nesting attempt, and all support at least one of the predictions of the predation-avoidance hypothesis. We also find support for the hypothesis in Prairie Warblers (*Dendroica discolor*): late-cycle losses resulted in a greater probability of dispersal. Two alternative hypotheses may explain within-season breeding dispersal: dispersal to permit more rapid renesting and dispersal to avoid depleted resources. Neither is supported in Prairie Warblers. Only one of the five earlier studies has tested either alternative. Although there is a clear need for further testing of all of these hypotheses the rather limited existing data do suggest that predation-avoidance is important in establishing within-season patterns of breeding dispersal.

Key words: Breeding dispersal; Prairie Warbler; Dendroica discolor; *nest predation; predation-avoidance.*

INTRODUCTION

Territorial birds that either raise multiple broods in a single season or that renest following nest failure have three options for subsequent nesting attempts. They can (1) remain on the same territory, (2) move to a new territory with the same mate, or (3) move to a new territory and change mates. These are the same three options available to birds that make only one nesting attempt per season, except in these cases the decision is made between years. In a general review of dispersal in birds, Greenwood and Harvey (1982) showed that between years individuals are more likely to move to a new breeding locality following a poor or unsuccessful breeding attempt than after a successful attempt and that the cause of nest failure can often be attributed to predation.

Although Greenwood and Harvey briefly discussed within-year breeding dispersal, the best review of this subject is found in a pioneering paper by Darley et al. (1971) on territoriality in catbirds.

In this paper we examine the hypothesis that avoidance of predation on the nest can also lead to breeding dispersal within a season. We test this hypothesis with data in the literature, and we present a summary and interpretation of Nolan's (1978) data on Prairie Warblers (*Dendroica discolor*); for this latter purpose we reanalyze original field notes to address the above questions, and we present information not available in his monograph. We also consider other hypotheses to explain the occurrence of within-season breeding dispersal in territorial birds. We hope this paper will stimulate publication of data that heretofore have not been analyzed with this problem in mind. The value of a better knowledge of renesting dispersal is illustrated by its

central importance in predicting whether replacement mates should adopt or kill dependent young (Rohwer 1986).

DISPERSAL TO ESCAPE NEST PREDATION

If the predecessor nest failed because of predation (herein this term includes parasitism by cowbirds or cuckoos), placement of the new nest at a distance from the location of the old nest may increase the probability of escaping another similar instance of predation. This hypothesis generates three predictions. First, after nest failure due to predation individuals might move to new territories before renesting, if such movements reduce the probability of subsequent nests being taken by predators. If predation events are correlated over space, so that the fate of a nest at a particular site predicts the fate of future nests built at the same site, more moves should occur after unsuccessful nests than after successful nests. Empirical support of this idea comes from Dow and Fredga (1983), who found that Common Goldeneye (*Bucephala clangula*) nest boxes in which clutches had been preyed upon by pine martens had nearest-neighbor boxes with a higher rate of predation than boxes in which clutches were never preyed upon. Furthermore, the rate of predation showed a significant decline with increasing distance from boxes in which clutches had been preyed upon. Sonerud (1985) found similar results for Boreal Owls (*Aegolius funereus*), and concluded that pine martens did not encounter nest boxes randomly, but revisited those they had found previously. Lastly, Blancher and Robertson (1985) found that rates of predation on Eastern Kingbird (*Tyrannus tyrannus*) nests in different sections of the study site were consistently different between years (i.e., predictable between years).

Second, the probability of an individual's moving after a failure might be correlated with the cause of failure. Predators that have hunting ranges smaller than the territory of the bird (e.g., mice) could be avoided by within-territory movements large enough to escape a local hunting area. Conversely, predators with hunting ranges larger than the territory of the bird (e.g., large raptors) could be avoided only by longer moves. Whether a bird disperses to a new territory in these cases depends on the time cost of re-pairing and/or moving (see Wunderle 1984).

