

SITE FIDELITY AND HABITAT QUALITY AS DETERMINANTS OF SETTLEMENT PATTERN IN MALE PAINTED BUNTINGS¹

SCOTT M. LANYON²

Museum of Zoology and Department of Zoology and Physiology, Louisiana State University,
Baton Rouge, LA 70803

CHARLES F. THOMPSON

Department of Biological Sciences, Illinois State University, Normal, IL 61761

Abstract. The spatial distribution of high and low quality Painted Bunting (*Passerina ciris*) territories on St. Catherines Island, Georgia, was determined through an examination of the distribution of food resources and polygynous pairings in 1976 and 1977. Based on the distribution of high and low quality territories, we predicted the pattern of territory settlement by males at the start of the breeding season. As predicted, males settled significantly earlier on high quality than on low quality territories in 1978 and 1979. However, not all males that initially acquired high quality territories were able to maintain them long enough to breed on them. Most of these males, which were subsequently displaced by returning site-faithful males, were settling for the first time on the study area, although some were returning males that had held low quality territories the previous year. New breeders and some returners initially settled in a pattern consistent with predictions based on territory quality; most returning males settled on the basis of site fidelity. Thus, the final settlement pattern was the result of an interaction between preference for areas of high quality and the return and site faithfulness of previous territory holders. The implications of this pattern of territory acquisition for the evolution of delayed maturation in males are discussed.

Key words: Site fidelity; Painted Bunting; *Passerina ciris*; territory establishment.

INTRODUCTION

Many bird species actively choose habitats during the breeding season. However, even among acceptable habitats, quality varies (Hildén 1965, Brown 1969, Fretwell 1972). Consequently, natural selection should favor those individuals that can recognize appropriate habitat and those that accurately assess the relative quality of acceptable areas. This is implicit in hypotheses concerning the evolution of polygynous mating systems (Verner and Willson 1966, Orians 1969).

Variability in territory quality, as well as the ability to assess it, has been hypothesized to be a driving force behind the evolution of polygyny (Orians 1969). As a partial test of this hypothesis, the ability of individuals to discriminate among territories of different quality has been studied for some migratory polygynous species: Indigo Buntings, *Passerina cyanea* (Carey and Nolan 1979), Pied Flycatchers, *Ficedula hypoleuca* (Alatalo et al. 1984), and Lark Buntings, *Calamospiza melanocorys* (Pleszcynska 1978). In these species early arriving males settled on territories that were considered to be of highest quality. Later arriving males, although expected to obtain territories of lower quality, should attempt to

evict territorial males from high quality areas if eviction or compression of existing territories are possible outcomes. In addition to a predictable temporal pattern of territory establishment, higher levels of aggression may be expected on good breeding areas as compared with low quality areas.

An additional factor that may affect settlement patterns is site fidelity. Returning to the same area to breed each year could be advantageous if familiarity with an area improves an individual's foraging efficiency or ability to avoid predators, as suggested by Hinde (1956). In this study we investigated the effect of territory quality and site fidelity on the settlement pattern of male Painted Buntings (*P. ciris*). Estimates of territory quality were based on the spatial distribution of both food and polygynous matings in the two breeding seasons preceding this study.

STUDY AREA AND METHODS

This study was conducted during the spring and summer of 1978 and 1979 on St. Catherines Island, a 5,600-ha barrier island located 50 km south of Savannah, Georgia. The study area consisted of 90 ha of mixed pine (*Pinus* spp.) and oak (*Quercus* spp.) bordered by extensive salt marsh dominated by cord grasses (*Spartina* spp.). Starting in 1976 and continuing through 1979, all but one of the males breeding on the study area were mist-netted and given unique color-band combinations. A 20 × 20 m grid system of labeled stakes was

¹ Received 1 April 1985. Final acceptance 21 October 1985.

² Present address: Division of Birds, Field Museum of Natural History, Roosevelt Rd. at Lake Shore Drive, Chicago, IL 60605.

