Philopatry and Correlates of Territorial Fidelity In Male Dickcissels

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Abstract.

Although female Dickcissels (*Spiza americana*) are not philopatric, an average of 49% of the males in a population followed for five years returned to the same area in the next subsequent year. Territory fidelity in these philopatric males is related to their previous reproductive success. Males that switched territories the next year had experienced lower degrees of polygyny and defended territories in which fewer nests were built. Although statistical significance was not demonstrated, males that did not change their territory the next year had produced more young than males that did change. Males that switched territories the next year also spent a significantly shorter length of time on territory the previous year compared to males that exhibited territory fidelity.

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Differences in the degree of philopatry to a particular area, as well as fidelity to a specific territory location, between reproductively successful and unsuccessful birds have been documented in some species (Doty and Lee 1974, Darley, et al. 1977, Newton and Marquiss 1982, Oring and Lank 1982, Shields 1984, Blancher and Robertson 1985, Petersen and Best 1987); however, such differential responses related to reproductive success do not occur in all species (Delvius 1965, Bedard and LaPointe 1984, Gratto, Morrison and Cooke 1985, Wiens and Cuthbert 1988). It may be that in some monogamous species like the Field Sparrow (Spizella *pusila*) (Best 1977), there is so little difference in the distribution of resources among territories (as should be expected, see Emlen and Oring 1977) that the benefit gained by switching to another location is not greater than the loss suffered by moving into an unfamiliar area. Furthermore, switching may not occur if the cost to preempt the resident of a higher quality territory is great (Lanyon and Thompson 1986). Alternately, if the habitat is so unstable temporally (e.g., in early successional communities), territory switching cannot be assured to result in a territory of a quality high enough to increase success the following year (Oring 1982).

The Dickcissel (*Spiza americana*) is a successional species, reaching its highest densities in mid-seral oldfield communities (Zimmerman 1971). The oldfield habitat is spatially heterogeneous, and the territorial system of the Dickcissel

results in significant differences in the quality of the territories among the males in a population (Zimmerman 1971). Indeed, males with the lowest quality territories may remain bachelors (Zimmerman 1966). Oldfield habitat heterogeneity is reflected in higher levels of polygyny and increased numbers of young fledged per male compared to the degree of polygyny and productivity in populations resident in less suitable, more homogeneous habitats, like prairie (Zimmerman 1982). Dickcissels provide a clear example of the value of polygyny in environments where resources for breeding are unevenly distributed among the territories of the males (Oring 1982). Since territory quality is so important in determining a male's reproductive success, males should demonstrate philopatry on the breeding range (Greenwood 1980) with a large proportion of the birds, even unsuccessful males, returning to the same habitat where success is potentially possible (Catchpole 1972). Gavin and Bollinger (1988) have demonstrated that philopatry in the ecologically similar Bobolink (Dolichonyx oryzivorous) is positively related to nesting success, but they did not investigate the relationship between success and territory fidelity.

In addition to being philopatric, successful males also should show a high level of site fidelity, that is, they should return to the same territory on which they were productive the previous year. Unsuccessful males should not demonstrate the same degree of site fidelity. Indeed, one should expect an unsuccessful male to switch territories the next year (Brooke 1979), even while remaining philopatric.

In this study we demonstrate the degree of philopatry in this seral species, assuming that if males are philopatric succession does not change the quality of the habitat significantly from one year to the next. Using the subset of philopatric males, we test the hypothesis that male Dickcissels that switch territories the next year have had significantly lower productivity the previous year compared to males that are faithful to the same territory the following year.

Methods

This analysis is based on a color-marked population that was followed from 1965 through 1969 in a 128 acre (52 ha) tract located in Riley Co., Kansas, that was 60% covered with brome grass and sweet clover with extensive stands of sun-