Third, the probability of dispersal might also depend on when in the nesting cycle the nest is lost. When the breeding season is long enough to allow several renesting attempts, dispersal after nest loss late in the nesting cycle should be more frequent than dispersal after loss early in the cycle, other things being equal. This prediction assumes that the probability of similar events happening that would cause replacement nests also to be lost late in the cycle is now predictably higher than it was before loss of the preceding nest. Thus our hypothetical females face a decision—whether to renest immediately in the same territory and gamble, against odds, that the new nest will succeed, or to sacrifice some time to try to find a new mate on a potentially safer territory. The decision should depend on the constraints that similar losses of replacement nests on the same territory will place on the remainder of their breeding season. Because late-cycle losses "waste" more of the breeding season, less time for additional renesting will be available after a repeated late-cycle loss; thus, after late-cycle losses females should be inclined to incur the time cost of dispersal rather than gamble on the success of a more immediate renesting attempt. Early-cycle losses, however, waste less of the breeding season and leave more time for future renesting attempts if the first replacement nest also fails. Consequently, following early-cycle losses, females should be more inclined to gamble on the success of an immediate renesting attempt in the same territory and thus to avoid the time cost of dispersal. In contrast, when breeding season is relatively short so that renesting after late-cycle losses is impossible when the time cost of dispersal is added, but possible without dispersal, dispersal after late-cycle losses should not occur.

This prediction that late-cycle losses should lead to greater dispersal also assumes that the daily probability of a nest failure is constant throughout the nesting cycle. If average nest failure is high early in the cycle but low late in the cycle, then dispersal after late-cycle losses might not be found. (To elaborate, a late-cycle failure may indicate that a territory is better than average because the nest did make it through the early, more vulnerable part of the nesting cycle.) If so, a female should renest on the territory and gamble on avoiding another (low probability) late-cycle loss. On the other hand, if the probability of nest loss is positively related to nest age, then our prediction is reinforced. Finally, if predators

can remember which nests they successfully visited, which, as noted earlier, may be the case with pine martens preying upon Common Goldeneye and Boreal Owl nests, there may be no correlation between probability of nest loss and nest age. In this case, age of nest at nest loss might be unimportant in a female's decision to disperse. Unfortunately, we have little data on any of these assumptions.

Two general observations about the applicability of these three predictions are, first, that relating movement to whether the preceding nest succeeded or failed is, of course, relevant only for species in which significant numbers of individuals attempt at least two broods. But second, relating movement to the cause or timing of the preceding failure is relevant to any species that renests after failure, regardless of whether second broods are attempted.

REPORTS IN THE LITERATURE

A number of authors report that movements to new territories often occur immediately after nest failures, and many have either suggested or implied that such movements function to reduce predation on replacement nests (Blanchard 1941, Ribaut 1964, Bell et al. 1968, Darley et al. 1971, Thompson and Nolan 1973, Nolan 1978). Lacking in all of these older studies, however, is any statistical evaluation of the data against a null hypothesis. If nest failure is to be considered a cause of movement, it must be shown either that dispersal after nest failure is more frequent than dispersal after success or that patterns of movement after nest predation differ according to characteristics of the animal responsible for the failure.

Five studies have reported adequate statistical tests of the predation-avoidance hypothesis. As predicted by this hypothesis female Bananaquits (*Coereba flaveola*) were steadily more likely to abandon males and their territories as the number of nests they had had taken by predators increased, and furthermore, this probability was much reduced if a prior nest with that male had been successful (Wunderle 1984). Likewise, for Eastern Bluebirds (*Sialia sialis*) (P. A. Gowaty, unpubl.; see Rohwer 1986, table 3), females that failed in their first nesting attempt of a season were much more likely to move to a new territory for their second nesting (69% of 36) than were those that succeeded (39% of 87; $\chi^2 = 9.41$ df = 1, $P < 0.002$). Great Tits (*Parus major*) did not

disperse further after their clutch was artificially reduced to three or four eggs (simulating predation) and their brood was completely removed 15 days after hatching than when their clutch was increased to 10 or 11 eggs and their brood was similarly treated (Slagsvold 1984). However all of these females which had their clutches manipulated tended to renest closer to their first nest than did seven females which deserted their nests because of being trapped by the investigators (115.6 m vs. 171.4 m, respectively, $0.05 < P < 0.10$) (the former group of females were marked in a less obtrusive way). Slagsvold suggested that the former group of females may have felt that a successful nesting attempt had been completed, while the latter group may have felt that a predator was in the area. He did not state whether these dispersal events involved movements between territories, however he assumed that most females probably renested with their original mate (but this was not checked).