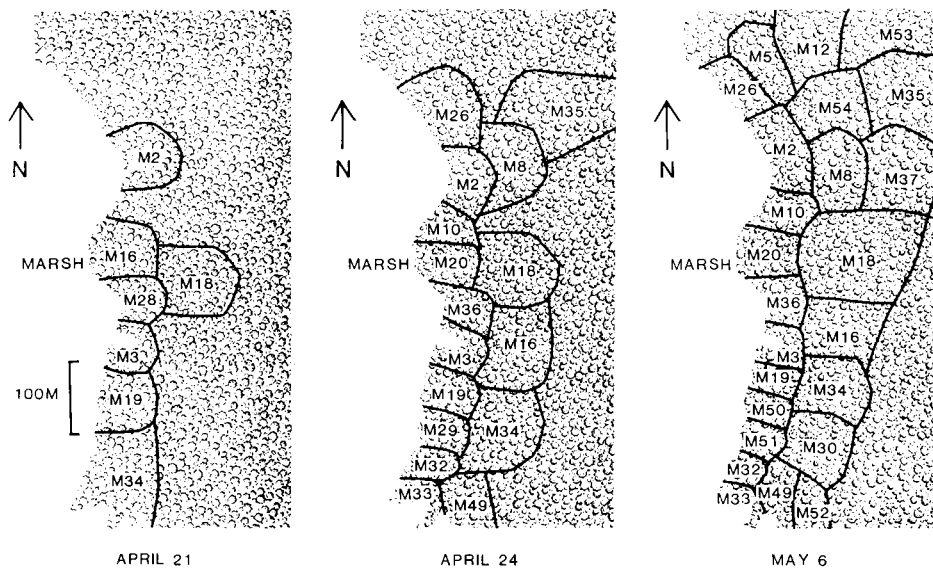


FIGURE 1. Distribution of territorial male Painted Buntings on the St. Catherines Island study area at three times during the settlement of breeding territories in 1978. Territorial boundaries are approximations only and are included to illustrate territorial shifts during the first few weeks of the breeding season. Codes (e.g., M2) identify each territorial male.

set up on the study area in 1977 to facilitate the mapping of territories.

Male Painted Buntings established territories either completely in the forest (interior territories) or on the forest edge, in which case they bordered on salt marsh (edge territories; Fig. 1). In 1976 and 1977 food supplies of males holding edge territories were significantly greater than those for males with interior territories because of the abundant and easily harvested marsh grasshoppers available in the adjacent salt marsh (Thompson, unpubl.). Eight of nine cases of polygyny during 1976 through 1977 occurred in edge territories. Because edge territories had both greater food supplies and a preponderance of polygynously mated males compared with interior territories, they were considered to be of high quality; interior territories were considered low quality.

Over 1,200 hr of observation were made in 1978 and 1979 between mid-April, when the first breeding males arrived, and mid-July. During this time the entire study area was walked several times each day, and all singing males were identified to ensure that any newly arriving males were seen. For each observation of an individual, its location and activity were noted until it was lost from sight. An attempt was made to observe each individual every day in order to determine the date of first pairing. Two age classes of male Painted Buntings could be distinguished in the field: brightly plumaged adults (two or more years old), and greenish female-like plumaged yearlings (Dwight 1900).

To eliminate any bias caused by differences in length of residency, only observations obtained after the last male had arrived were used when comparing levels of aggression. We assumed that all newly arriving males sang on the day they returned, and we defined the date of first observation as the date of arrival. This seems likely as 94% (46 of 49) of the males were seen singing on the same day as they were first observed.

RESULTS

ADULT MALE AGGRESSION

We compared the number of observations of agonistic encounters between interior males and edge males (i.e., agonistic displays, displacements, chases, and fighting; Lanyon and Thompson 1984). Only data from adult males were used because yearling males, which frequently do not breed, are likely to react differently in aggressive situations. Edge males were involved in significantly more aggressive encounters with other males in both 1978 ($U = 77$; $df = 10,8$; $P < 0.001$) and 1979 ($U = 33$; $df = 8,5$; $P < 0.05$; Table 1).

