# The reproductive success of Blackbirds *Turdus merula* in relation to habitat structure and choice of nest site

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The reproductive success of a population of Blackbirds *Turdus merula* occupying farmland and woodland was studied over 3 years to investigate the effects of habitat on breeding success. Territory distribution was patchy in both farmland and woodland; some areas were unoccupied, while other areas were occupied at variable densities. Habitat structure appeared to influence occupation: the index of habitat complexity ("cover score") was higher in occupied areas than in unoccupied areas and high-density territories had higher cover scores than low-density territories. However, habitat structure had no significant effect on reproductive success because the cover scores of territories where pairs were successful did not differ significantly from those of territories where there were no successful breeding attempts. There was no evidence of differential mortality rates in adults according to habitat. The height, bulk and exposure of *c*. 430 nests were measured to determine the effect of nest and nest-site characteristics on reproductive success. Nest exposure was the only feature that differed between successful and failed nests, successful nests being less exposed than failed nests. The major cause of breeding failure was nest predation, but the effect of nest exposure operated only during the laying and incubation period and not during the nestling period. The significance of habitat structure for variation in population densities between habitats is discussed.

The numbers of many farmland bird species have declined in the last two decades (Marchant et al. 1990, Lack 1992, Fuller 1993, Gibbons et al. 1993), prompting intensive studies of the causes of decline. A key goal of such studies is the identification of habitat requirements and the factors that determine reproductive success. The effects of habitat on productivity have been assessed by various methods (Ens et al. 1992). These include (1) the observation of clusters of successful nests, presumed to be in good habitat (Hochachka et al. 1989); (2) the ranking of territories on the basis of permanency or priority of occupancy, with that ranking related to reproductive success (Newton 1989, Bensch & Hasselquist 1991) and (3) identification of specific habitat features related to success, although the precise effect of those features may (Weatherhead & Robertson 1977, Ens et al. 1992, Komdeur 1992) or may not (Hotker 1989) be identified. The key to such studies is to find territory features

that can be measured independently of reproductive success. Few studies (Ens et al. 1992) have been able to determine the role of habitat quality in this way.

This article examines the effect of habitat structure on the reproductive success of the Blackbird *Turdus merula*. The Blackbird is a good model species because while its ancestral habitat was either woodland edge and clearings (Marchant et al. 1990) or forests (Gibbons et al. 1993), it is now among the most conspicuous and most common bird species of woodland, farmland and urban habitats (Gibbons et al. 1993, O'Connor & Shrubb 1986). The spread into urban habitat has resulted in increased abundance and a much higher density than in rural habitats (Snow 1958). The U.K. population has remained relatively stable for the last 50 years, despite a recent slight decline in rural habitats (Gibbons et al. 1993). Although urban Blackbirds have been extensively studied (Snow 1958, Batten 1973, Magrath 1991, Desrochers 1992a,b), there have been few rural studies. Nest records from the British Trust for Ornithology are a useful source of data for large-scale comparisons (O'Connor & Shrubb 1986), but this source is limited when considering habitat requirements on a fine scale. Here, we consider habitat requirements of rural Blackbirds at two levels: first, the effect of habitat on breeding density and success, and, second, the effect of habitat and nest location on reproductive success.

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## METHODS

### Study site and population

The study was conducted on 54–76 pairs of Blackbirds in 350 ha of farmland and woodland on the Wytham Estate, Oxford, during 1991–1993. Most breeding birds (64–72%) were colour-ringed. Breeding territories were identified by the presence of a pair, not simply the presence of singing males, because some unpaired males held territories in each year of the study. There were also some non-territory-holding, unpaired males during the breeding season. Unpaired males are excluded from analyses of territory density. Territory boundaries were estimated from nest distribution, augmented by observations of singing males. Foraging is not confined to the territory, so observations of foraging birds could not be used to delineate territories. However, we use breeding density rather than territory size when considering habitat occupation, so a more precise definition of territory size was not necessary.