In accordance with the second prediction female Red-winged Blackbirds (*Agelaius phoeniceus*) moved only short distances to renest after failures attributable to predators whose home ranges were very small; with such predators even short moves would be likely to put the new nest beyond the range of the animal that caused the failure of the old. In contrast, female redwings made large movements before renesting after failures attributable to predators with large hunting areas (Monnett and Rotterman 1980). No data on whether the short movements involved territory shifts were provided. Greig-Smith (1982) showed that pairs of Stonechats (*Saxicola torquata*) moved further after predation on the nest or desertion caused by human disturbance than after poor success for other reasons. In contrast to our third prediction, however, dispersal distance was not correlated with the length of time the previous nest had survived. Greig-Smith did not state whether pairs changed territories, but he suggested that within-season dispersal in Stonechats is unlikely to be affected by territorial boundaries as distances moved were unrelated to population density.

Shields (1984) showed that Barn Swallows (*Hirundo rustica*) were more likely to change nests without moving from one nest cluster to another within seasons following a successful nesting attempt than a failed attempt. However females that failed moved a greater distance to disperse than those that succeeded. Shields did not state whether failures were due to predation or some

other cause, so it is unclear how these data relate to the predation-avoidance hypothesis. Shields suggested that the increased probability of changing nests after a success might be due to factors (e.g., ectoparasites) that reduce the quality of an active nest over the course of the breeding season.

THE PRAIRIE WARBLER DATA

For general methods used in the Prairie Warbler study we refer the reader to Nolan's (1978) monograph. In testing the predictions of the predation-avoidance hypothesis for Prairie Warblers it is necessary to know the approximate date at which females begin to pass out of breeding condition because movement after that date cannot be expected to be followed by renesting. For this cut-off date we chose 10 June. After this date females that nested in the study area, but failed, began to remain in the area without attempting to renest. In addition, females that nested elsewhere earlier in the season (judging by the presence of a brood patch on arrival; see Nolan 1978, chapters 30 and 34) began arriving on the study area without attempting to renest. Thus, if a female either lost her nest or produced fledglings on or before 10 June and then disappeared from the study area, we treated her as having dispersed and renested elsewhere. If disappearance following a loss or success took place after this date, we excluded the case from our analysis because the significance of the disappearance was ambiguous—the female may have been incapable of renesting.

Contrary to our first prediction, that females should move more often after unsuccessful nestings than successful ones, female Prairie Warblers were equally likely to leave their mate's territory (and remate) in the first case as in the second (18% of 128 vs. 17% of 12; χ^2 with continuity correction = 0.08, df = 1, $P > 0.05$).

To test our second prediction, that moving after nest failure may be affected by the type of animal responsible for the failure, we categorized failures into those presumed due to Brown-headed Cowbirds (*Molothrus ater*), snakes, eastern chipmunks (*Tamia striatus*), and larger predators, presumably mostly raccoons (*Procyon lotor*), or opossums (*Didelphis virginiana*) (see Nolan 1978, chapter 33). Losses were attributed to cowbirds when nests that contained Prairie Warbler eggs were abandoned after being parasitized. Failures were attributed to snakes when all the eggs or young disappeared without trace, apparently in a single bout of predation, and without damage to the nest. Failures were attributed to chipmunks when fewer than all eggs disappeared from undamaged nests, followed by nest desertion, or when eggs or young disappeared one at a time during several nest inspections until all were gone and the nest remained undamaged. (An occasional such case may have been caused by Blue Jays, *Cyanocitta cristata*.) Failures attributed to larger mammals were characterized by major damage to the nest itself. We then divided causes of failure into two groups—those due to predators with home-range sizes smaller than Prairie Warbler territories (mean Prairie Warbler territory size = 1.56–1.62 ha; Nolan 1978, p. 332) and those due to predators with larger home-range sizes. In the former group were chipmunks (mean home-range size = 0.11 ha; Yerger 1953) and in the latter group are larger mammals and snakes, as well as cowbirds. Contrary to our second prediction, females were no less likely to move following predation due to chipmunks than they were following predation due to larger predators (6% of 17 vs. 19% of 100; $P = 0.164$, one-tailed Fisher's exact test).