This analysis might not accurately reflect the actual frequency of interactions because edge males were observed significantly more often than interior males in both 1978 ($U = 72$; $df = 10,8$; $P < 0.005$) and 1979 ($U = 32$; $df = 8,5$; $P = 0.05$). The data were therefore re-analyzed by comparing the proportions of observations of aggression and nonaggression (Table 1). Edge males were involved in a greater proportion

TABLE 1. Adult male-male aggressive interactions as a function of territory location.^a

	1978		1979	
	Interior	Edge	Interior	Edge
No. males	8	10	8	5
No. (%) observations of aggression	43 (10.9)	180 (17.3)	48 (11.6)	83 (15.4)
Total no. of observations	395	1,042	434	539

^a Data are observations made after the arrival of the last male and include only those males for which ten or more observations were made.

of aggressive encounters than were interior males in 1978 ($\chi^2 = 6.28$, $df = 1$, $P < 0.025$) but not in 1979 ($\chi^2 = 2.66$, $df = 1$, $P > 0.05$).

MALE SITE SELECTION

In 1978, males settling initially on edge territories arrived significantly earlier (\bar{x} arrival date = 20 April) than those on interior territories ($\bar{x} = 23$ April; $U = 110.5$; $df = 16,9$; $P < 0.025$; Fig. 2). Four males that held interior territories in 1977 initially settled on the edge in 1978. Three of these subsequently moved to the interior territory they occupied the previous year when the resident from the previous year returned (e.g., M16 and M34, Fig. 1); the remaining male (M20) continued to hold an edge territory throughout 1978 when the resident from the previous year did not return. Seven additional interior males returning from 1977 settled first on interior territories and all nine edge males returning from 1977 settled first on edge territories.

In 1979, edge territories again were settled significantly earlier ($\bar{x} = 18$ April) than interior territories ($\bar{x} = 22$ April; $U = 111.5$; $df = 15,9$; $P < 0.005$; Fig. 2). However, there was much less temporal overlap in settlement of edge and interior sites than in 1978 (Fig. 2). The late settlement of two yearling males on the edge on 7 May caused most of this overlap. Two interior males from the previous year first tried to acquire edge territories, but both returned to their interior territory of 1978 upon the return of the residents from the previous year. Eight additional returning interior and all three returning edge males regained the territories they had occupied in 1978.

EFFECT OF SITE FIDELITY ON FINAL SETTLEMENT

The relative importance of arrival date and site fidelity on the quality of territories acquired by males can be determined from partial life histories of marked individuals. Of 25 breeding males in 1978, 19 (76%) bred where they had the previous year. Of the remaining six, one was an adult-plumaged male, about which we had no prior information; four were yearling males; and one was the male noted earlier (M20) that successfully moved from the interior to an adjacent edge territory. Thus, only

one of 20 returning males occupied a territory different from that held the previous year.

Of 24 breeding males in 1979, 12 (50%) settled where they had the previous year. Of the remaining 12 males, one was a two-year-old that moved from one interior territory to another; two were adult-plumaged males about which we had no prior information; and nine were yearlings. Thus, most returning males (12 of 13) ultimately occupied the same territories as they had in previous years. To determine the influence of site quality on settlement patterns, we investigated settlement of those males that have no known prior experience on the study area. Of five new males arriving in 1978, the first three settled on the edge and the last two in the interior. There was more overlap in the settlement of edge and interior territories by new males in 1979, and their arrival dates are not significantly different ($U = 22$; $df = 7,4$; $P = 0.1$).

EFFECT OF AGE ON SETTLEMENT

Yearling males arrived significantly later in 1978 than adult males ($\bar{x} = 9.5$ days later, $U = 77.5$; $df = 22,4$; $P < 0.01$), with three of the four arriving after the last adult male. In 1979, all nine yearlings arrived after the last adult male and averaged 17 days later than adults. Because yearlings arrive later than adults and because most edge territories are filled when yearlings arrive, if yearlings are to breed most would have to settle on low quality interior territories. Thirteen of 16 (81%) territorial yearling males over the course of this study settled in the interior. The three males that bred on the edge fitted between existing territories. This was apparently accomplished through reduction in size of the previously settled territories, as all of the edge habitat seemed to be defended prior to the arrival of the first yearling males.