### Reproductive success

The most effective method of finding nests was to search likely breeding sites. A few were found by observation of nest-building females or of provisioning parents. We could not locate all nests in all territories, but the proportion found increased with our experience (see below). Some nests were abandoned by females before egg-laying, usually before completion of the lining, and these are not included in analyses of breeding success. The total number of nests found (in which at least one egg was laid) increased from 128 in 1991 to 178 in 1992 and 246 in 1993. The number of pairs in the study area increased from 54 in 1991 to 76 in 1993, but there was also a significant increase in the mean (± s.d.) number of known attempts per pair from 2.37 ± 1.25 ($n =$ 54) in 1991 to 2.70 ± 1.15 ($n = 66$) in 1992 and 3.24 ± 1.59 ($n = 76$) in 1993 (ANOVA, $F_{2,193} = 6.76$, $P < 0.001$). There was no significant difference in the timing of breeding between years (first-egg dates for first clutches: ANOVA, $F_{2,133}$ = 2.85, n.s.) nor in the seasonal distribution of first-egg lay dates (first-egg dates for all clutches: ANOVA, $F_{2,446} = 0.10$, n.s.).

Nests were visited about every 2 days until clutch completion to determine first-egg dates and clutch size. To avoid excessive disturbance of nests and vegetation, we checked nests only once during incubation, approximately 6 days after clutch completion. Nests were visited daily from day 10 or 11 of incubation (day 0 = day of clutch completion), so the hatching date could be determined to within 24 h. Nests found after clutch completion were visited every 2 or 3 days, so the hatching date could not be determined with the same accuracy. In these cases and in broods found after hatching, chicks were aged by reference to growth curves of tibia length determined in 1991 by daily measurement of 12 broods. Broods were ringed when the oldest nestling was

8 days old; gape length, tibia length and weight were recorded for each nestling.

### Habitat structure and nest sites

A habitat survey was conducted in 1993 by a naive observer with no previous experience of the study site, territory distribution or reproductive success at sampling sites. One sampling point was assigned to each territory (marked on maps of the study site), using 1992 territories as a guide, although these did not exactly coincide with territories in 1991 or 1993. Extra sampling points were assigned to areas thought to be occupied at higher densities. Further sampling points in unoccupied areas spaced evenly around the study area were also assigned to represent false territories. At each sampling point in woodland, the observer scored the surrounding area (10 m radius) on an index from 1 to 5 according to vegetation density. The cover score was based on the difficulty of finding a Blackbird nest 1.0 to 1.5 m above the ground. In farmland, the observer scored 20 m of hedgerow in the same way. The results for each habitat are presented separately. This habitat survey was conducted in both farmland and woodland in early April (the start of the breeding season) and in woodland only in early June (the end of the breeding season).

To determine the effects of nest and nest-site characteristics on productivity, the following features were measured: (1) nest height (m), the height of the nest rim above the ground; (2) nest bulk (cm³), the nest "volume", calculated as depth × diameter × diameter, the two diameters being measured at 90° to each other and, (3) nest exposure (%), the proportion of ambient light reaching a point 2 cm above the nest cup. Light was measured using a light meter, but only on overcast days because the reading was highly sensitive to direct sunlight.

Nest measurements were normally taken shortly after fledging or breeding failure. However, this was not possible for all nests because the weather did not permit measurement during overcast conditions for several days or even weeks in a few cases.

Our increasing nest-finding ability could have biased the sample of nests found, so measured nests may not truly reflect the characteristics of all nests. There were significant differences between years in the exposure, height and bulk of nests (Table 1). Most nests were in mature woodland and long-established hedges, so it is unlikely that there was significant variation between years in the availability of high and low sites or exposed and concealed sites. Indeed, the differences between years were consistent with an improvement in our ability to find nests, i.e. exposure and bulk decreased and height increased (nests high in ivy-covered trees were harder to locate than nests close to the ground). Therefore, years were combined when considering the effects of nest characteristics on breeding success. Furthermore, we considered each nest to be independent, even