Finally, we considered the probability of movement according to the stage in the nesting cycle at which the prior nest failed. As predicted, females whose nests were lost during laying were less likely to change sites between nesting attempts than were females that lost their nests during incubation or while nestlings were present (Table 1). As noted above, this prediction that females will change territories less frequently after losses early rather than late in the nesting cycle requires the assumption that causes of nest loss vary according to the stage of the cycle. This assumption appears justified in the Prairie Warbler. A major cause of early-stage failure was desertion after cowbird parasitism (Nolan 1978, p. 383–385). Cowbirds parasitized 83 of 248 nests (33%) that received the first warbler egg on or before 10 June (Nolan 1978, table 126); but, of 106 cowbird eggs whose laying date could be related precisely to the host female's nesting cycle only eight (8%) were laid after day 2 of the incubation period (Nolan 1978, table 129). Thus cowbird eggs were usually laid no later than about the ninth day of an approximately 28-day cycle and, in most cases, several days earlier than that. Failures caused by some important predators, e.g., snakes, probably were randomly distributed.

Whether still other predators imposed greater risks late in the cycle is not known, but losses rose when the eggs hatched and were high thereafter, and Nolan's view (1978, p. 402–404) that both parental and nestling behavior made nests more conspicuous at this time suggests that mammalian predation may have increased after hatching.

WHY NOT DISPERSE?

When either females or mated pairs fail to move after predation, this could be either because selection does not favor dispersal or because there are constraints on movement caused by saturation of local habitat. Greenwood and Harvey (1982) concluded that in territorial birds males are more constrained than females because they are primarily responsible for establishing a territory. Thus the greater probability of a female dispersing between years than a male is because females are more likely to find a new site with an unpaired male.

Species in which females (and their mates) have been found either not to move within a season following nest failures or to move at very low frequencies are Wrentits (*Chamaea fasciata,* Erickson 1938), Song Sparrows (*Melospiza melodia,* Tompa 1964), European Blackbirds (*Turdus merula,* Ribaut 1964), Eurasian Skylarks (*Alauda arvensis,* Delius 1965), Cactus Wrens (*Campylorhynchus brunneicapillus,* Anderson and Anderson 1973), Barn Swallows (*Hirundo rustica,* Shields 1984), Scrub Jays (*Aphelocoma coerulescens,* Woolfenden and Fitzpatrick 1984) and Acorn Woodpeckers (*Melanerpes formicivorus*; Koenig, pers. comm.).

Unfortunately, we do not know for any of these species whether nest predation events are correlated over space, thereby favoring mid-season dispersal for renesting; such correlations, however, seem likely to exist for most species in at least some breeding areas and some seasons. Data in most of the reports cited suggest that local habitats were saturated by mated pairs or by breeding groups containing females. For Barn Swallows, Shields (1984) argued that within-season dispersal following nest failure is unlikely because of the strong seasonal decline in nesting success and the time costs of dispersal and building a new nest.

Darley et al. (1971) argue that predation-related breeding dispersal might not be expected to be accompanied by pair dissolution because

TABLE 1. Response (change or no change of territory and mate) of female Prairie Warblers after failures on or before 10 June, according to stage of nest at failure.

