EFFECTS OF AGE, SEX, AND BREEDING SUCCESS ON SITE FIDELITY OF GRAY CATBIRDS

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INTRODUCTION

In a study of territorialism of Gray Catbirds (*Dumetella carolinensis*) we observed some returns of our color-banded catbirds (Darley et al., 1971). The degree to which birds returned to their former territories varied greatly. This paper considers three variables (age, sex, and breeding success in the preceding year) that might influence variability in site fidelity.

METHODS

The study was made between 1963 and 1966 on the campus of the University of Western Ontario, London, Ontario. Darley et al. (1971) presented details of banding procedures and of the delineation of territories in 1963 and 1964. Territories were less accurately defined in 1965 and 1966. In 1965, we visited territories only to determine if a pair remained throughout the breeding season and if it was successful (i.e. produced at least one fledgling). In May and June 1966, we searched the study area for color-banded catbirds but did not study territories of unbanded pairs.

We assigned each returning bird to one of three categories of territories: same, adjacent, or elsewhere. First, a bird could occupy essentially the same territory in successive years. Second, a bird could occupy a territory adjacent to and usually abutting that held in the preceding year. In occupying an adjacent territory the returning bird replaced one that had previously occupied this territory. In turn, the returning bird was itself replaced on its former territory by another bird. Where suitable habitat was discontinuous, e.g. on opposite sides of the river that flows through the campus, territories unseparated by intervening territories were regarded as being adjacent. One successful male in 1963 was not found in 1964 but occupied in 1965 a territory adjacent to his 1963 territory. We have assumed that in 1964 this bird occupied another territory adjacent to the 1963 territory but in a habitat around some houses, just outside the study area, which we did not inspect. Finally, some birds returned and occupied territories clearly separated by intervening territories from those previously held; we designate such territories as being "elsewhere." The recorded distances separating "elsewhere" territories from the preceding ones ranged from 100 m to 1000 m. The actual territories of three males and two females assigned to this category were not found. Two males were each seen only once, in May, each about 450 m distant from his former territory. Another male seen once in May near a territory that he had deserted in the preceding year was found a month later about 1,000 m from his former territory. A female was seen once in May near her previous territory which already had a nesting pair. We assume that these four birds lived outside the study area. The other female, which occupied a known

territory in 1964, was not seen in 1965 but returned in 1966 to nest about 700 m from her 1964 territory. We have assumed that in 1965 she was elsewhere, not adjacent to her 1964 territory.

Because age might influence return to a particular territory, we separated returns of birds, present at the end of the breeding season, and that had been banded for at least two years, from returns of birds that were first banded in the year preceding their return. In Table 1 we designate these two groups as old and young. Most birds new to the study area were likely entering their first breeding season but some may have previously bred in earlier years outside the study area.

TABLE 1.

Location of territories of returning catbirds in year following banding (young) and in second or third year following banding (old).

Breeding history	Territory in year of return			No return
	Same	Adjacent	Elsewhere	
Males				
Old successful	8	1	1	7
Young successful	6	1	2	3
Old unsuccessful	1	2	1	4
Young successful	1	0	0	7
Females				
Old successful	1	2	1	6
Young successful	3	1	5	10
Old unsuccessful	0	0	2	2
Young unsuccessful	0	2	1	6

The members of the catbird population and their distribution in the study area changed between May when breeding begins and July towards the end of the breeding season. Darley et al. (1971) showed that some of the first settlers deserted their territories, usually after a nesting failure. Some of these deserters relocated in the study area whereas others probably resettled outside it. Apparent newcomers (perhaps present earlier but undetected) established territories in the study area throughout June so that the known population each year was about the same size at the end as at the beginning of nesting.

A factor, such as unsuccessful reproduction, that might influence site fidelity between successive years could operate early or late in the breeding season. To determine to what extent events occurring relatively early as opposed to those occurring late in the breeding season influence site fidelity we analysed returns of two groups of birds. The first group (Table 2) comprises birds that established their first territory within the study area. The second group (Table 3) comprises birds that were still present at the end of the breeding season. It includes those members of the first group that were

faithful to their territory throughout the breeding season plus those of the first group that moved to other territories in the study area and some birds that apparently moved into the study area in late May or early June.

The analysis is based on returns from 51 males and 58 females whose reproductive success was known. Three females and two males that died during the breeding season are excluded. Seventeen males returned only once, 7 twice, and 1 three times; 18 females returned only once and 6 twice. As shown later, age did not apparently influence the likelihood of return. Accordingly, each return of a bird has been treated independently.

For statistical analyses, unless otherwise specified, we used Fisher's two-tailed exact test (Sokal and Rohlf, 1969: 593).