**Table 1.** *Between-year variation in nest and nest-site characteristics of Blackbirds, 1991-1993. All three measures differed significantly between years (height: Kruskal-Wallis ANOVA, H = 20.31, P < 0.001; bulk: ANOVA, $F_{2,430}$ = 5.62, P < 0.004; exposure: Kruskal-Wallis ANOVA, H = 18.4, P < 0.001)*

|  | 1991 mean ± s.d. (n) | 1992 mean ± s.d. (n) | 1993 mean ± s.d. (n) |
|---|---|---|---|
| Height (m) | 0.97 ± 0.76 (102) | 1.11 ± 1.14 (159) | 1.58 ± 1.67 (185) |
| Bulk (cm³) | 4627 ± 1509 (101) | 4108 ± 1224 (152) | 4031 ± 1667 (180) |
| Exposure (%) | 10.7 ± 16.0 (102) | 4.22 ± 5.58 (154) | 4.98 ± 6.69 (192) |

though some females contributed several nests to the total. This is justified because we are interested in the effects of habitat and nest site on breeding success, and even though several nests in the sample belonged to the same birds, each was located in a different site and nesting occurred at a different time.

## RESULTS

### Territory distribution and habitat

The occupation of available habitat was not uniform; some areas were occupied at high densities, some at low densities, while others remained vacant (Fig. 1). Blackbirds apparently prefer relatively dense vegetation because cover scores were significantly higher in occupied areas than in unoccupied areas in each year and in both habitats (Table 2). However, territory density varied within the occupied areas of both habitats (Fig. 1), e.g. in woodland there were two extensive areas which were occupied at more than twice the average density of woodland territories in all years. These patches of high-density occupation in woodland are referred to as

"hot spots", and other territories are referred to as "sparse" territories. This nonuniform distribution might result from a habitat preference or from differential survival of birds in different areas. The mean cover scores of sampling sites in hot spots and sparse territories in woodland are shown in Table 3. At the start of the breeding season (April), cover scores did not differ significantly, but at the end of the breeding season (June), hot-spot sampling sites had significantly higher scores than sparse sites in all years.

Survival estimates of those birds breeding in hot spots and those in sparse territories from one year to the next did not differ significantly when years were considered separately or together (1991-1992: hot spot 72% [n = 36], sparse 51% [n = 35], $\chi^2_1$ = 2.43, n.s.; 1992-1993: hot spot 51% [n = 43], sparse 45% [n = 49], $\chi^2_1$ = 0.15, n.s.; 1991-1993: hot spot 61% [n = 79], sparse 48% [n = 84], $\chi^2_1$ = 2.33, n.s.). This suggests that there was no effect of differential adult survival on breeding density.

### Habitat structure and reproductive success

The overall breeding success from nesting attempts was 19.2% (n = 552). The success rate decreased from 25.8% (n = 128) in 1991 to 19.7% (n = 178) in 1992 to 15.4% (n =
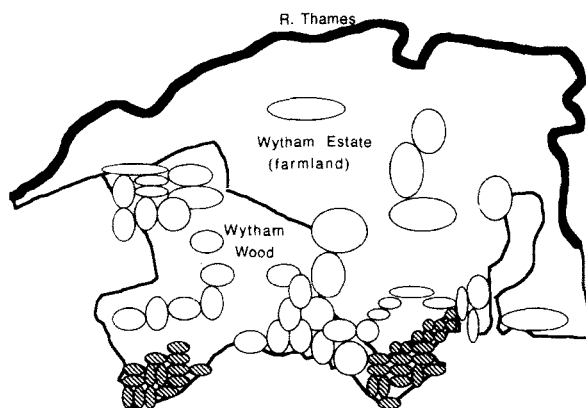


**Figure 1.** Distribution of Blackbird territories in woodland and farmland on the Wytham Estate in 1993. Shaded territories were classified as "hot-spot" territories; unshaded territories were classified as "sparse".