Response of females	Stage of nest at failure		
	Laying[1]	Incubation	Nestling
No change	38	56	11
Change	2	17	4
% Changing	5.0	23.3	26.7

[1] $\chi^2 = 6.77$, df = 2, $P < 0.05$.

of the time that would be lost in finding a new mate and re-pairing. Mid-season pair formation (after one member of a pair was lost) followed by nesting has been reported for some of the species listed above (Song Sparrows, Smith et al. 1982; Cactus Wrens, Anderson and Anderson 1973; Barn Swallows, Crook and Shields 1985; Acorn Woodpeckers, Stacey and Edwards 1983). We know of one set of measurements that demonstrates this time cost. For Bananaquits, Wunderle (1984) found that females that moved to distant mates (and territories) took averages of 4 (1981) and 14 (1978) days *longer* to renest than did females that refrained from dispersal after failure and renested with the same mate. In contrast, Lifjeld and Slagsvold (1988) found no difference in reproductive success between female Pied Flycatchers (*Ficedula hypoleuca*) that changed mates and those that remained paired with their mates following experimental destruction of their nests (although the former tended to take slightly longer to renest than the latter— 6.6 days vs. 6.2 days, respectively). No data on the distances that these two types of females moved were presented. Likewise, Slagsvold found no correlation between renesting time and renesting dispersal for Great Tits, but we do not know how dispersal was related to mate or territory changes in this study. At present, renesting dispersal by mated pairs is well-documented only for Gray Catbirds (*Dumatella carolinensis,* Darley et al. 1971).

The difficulty with the argument that dispersal by pairs should be favored over breaking of the pair bond and dispersal by the female alone is that there must exist a considerable amount of suitable but unoccupied breeding habitat. In most species, however, local habitats are saturated by territorial males, some of which may be unmated because tertiary sex ratios are often male-biased (Mayr 1939, French 1959, Wiseman 1975, Sampson 1976, Yom-Tov and Ollason 1976,

Craig and Manson 1979, Shreeve 1980). The presence of unmated males, together with the fact that the male rather than the female usually has the primary role in territory defense, means that females should be much freer to move than males. A female bias in within-season breeding dispersal occurs in Song Sparrows (Nice 1937), Northern Cardinals (*Cardinalis cardinalis*; Scott, fide Darley et al. 1971), Yellow-breasted Chats (*Icteria virens,* Thompson and Nolan 1973), Prairie Warblers (Nolan 1978), and Eastern Bluebirds (P. A. Gowaty, unpubl.; see Rohwer 1986, table 3). We know of no species in which males exhibit greater within-season breeding dispersal following nest failures than do females and would expect such male-biased dispersal only when females are the primary territory defenders, as is true in some polyandrous species.

ALTERNATIVE HYPOTHESES

Two other hypotheses have been suggested to explain within-season breeding dispersal. These hypotheses are not mutually exclusive either of one another or of the predation-avoidance hypothesis.

DISPERSAL FOR MORE RAPID RENESTING

The first hypothesis proposes that moving to a new territory may permit more rapid renesting if the preceding nest succeeded (herein, produced one or more fledglings) or no longer required biparental care. Such movement could be used by one member of a pair to terminate care of the nestlings or fledglings, thus improving the probability that it could attempt to raise a subsequent brood elsewhere. This might be especially likely to happen when the first brood is small enough for a single parent to raise it to independence.

The only detailed information relating the presence or absence of pair dissolution to the time interval between the fledging of the first brood and the initiation of the second brood attempt comes from Kendeigh's (1941) monograph on House Wrens (*Troglodytes aedon*). In 42 cases where the behavior of the male was known he helped the female care for the fledglings of the first brood in 21 instances and did not help in the other 21. When he did not help he usually moved to a new territory and began advertising for a mate. Males that did help repaired with the same female for the second-brood attempt in 65% of the cases, while males that did not help re-paired with the same female in only

33% of the cases and attracted new mates in the other 67%. When males helped, their average renesting interval was 10 days (ranging from 7 to 32 days), but when they did not help this interval averaged 8 days (ranging from 1 to 18 days). These intervals apparently include both cases of remating with the same female and cases of mate change, but the text is unclear on this point (Kendeigh 1941, p. 52). Whether these averages are statistically different is unknown; however, the difference is in the direction predicted by this hypothesis.