Tables 2 and 3 show the numbers of returns for four main categories of birds: reproductively successful and unsuccessful males and females. The recorded values may be biased in two ways.

TABLE 2.

Location of returning catbirds relative to first territory held in preceding year.

Sex, success, and territorial fidelity in preceding year	Territory upon return			No return
	Same	Adjacent	Elsewhere	
Males				
Successful and faithful	15	1	3	9
Unsuccessful and faithful	2	1	1	10
Unsuccessful and deserted	0	3	3	8
Females				
Successful and faithful	6	3	3	15
Unsuccessful and faithful	0	1	1	7
Unsuccessful and deserted	0	3	4	7

First, some birds may have returned to sites outside the study area. Second, we may have failed to find some birds that returned to the study area.

The frequencies of returns of birds present at the end of the preceding breeding season ranged from a high of $25/39 = 0.64$ for successful males to a low of $7/20 = 0.35$ for unsuccessful males and females (Table 3). This variation suggests that the probability of return to the study area or nearby was not independent of sex or reproductive success (2×4 G-test of independence with 3 d.f., $G = 6.820 > \chi^2\ 0.1 = 6.251$, Sokal and Rohlf (1969: 599)). If chance is excluded, the differences in the observed frequencies of return mean either that the annual survival rate of successful males was actually greater than that for the other catbirds or that we found fewer females and unsuccessful males because some returned to locations outside the study area. The latter explanation seems more likely because the observed survival rate of 0.42 (34/82) of females and unsuccessful males is much less that that recorded for adults of several passerine species (Perrins, 1971; Roberts, 1971;

TABLE 3.

Location of returning catbirds relative to last territory held in preceding year.

Sex and success in preceding year	Territory upon return			No return
	Same	Adjacent	Elsewhere	
Males				
Successful	19	3	3	14
Unsuccessful	4	2	1	13
Females				
Successful	6	5	9	27
Unsuccessful	0	3	4	13

Savidge and Davis, 1974). On the other hand, the observed survival rate of 0.64 for successful males is so close to the upper survival estimates stated in the above references that we must have found almost all surviving successful males. If this interpretation of the variation in the frequencies of returns is correct, then the numerical distribution of returns assigned to the three categories of territories in Tables 1, 2, and 3 must be biased. If all surviving birds had been located, the number of birds recorded in the "elsewhere" category of territories would have relatively increased, especially for females.

Our search for banded birds was thorough in 1964 and 1965 and it seems unlikely that we failed to find any returns that had their first territories in the study area in those years. In 1966, our search was less intensive and, judged on the number of birds present in previous years, we found only about 70% of the birds that nested in the study area. Thus we could have missed some returned birds, particularly females because they are less conspicuous than males. Consequently the observed rates of return are possibly slightly biased in favor of males. There should, however, be no bias in favor of either reproductively successful or unsuccessful, because reproductive status in the preceding year should not have influenced the chance of finding a bird if it had returned to the study area.

RESULTS

There is no evidence that age was important in determining return to the study area (Table 1). For example, old successful males returned less frequently than young successful males (10 returns:7 no returns for old males vs 9 returns:3 no returns for young males) but old unsuccessful males returned more frequently than young unsuccessful males (4:4 vs 1:7). No difference between age-groups within either sex is statistically significant.

Successful birds returned more frequently than did unsuccessful birds (Table 3). The difference between the two groups of males is close to significance at the 0.05 level (25:14 vs 7:13; $P = 0.064$) but that for females is clearly not significant (20:27 vs 7:13; $P = 0.76$). If the sexes are combined the difference between successful

and unsuccessful birds is also close to significance (45:36 vs 14:26; $P = 0.052$).

Although proportionately more successful than unsuccessful returning birds of each sex reoccupied the same territory, the differences between the proportions were not significant (males, 19:6 vs 4:3; $P = 0.59$; females, 6:14 vs 0:7; $P = 0.26$).

Nest failure early in the breeding season is sometimes followed by desertion of the first territory (Darley et al., 1971). No bird that deserted a first territory returned to it the following year (Table 2). In this respect, such birds differed from those that were successful on their first territory (males, 0:6 vs 15:4; $P = 0.0024$; females, 0:7 vs 6:6; $P = 0.068$).

Thus the likelihood of a bird returning to its former territory seems to be clearly influenced by lack of reproductive success only when it has led to desertion of a territory early in the breeding season.