**Table 2.** *Cover scores for sampling sites that were occupied or unoccupied by breeding Blackbirds in farmland and woodland in April. Sample sizes represent sampling sites rather than territories*

| Year | Habitat | Occupied mean ± s.d. (n) | Unoccupied mean ± s.d. (n) | z |
|---|---|---|---|---|
| 1991 | Woodland | 3.76 ± 1.26 (48) | 2.11 ± 1.44 (52) | 5.20[b] |
|  | Farmland | 3.47 ± 0.99 (15) | 2.72 ± 0.99 (47) | 2.52[a] |
| 1992 | Woodland | 3.77 ± 1.22 (57) | 1.64 ± 1.16 (43) | 6.68[b] |
|  | Farmland | 3.78 ± 1.06 (18) | 2.52 ± 0.82 (44) | 4.02[b] |
| 1993 | Woodland | 3.75 ± 1.18 (57) | 1.70 ± 1.21 (43) | 6.12[b] |
|  | Farmland | 3.64 ± 1.09 (22) | 2.51 ± 0.79 (40) | 4.05[b] |

[a] Mann-Whitney U-tests, P < 0.05.
[b] Mann-Whitney U-tests, P < 0.001.

**Table 3.** *Cover scores for hot-spot and sparse Blackbird territories in woodland in early April and early June. Cover scores were allocated on a relative rather than absolute scale within each sampling period, hence the lower scores for sparse territories in June compared to April, despite bud-burst and vegetation growth*

| Date | Hot-spot mean ± s.d. (n) | Sparse mean ± s.d. (n) | z |
|------|--------------------------|------------------------|---|
| April | | | |
| 1991 | 3.91 ± 1.41 (29) | 3.61 ± 1.12 (19) | 1.23 |
| 1992 | 3.86 ± 1.33 (28) | 3.68 ± 1.12 (29) | 0.88 |
| 1993 | 3.82 ± 1.33 (26) | 3.70 ± 1.06 (31) | 0.70 |
| June | | | |
| 1991 | 4.14 ± 0.74 (29) | 3.11 ± 0.88 (19) | 3.89[b] |
| 1992 | 4.14 ± 0.89 (28) | 3.03 ± 1.12 (29) | 3.78[b] |
| 1993 | 4.08 ± 0.89 (26) | 3.13 ± 1.15 (31) | 3.25[a] |

[a] Mann-Whitney $U$-tests, $P < 0.01$.
[b] Mann-Whitney $U$-tests, $P < 0.001$.



**Figure 2.** Relationship between mean exposure (% ± s.e.) of Blackbird nests and date, pooling data from 1991–1993. Spearman rank correlation: $r_{s437} = 0.42$, $P < 0.001$.
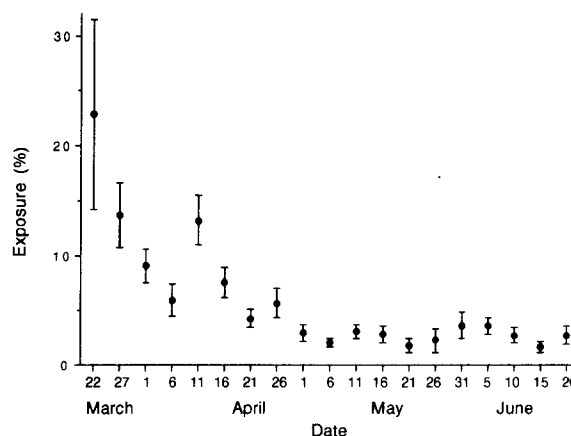
246) in 1993 ($\chi^2_2 = 5.83$, $P < 0.05$). This decrease was probably, in part, an artifact of our improving nest-finding ability, i.e. as we located nests earlier, we were more likely to find nests preyed upon early in the nesting cycle. To illustrate this, a separate analysis including only those territories where a complete breeding record was obtained revealed no significant difference between years in success rate (1991: 22.9% [$n = 70$]; 1992: 22.0% [$n = 127$]; 1993: 14.7% [$n = 198$]; $\chi^2_2 = 3.89$, n.s.).

The vegetation cover scores on territories with at least one successful breeding attempt were compared with those on territories with no successful attempts (Table 4). The cover scores did not differ significantly in early April, and in June there was a significant difference in only one year. Therefore, if there was any effect of habitat on reproductive success, it occurred at a level finer than that measured by cover scores.