flowers and giant ragweed in damper areas, 25% covered by wheat stubble, sweet clover, and annual forbs, and 15% covered by mixed perennial grasses. Male territories were delineated by repeatedly flushing the male from his song perches, and mapping of territories was completed each week throughout the nesting season. Females were also counted weekly, and the number of females resident in a particular male's territory was based upon the number of active nests plus any females he was actively courting during that week and for which copulation was observed. Mean male density mid-June in these years was 34 males/40 ha and each male was simultaneously mated in June to an average of 1.1 females. Considering the range of habitats occupied in Kansas by Dickcissels, this site is of moderate quality (Zimmerman 1971). Males were considered philopatric if they returned to the study area or were discovered in the immediate vicinity in the next year. Males were considered to demonstrate territory fidelity if their territory in a subsequent year overlapped any part of their territory of the previous year. Hence philopatric males were scored as switching if their next year's territory was spatially exclusive of last year's territory. A variety of measures of reproductive success (see Table 2) was used to test the hypothesis. The mean number of females is the average number of the females/week in a male's territory during all the weeks the territory was extant, while the maximum number of females is the mean of the highest number of females observed on each territory during those weeks. The number of nests is the mean of the total nests built on males' territories during the season. Young produced is the average total number of both Dickcissels and cowbirds (Molothrus ater) fledged per season in each territory. Schartz and Zimmerman (1971) demonstrated that the amount of time a male spends off his territory each day is inversely related to his degree of polygyny. It was suggested that the male left to search for more suitable sites for territory establishment. Thus a comparison was also made between males on the length of territory maintenance. It is hypothesized that males demonstrating territory fidelity would have maintained their territory for a longer period the previous year than males that switched in the next year. Data for males returning for the next subsequent year were combined for all four years, regardless of year and how many times he had previously returned. Comparisons of means was done with Student's t-tests.

Results and Discussion

Over four years of return data, an average of 49% of the banded territorial males returned the next year (Table 1). This degree of philoptary is similar to other oldfield, grassland, and rangeland birds (Best 1977, Bedard and LaPointe 1984, Blancher and Robertson 1985, Petersen and Best 1987). Over this entire four year period, an average of 69% of these philopatric males switched territories the next year. The results of testing the hypothesis that males switching territories have lower reproductive success is presented in Table 2. If the hypothesis is valid, then the value for each of these variables would be significantly greater for males that did not change compared to males that did switch. This prediction is supported for all variables except the total young produced per male. While the difference in the number of young produced is in the expected direction, 0.4 young/male for switchers vs. 2 young/male for males that did not change territories, the numerous zeros in the data (poor nesting success) make demonstrating statistical significance difficult. A comparison of the proportion of territories producing young, 0.29 for switchers vs. 0.50 for males that did not change, using the Fisher Exact Test also did not indicate a significant difference.

The comparison between males on the length of territory maintenance showed the expected difference. The mean weeks in residence (\pm S.E.) for males that changed territories ($x = 7.50 \pm 0.84$, n = 8) was significantly less than that for males that did not switch ($x = 10.3 \pm 0.67$, n = 10) (Student's t = 2.64, df = 16, P < 0.01). Since those males that switched territories were less successful in attracting mates, it is not surprising that territory tenacity was lower (see Schartz and Zimmerman 1971).

It is not clear how males assess suitability of a territory and how well they do when changing to a new territory for a subsequent year. When these same measures of reproductive success were compared between old territories and the new territories of males that switched, the means were greater for the new territory, but the increase was not significant. As Petersen and Best (1987) caution, however, patterns between years may be confounded by increasing reproductive success with age (see Middleton 1979).

Male Dickcissels are philopatric even though their preferred habitat is in a seral community. Furthermore, their fidelity to the territory of the previous year is related to the magnitude of their success in attracting females and perhaps to their production of young. Males that are not as successful have a higher probability of switching territories than males that are more successful. Unlike the pattern in Bobolinks (Gavin and Bollinger 1988), we have obtained no returns that demonstrate philopatry in females in all the years of banding Dickcissels, not only at this site, but in more mature oldfields as well as tallgrass prairie. This is perhaps not surprising, since nesting success for females is not habitat dependent; they do just as well in preferred or less-preferred habitats, success being more dependent on the highly localized quality of the nest site (Zimmerman 1982).

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Table 1. Returns of Banded Territorial Males.

	Total	% Returned	% of Returned
Year	Banded	The Next Year	Males Territory Faithful
1965	12		
1966	15	58	29
1967	23	53	25
1968	18	35	50
1969	14	50	22
Mean		49	32

Table 2. Mean measures of reproductive success (+ s.e.) for males that switched territories and males that did not change territories.

	Switched	No Change	P(1-tailed)
Mean Females Per Week	0.75 + 0.21	1.52 + 0.25	< 0.025
Max. Females Per Week	1.88 + 0.21	3.40 + 0.58	< 0.05
No. of Nests	2.00 + 0.49	4.80 + 0.89	< 0.025
Young Produced ¹	0.43 + 0.30	2.00 + 0.77	>0.05
n	8 ²	10	

¹ Includes both Dickcissel and cowbird (*Molothrus ater*) young. ² For "no. of nests" and "young produced". n = 7.