Two-year-old males arrive at approximately the same time as older adults, thus they should be more likely than yearlings to acquire high-quality edge territories. A significantly higher proportion of new, adult-plumaged males, which we assumed were two-year-olds, acquired edge territories (8 of 9, 89%) than did yearling males (3 of 16, 19%; $\chi^2 = 11.5$, $df = 1$, $P < 0.005$).

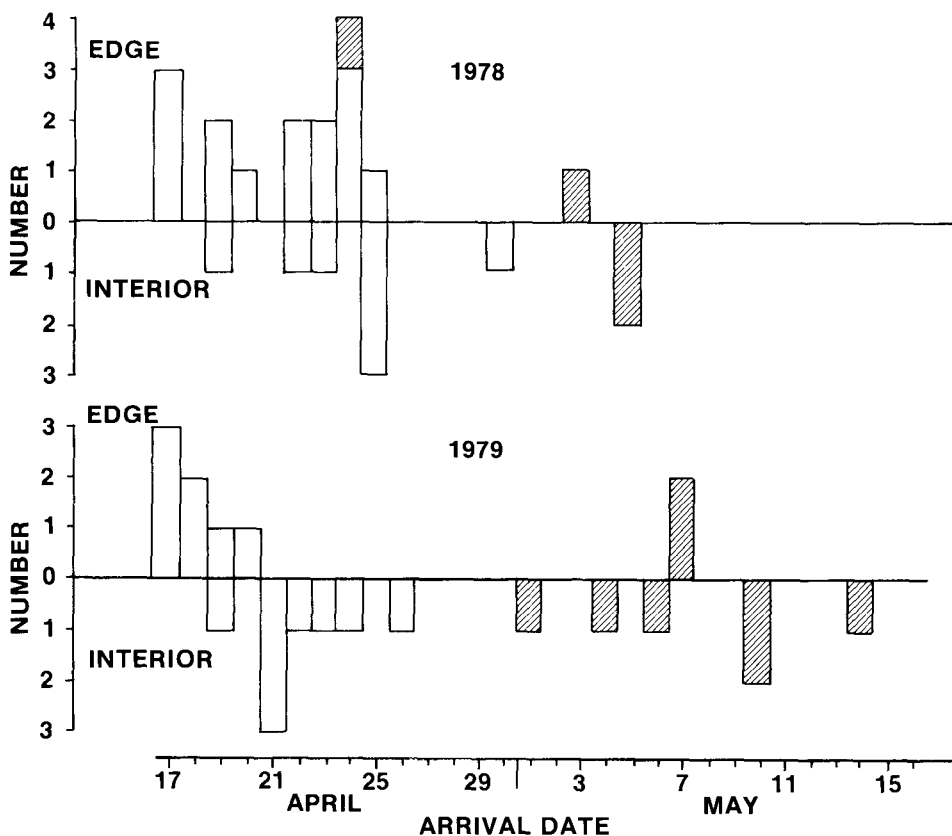


FIGURE 2. Number of male Painted Buntings acquiring edge and interior territories as a function of arrival date. The initial territory for each male was considered to be that territory upon which he was observed singing for a minimum of one day. Open bars denote males two or more years old; hatched bars denote yearling males.