## Nest-site selection and reproductive success

The characteristics of c. 430 nests were assessed. There was no seasonal variation in nest height ($r_{434} = 0.03$, n.s.) or bulk ($r_{420} = 0.09$, n.s.), but nest exposure declined significantly

**Table 4.** *Comparison of cover scores for Blackbird nests in early April and early June on territories where there was at least one successful breeding attempt and where there were no successful breeding attempts*

| Date | Habitat | Cover scores mean ± s.d. (n) Successful breeding territories | Unsuccessful breeding territories | z |
|------|---------|------------------------|-----------------------------------|---|
| April | | | | |
| 1991 | Woodland | 3.54 ± 1.25 (24) | 3.69 ± 1.27 (18) | 0.42 |
| | Farmland | 3.50 ± 0.58 (4) | 3.75 ± 1.50 (4) | 0.30 |
| 1992 | Woodland | 3.80 ± 1.35 (25) | 3.69 ± 1.32 (32) | 0.65 |
| | Farmland | 3.96 ± 0.97 (5) | 4.25 ± 0.50 (4) | 0.76 |
| 1993 | Woodland | 4.04 ± 0.87 (23) | 3.74 ± 1.23 (36) | 0.80 |
| | Farmland | 3.75 ± 0.96 (4) | 3.75 ± 0.68 (6) | 0.11 |
| June | | | | |
| 1991 | Woodland | 3.65 ± 0.98 (24) | 3.64 ± 0.90 (18) | 0.43 |
| 1992 | Woodland | 4.29 ± 1.00 (24) | 3.22 ± 0.87 (32) | 4.11[a] |
| 1993 | Woodland | 3.60 ± 1.03 (24) | 3.99 ± 0.87 (31) | 1.40 |

[a] Mann-Whitney $U$-test, $P < 0.001$.

**Table 5.** *Nest and nest-site characteristics and reproductive success, hatching success (whether an initiated clutch hatched or not) and fledging success (whether a hatched brood fledged or not) of Blackbirds in 1991–1993*

| | Breeding attempt mean ± s.d. (*n*) | | |
| --- | --- | --- | --- |
| | Successful | Unsuccessful | *z* |
| **Breeding success** | | | |
| Height (m) | 1.26 ± 1.24 (72) | 1.27 ± 1.38 (361) | 0.10 |
| Bulk (cm³) | 4010 ± 1340 (70) | 4237 ± 1521 (351) | 1.16 |
| Exposure (%) | 3.70 ± 6.23 (70) | 6.57 ± 10.32 (365) | 3.47[b] |
| **Hatching success** | | | |
| Height (m) | 1.14 ± 1.25 (148) | 1.33 ± 1.40 (283) | 2.26[a] |
| Bulk (cm³) | 4052 ± 1233 (139) | 4274 ± 1604 (281) | 1.43 |
| Exposure (%) | 3.45 ± 5.12 (145) | 7.42 ± 11.26 (288) | 4.85[b] |
| **Fledging success** | | | |
| Height (m) | 1.26 ± 1.24 (72) | 1.03 ± 1.25 (76) | 1.63 |
| Bulk (cm³) | 4010 ± 1340 (70) | 4096 ± 1121 (69) | 0.41 |
| Exposure (%) | 3.70 ± 6.23 (70) | 3.22 ± 3.84 (75) | 0.95 |

[a] Mann-Whitney *U*-tests, $P < 0.05$.
[b] Mann-Whitney *U*-tests, $P < 0.001$.

through the season (Fig. 2), reflecting leaf emergence and growth of the ground layer, e.g. nettles *Urtica dioica*. If this relationship is assumed to be linear, the regression slope is −0.15 (i.e. over 10 days, the nest exposure decreased by 1.5%).