Prairie Warblers. In Prairie Warblers some females do desert males, leaving them to take over care of fledglings (Nolan 1978, p. 321). Under the hypothesis being considered, females that moved should have renested sooner than females that did not. Two females moved within 1–2 days of bringing off first broods (Nolan 1978, p. 346), but only one was found soon enough to provide useful information. Judging by her behavior (her nest was too high to inspect), she laid the first egg of her subsequent clutch 6 days after her previous brood fledged. Seven females that did not desert and that renested on their original territories and whose first-egg date we know laid that egg an average of 14 days (extremes 2 and 30 days) after the previous brood fledged. More data on this point are needed before we can draw any conclusions.

If moving after nest success is strongly advantageous in accelerating renesting and moving is not advantageous in avoiding nest predation, or not greatly so, then we might expect females to move more frequently after successful nesting attempts that after failures. As noted earlier, however, dispersal to a new territory was no more likely to follow successful than unsuccessful nesting attempts in Prairie Warblers.

The predictions of this hypothesis and of the predator-avoidance hypothesis are in conflict. That is, if dispersal can accelerate renesting, dispersal should more often follow successful than unsuccessful nests; but, to avoid future nest predation, dispersal should more often follow unsuccessful nests. Selection could have favored both patterns of dispersal, and their opposing effects could be sufficiently balanced that neither appears to be confirmed by the data. There are two reasons why we believe changing territories and mates to increase the speed of renesting is unlikely to confer benefits on female Prairie Warblers. First, males do not feed females during the

period preceding laying, so females do not require this kind of attention to initiate new clutches. Second, males assume care of the fledglings when females attempt a new brood, regardless of whether females disperse or remain on the territory; females are thus free for rapid renesting without incurring a time cost of dispersal.

DISPERSAL TO AVOID DEPLETED RESOURCES

The second additional hypothesis to explain within-season breeding dispersal proposes that avoidance of the vicinity of the earlier nest may have the consequence of avoiding an area in which food resources have been depleted. To avoid renesting in areas of resource depletion, females could either change territories or could remain on the same territory but vary the distance between successive nests according to the degree of depletion around the preceding nest. Under this hypothesis we should expect (1) more movement either to a new territory or more movement within a territory after success than after failure, and (2) more movement when the preceding nest failed in the nestling stage than when it failed during laying or incubation, i.e., before the food requirements of the young had depressed food levels on the territory.

This idea has been supported by data on Stonechats. Greig-Smith (1982) found that pairs that successfully raised large broods moved greater distances *within their territories* before renesting than did pairs whose broods were small. Apparently, these movements were related to local food depletion, because nestling growth in subsequent broods was better for those parents that moved greater distances from successful nests before nesting again.

Movements of some female Song Sparrows may have a similar basis. Nice (1937, p. 181) observed four females that followed their fledglings off their mates' territories to new locations, where each female renested with a new male. The loosely colonial cardueline finches, no species of which defends a feeding territory, are well-known to move considerable distances for renesting. Such movements could represent adjustments to changing food distributions (Newton 1973) or could be undertaken by the deserting member of a pair to terminate parental care. In House Finches (*Carpodacus mexicanus*) successful females that attempted to renest probably would be seriously delayed unless they first deserted

mate and brood and dispersed to another location; the reason is that in this species dependent fledglings will vigorously attack a courting parent (Rohwer, unpubl.).

Prairie Warblers. As already noted, the probability of dispersal did not depend on the fate of the previous nest. Also, Prairie Warblers did not parallel Stonechats (Greig-Smith 1982) by moving greater distances for renesting within their territories following successful than following unsuccessful nest attempts. The mean distance between 22 successful nests and the following second-brood nest was 81 m (SD = 47 m); the mean between 193 unsuccessful nests and their successors was 85 m (SD = 53 m; Nolan 1978, p. 136). Lastly, although movement did depend on when in the cycle the nest was lost (Table 1), females were as likely to leave when the nest was lost when eggs were present (i.e., during laying and incubation) as when it was lost while nestlings were present (see Table 1; $\chi^2 = 0.33$, df = 1, $P > 0.05$).