Males, successful or unsuccessful, showed greater site fidelity than corresponding females. More returning successful males than successful females returned to their first territory but the difference is not significant (Table 2, 15:4 vs 6:6; $P = 0.200$). However, the difference in fidelity to the last territory of the year is significant (Table 3, 19:6 vs 6:14, $P = 0.0049$). It may be noteworthy that those females that apparently arrived late on territories and were successful showed little site fidelity to the last territory occupied. None of 8 such females (difference between distributions of female returns in Tables 2 and 3) returned to the territory where she had been successful. This contrasts strikingly with the behavior of females successful on their first territories; the difference in site fidelity between these two groups is significant (6:6 vs 0:8, $P = .048$). On the other hand there was no significant difference between males successful on first territories and males that arrived late and were successful (15:4 vs 4:2, $P = 0.91$). None of 7 unsuccessful females returned to the last territory but 4 of 7 unsuccessful males did so (0:7 vs 4:3, $P = 0.069$).

Mate fidelity from one year to the next was not great. We found both members of only 12 of the 56 pairs that had been present at the end of the previous breeding season. The same birds mated again in four cases; in each case the pair had been successful and reoccupied the same territory. Six males but no females of the remaining eight former pairs returned to the same territory.

DISCUSSION

Our data indicate that site fidelity in the Gray Catbird is strongly influenced by sex, slightly by reproductive success, and apparently not at all by age and thus agree with reports on site fidelity in other passerines.

Many studies have shown that male passerines have much greater site fidelity than females (Nice, 1937; Mayfield, 1960; Delius, 1965; Nolan, 1966; Berndt and Sternberg, 1969). Site fidelity is so strongly developed in the males of so many passerines that reoccupation of a familiar territory must be advantageous. It is not

clear, however, why site fidelity should not be equally well-developed in females as presumably it would also be advantageous to them.

Only six females returned to their previous territories. Four remated with their mates of the previous year but we are uncertain about the identity of the mates of the remaining two. Thus, as Delius (1965) noted in Skylarks (*Alauda arvensis*), there is some evidence that site fidelity in females is associated with mate fidelity. That is, if the male has not returned to his territory the female is unlikely to do so. Old male catbirds return first in the spring followed shortly by old females and unbanded males (yearlings?) and finally by unbanded females (Darley et al., 1971). If the former mate of a female is dead, then his former territory is likely to be still unoccupied by a male when she returns. She must then pair with any unpaired male that is back and this will usually involve a shift to another territory. Consequently old females usually mate with old males (17 of 21 old females mated with known old males). Furthermore strong female site fidelity requires that a returning male defer pairing until his former mate returned. Unless the advantages of mate fidelity are very great, such male behavior seems unlikely. Also, because of variation in time of return, a female may return to a territory occupied by another old female, which has paired with the former mate of the first female.

Other studies have shown that reproductive success increases the likelihood of return to the breeding site (von Haartman, 1949; Richdale, 1957; Delius, 1965; Nolan, 1966; Doty and Lee, 1974). Usually there is insufficient information to ascertain the proximate cause of such site fidelity. Delius (1965) thought that differences in breeding success influenced mate fidelity of Skylarks. He showed that mate fidelity was strongly associated with site fidelity and hence the most successful birds tended to return to their former territories. Our data that the only pairs that remated had been previously successful and returned to the same territory suggest that in the Gray Catbirds mate fidelity, site fidelity, and breeding success may be similarly interrelated. Nolan (1966) showed clearly that female Prairie Warblers (*Dendroica discolor*) that had produced fledglings returned significantly more often to their former territories than unsuccessful females. He argued that females remained with their young near the breeding site until they began to molt, whereas unsuccessful females were free to drift away. Regrettably, we lack detailed information on postbreeding movements of catbirds and consequently are unable to test Nolan's hypothesis. There was a significant difference between the strong site fidelity shown by females successful on their first territory and the absence of site fidelity of successful females that appeared late in the study area. This suggests that the length of time spent on a particular territory may influence site fidelity.

Little is known about the effect of age on site fidelity in passerines. We found no evidence of an effect in Gray Catbirds, nor did Delius (1965) in Skylarks or Nolan (1966) in Prairie Warblers. However, von Haartman (1949) showed that site fidelity of both male and female Pied Flycatchers (*Ficedula hypoleuca*) increased with age, as it does in some nonpasserines (Austin, 1949; Richdale, 1957).

Unfortunately it is difficult to obtain samples of passerines, which generally are shorter lived than nonpasserines, large enough to permit analysis of the effects of age.

SUMMARY

The returns from 51 male and 58 female Gray Catbirds, color-banded as breeding adults, are analysed in relation to sex, age, previous reproductive success, and degree of fidelity to the territory occupied in the year preceding return.

Age apparently did not influence the probability of return to the breeding area. Successful reproducers (sexes combined) returned in proportionately greater numbers to the study area than did unsuccessful birds and showed slightly stronger site fidelity. Males showed stronger site fidelity than females.

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