Nest exposure was the only characteristic to differ significantly between successful and unsuccessful nests: successful nests were less exposed than failed nests (Table 5). How-



**Figure 3.** Hatching success (% of initiated clutches which hatched) of Blackbird nests in relation to nest exposure (% of ambient light reaching nest cup); *n* = 432 nests.

ever, this effect of exposure on the success or failure of breeding attempts did not operate throughout the breeding cycle. There was a significant effect of exposure on hatching success (Table 5), but there was no effect of any nest characteristics on fledging success (Table 5). Figure 3 shows the proportion of attempts that hatched successfully in relation to nest exposure. If the relationship is assumed to be linear, the regression slope is −0.67, i.e. as nest exposure decreased by 10% (e.g. from 15% to 5% in Fig. 3), the probability of the clutch hatching successfully increased by 6.7%. The seasonal decline in nest exposure (Fig. 2 and above) would therefore result in an expected increase in hatching success of only about 10% over a 3-month period.

The effect of exposure on reproductive success might be mediated by biotic or abiotic factors. In fact, most nest failures were caused by predation (Table 6), the main predators being birds, probably corvids. Of nine predation events witnessed, five were by Magpies *Pica pica* and four were by mammals (three Weasels *Mustela nivalis* and one Fox *Vulpes vulpes*). The accuracy of predator identification from nest appearance and the presence or absence of egg or nestling remains is limited, so these estimates were checked using plasticine eggs in artificial clutches of quail eggs to identify predators (Chamberlain *et al.* 1996). There was no significant difference in the overall proportions of avian and mammalian predators identified by observation and experiment ($G_1$ = 1.12, n.s.).

These results indicate two levels of habitat preference determining territory distribution and nest-site selection. We investigated whether these were different processes or simply two effects of a single choice for densely vegetated territories by examining the relationship between nest exposure
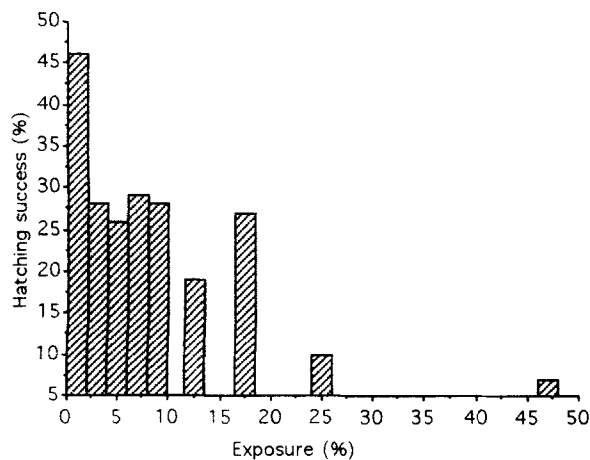
**Table 6.**  *Causes of reproductive failure in Blackbirds and identity of nest predators in farmland and woodland territories*

| Territory | Cause of failure | | |
|---|---|---|---|
| | Predation | Desertion | Death of adult |
| Farmland | 51 (94%) | 2 (4%) | 1 (2%) |
| Woodland | 345 (91%) | 25 (7%) | 8 (2%) |
| Total | 396 (92%) | 27 (6%) | 9 (2%) |
| | Predator | | |
| | Avian | Mammalian | |
| Farmland | 13 (54%) | 11 (46%) | |
| Woodland | 175 (72%) | 69 (28%) | |
| Total | 188 (70%) | 80 (30%) | |

and cover scores. There was no significant correlation between nest exposure and cover score in farmland in any year (Spearman Rank correlations: 1991, $r_{s11}$ = −0.09, n.s.; 1992, $r_{s21}$ = −0.03, n.s.; 1993, $r_{s14}$ = 0.24, n.s.) nor in woodland using the April cover scores (1991, $r_{s89}$ = −0.14, n.s.; 1992, $r_{s133}$ = 0.02, n.s.; 1993, $r_{s173}$ = −0.05, n.s.). There was a significant negative correlation between nest exposure and the June cover score in woodland in 1991 ($r_{s89}$ = −0.25, $P$ < 0.02), but not in other years (1992, $r_{s133}$ = 0.05, n.s.; 1993, $r_{s173}$ = −0.12, n.s.). In general, it appears that the degree of nest exposure did not reflect the cover index.