The hypothesis that dispersal in the Prairie Warbler prevents renesting in areas in which food has been locally depressed also makes conflicting predictions concerning dispersal as affected by the fate of the preceding nest. Here too, if both hypotheses are correct, data supporting their conflicting predictions may have cancelled each other out in the Prairie Warbler analysis, resulting in no observed relationship between mid-season territory change and the success or failure of the preceding nest. We doubt this interpretation. To avoid areas of resource depression, even females that did not move to a new territory to renest should have placed the new nest farther from its predecessor when the latter was successful than when it was unsuccessful. This did not occur, and the sample for this intraterritorial test is considerable (see data from Nolan 1978, p. 136, cited above). Because this intraterritorial test does not conflict with predictions from the other hypothesis and, furthermore, is not confirmed, we believe that avoiding areas of food depletion is not an ultimate cause of mid-season breeding dispersal by female Prairie Warblers.

CONCLUSIONS

In sum, our finding in Prairie Warblers that the probability of dispersal prior to renesting is dependent on the stage at which the preceding nest failed, together with evidence supporting the critical assumptions behind this prediction, suggests

that renesting dispersal in Prairie Warblers may indeed function to reduce losses of replacement nests. Neither dispersal for more rapid renesting nor dispersal to avoid areas of resource depletion was supported, although as noted some of the predictions of these two hypotheses concerning the probability of dispersal according to the fate of the previous nest conflict with the predictions of the predation-avoidance hypothesis. However, neither of these two hypotheses is likely to apply to Prairie Warblers: Dispersal is unlikely to lead to more rapid renesting, because males assume care of the fledglings regardless of whether the female disperses; and females do not move further within their territories following successful nests than following unsuccessful nests, even though in the former case resources might be more depleted near the nest than elsewhere.

We were surprised that we did not find a difference in the probability of a female Prairie Warbler's changing territories following a successful as opposed to an unsuccessful breeding attempt. We offer the following as a possible explanation. When testing our second prediction of the predation-avoidance hypothesis (that the probability of moving should depend on the cause of nest loss), we included cowbirds in the same category as snakes and large mammals. This grouping may not be appropriate. The distribution of cowbirds may be tied more closely to the distribution of Prairie Warblers than are the distributions of the predators. In addition, cowbirds may have a relatively more ideal-free distribution than snakes and large mammals, that is, individual cowbird ranges may overlap one another relatively more than do individual snake or large mammal ranges. In support of this, Fleischer (1985) found extensive spatial overlap in the laying areas of different females.

If the Prairie Warbler range is completely encompassed by the cowbird range, and if the movements of individual cowbirds are relatively unrestricted by other cowbirds (thereby increasing the uniformity of the cowbird distribution), then while movement following cowbird parasitism may place the new nest outside of the range of that particular cowbird, it may not place it outside the range of other cowbirds. If this is true, Prairie Warblers should *not* move following parasitism by cowbirds. If we regroup cowbirds with chipmunks and compare the probability of a female Prairie Warbler's moving following nest loss due to these two animals with the probability

of moving following losses due to snakes and large mammals, we find that the former is lower than the latter (8% of 40 vs. 22% of 77; $P = 0.041$, one-tailed Fisher's exact test). Thus our inability to detect a difference in the probability of dispersal following successful vs. unsuccessful breeding attempts may be explained by the facts that a large proportion of the nest failures that occurred before 10 June was due to cowbird parasitism, and that females may not be selected to disperse following cowbird parasitism.

As summarized earlier, of the five other species for which the predation-avoidance hypothesis has been adequately tested against a null hypothesis, some evidence supporting at least one of its predictions has been found for all. Only one of these five studies has examined either of the alternative hypotheses: Greig-Smith (1982) found support for the depleted resources hypothesis in Stonechats. Thus neither of these alternatives can be excluded. However, it appears that predation avoidance is important in establishing within-season patterns of breeding dispersal. This finding is in accordance with studies on between-season breeding dispersal. It remains for future workers to test the fundamental prediction of this hypothesis, that such dispersal actually improves, for any species, the odds of replacement nests succeeding.

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