## DISCUSSION

The low density of rural Blackbirds compared to urban populations may result from relatively low winter survival rates (Snow 1958, Lack 1966). Differential mortality might also explain density variation within habitats, e.g. Song Sparrows *Melospiza melodia* (Hochachka *et al.* 1989), but we found no evidence of differential mortality according to habitat. The patchy occupation of both habitats was associated with vegetation density, and breeding success was strongly influenced by microhabitat selection (i.e. nest-site characteristics). Therefore, a preference for dense vegetation is a more plausible explanation for the observed territory distribution. Similar results have been obtained for other woodland species (Yapp 1962).

Pairs breeding in hot spots were more successful than those breeding in sparse territories, so why did not more pairs establish territories in hot spots as would be expected if birds were distributed in an ideal free manner (Fretwell & Lucas 1970)? Territories were more closely packed in hot spots than elsewhere (Fig. 1), and Chamberlain *et al.* (1996)

showed that artificial nests placed at twice the usual hot-spot density tended to be preyed upon at a higher rate than medium-density nests (as found on hot spots), while average-density nests were preyed upon at a lower rate. Therefore, if high-density breeding carries costs, a lower limit might be set to territory size, with behaviour by territory holders preventing further settlement. Despite the plastic nature of territories and the potential for high territory density in hot spots (e.g. 1993), poor-quality habitat was occupied even when there was a relatively low population in hot spots (e.g. 1991). Urban Blackbirds move territory (even when this entails divorce) to increase their breeding success (Desrochers & Magrath 1993), but the costs of forcing a vacancy in occupied habitat may limit movement into optimal habitat.

If territoriality constrained an individual's ability to acquire a good territory, then hot-spot territory holders should have a higher competitive ability than sparse territory holders. Blackbirds exhibit age-related foraging ability and breeding success (Desrochers 1992a, b), so age might reflect competitive ability. Over 3 years, fewer yearling males held hot-spot territories (6%, $n$ = 66) than held sparse territories (17%, $n$ = 69; $G_1$ = 4.33, $P$ < 0.05), but female age structure did not differ between habitats (hot spot 25%, $n$ = 69; sparse 16%, $n$ = 62; $G_1$ = 1.46, n.s.). This suggests that males in hot spots had higher competitive ability than those in sparse territories.

Territory and individual effects are confounded if male age structure varies with habitat and if reproductive success is age-related (Desrochers 1992a, b). Nest predation was the primary cause of breeding failure, but nest-site selection is primarily done by females (Snow 1958), and female age structure did not differ between habitats. Males may play a role in reducing nest predation (A. Desrochers & R.D. Magrath pers. comm.), so the possibility of male effects on reproductive success cannot be excluded.

The main cause of reproductive failure was predation. High rates of predation in sparse territories may have been due to high predator densities, but potential predators were present throughout the area, and a positive association between predator and prey densities is more likely. Predation is also the primary cause of breeding failure in urban Blackbirds (Osborne & Osborne 1980), and cover has a similar effect on reproductive success. The effect of nest exposure on hatching success but not fledging success could result from variation in the process of predation. During egg-laying and incubation, predators are likely to find nests by searching or by accident, and in both cases the probability of discovery will be a function of nest conspicuousness (i.e. exposure). During the nestling period, further cues are available to predators, including begging calls and increased parental activity. Neither of these cues are likely to be a function of nest conspicuousness, so predation at this stage may be relatively indiscriminate with respect to nest characteristics.

What do the results tell us about the function of Blackbird territories? Lack (1968) noted the selective advantage of widely spaced nests for reducing predation, and two results

suggest that this is an important function. First, spacing of nests reduces the predation rate (Chamberlain *et al.* 1996), and, second, the importance of habitat structure and nest-site selection in reducing predation means that cover represents a valuable resource to be defended. By contrast, food supplies on territories are probably unimportant because much foraging occurs off territory, particularly during the nestling phase, and food supplementation experiments do not result in higher breeding densities (A. Desrochers pers. comm., B. J. Hatchwell & D. E. Chamberlain unpubl.).

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