DISCUSSION

Male Painted Buntings settled first in areas considered to be high in quality. Furthermore, the most intense aggression between males occurred in areas of high quality. We conclude, therefore, that the data support the hypothesis that male Painted Buntings prefer and will attempt to settle in high quality areas. This is not to say, however, that males will breed on the highest quality territory available when they return. Much of the final distribution of breeding males is explained by site fidelity of returning individuals. Early arriving males that obtained high quality territories frequently were displaced by a later arriving male that had held the high quality area the previous year. Thus, local variation in habitat quality appears to be important mainly for birds breeding for the first time. Experienced breeders apparently are strongly influenced by the advantages of breeding on a familiar site. Such males, although they may settle initially in high quality areas (e.g., M34 in Fig. 1), rapidly return to the breeding site of the previous year rather than incur the cost of fighting the previous year's resident (e.g., M32 in Fig. 1) for the high qual-

ity area. These observations suggest that males recognized that edge territories were generally higher in quality than interior territories. However, if acquisition of a high quality territory involved aggressive interactions with a returning male, then the retention of a low quality area was the most advantageous strategy.

Nolan (1978:454) presents several cases in which male Prairie Warblers (*Dendroica discolor*) established territories from which they were later evicted by returning former owners. Some previous studies have concluded that site fidelity is unimportant to territory settlement (Best and Rodenhouse 1984), whereas others (Bédard and LaPointe 1984) have concluded that territory acquisition is "influenced primarily by previous occupancy." There is even variation from population to population in terms of the degree of site tenacity (Best and Rodenhouse 1984). In an experimental study of site tenacity, Krebs (1982) temporarily removed resident pairs of Great Tits (*Parus major*), which allowed their vacant territories to be settled by replacements. The probability that the original owners, upon release, would regain their territory was a function of replacement time: 10% after an absence of ten days. As

pointed out by Oring (1982), site tenacity should vary as a function of intra- and inter-annual variation in resources. If individuals are unable to assess territory quality at the time they establish territories, then the advantages of returning to the same site to breed may offset any fitness gain associated with an attempt to acquire a territory of higher quality.

Site fidelity may also be a factor in the evolution of delayed maturation. Although the development of bright nuptial plumage in male Painted Buntings is delayed until the second year (Dwight 1900), some males breed in their first year (Thompson and Lanyon 1979; pers. observ.) Because yearling males arrive one to two weeks later than adults, they tend to acquire poorer territories; birds that wait until their second year to breed arrive with other adults and thereby have the opportunity to acquire higher quality areas. Thus, yearlings that breed gain an initial advantage by entering the breeding population at the earliest possible time (Cole 1954, Stearns 1976), but they experience a reduced probability of acquiring a high quality territory. Most males ultimately continue to breed in future years on the same areas as first occupied. Therefore, not obtaining a high quality territory in its first breeding attempt may result in reduced productivity in all subsequent breeding seasons. Males that delay breeding until their second year experience a delay in producing progeny, but in so doing they may acquire high quality territories.

Site fidelity clearly plays an important role in determining the dispersion of breeding birds among habitats. Individuals breeding in low quality habitats may have attempted to settle initially in high quality areas but were ousted by former residents, or they may have settled an area they had occupied in previous seasons. Thus, the final settlement pattern is, in part, the outcome of trade-offs between (1) the advantages associated with obtaining a high quality territory and the costs of defending it against a site-faithful resident, and (2) the advantages associated with being site faithful and the cost of occupying a low quality territory.

ACKNOWLEDGMENTS

This research was funded by NSF grant DEB77-07246 and by grants from the St. Catherines Island Research Program of the American Museum of Natural History,

supported by the Edward J. Nobel Foundation. The Department of Biology, State University of New York, College at Geneseo provided additional support. We thank M. A. Finke, C. A. Finke, and K. M. Thompson for field assistance. Logistical support on St. Catherines Island was provided by J. T. Woods, island superintendent; R. Hayes; J. Evans; L. Holman; and J. Lukas. A draft of this paper was greatly improved by the comments of J. Picman and an anonymous reviewer.

LITERATURE CITED

- ALATALO, R. V., A. LUNDBERG, AND K. STAHLBRANDT. 1984. Female mate choice in the Pied Flycatcher *Ficedula hypoleuca*. *Behav. Ecol. Sociobiol.* 14:253-261.
- BÉDARD, J., AND G. LAPOINTE. 1984. The Savannah Sparrow territorial system: can habitat features be related to breeding success? *Can. J. Zool.* 62:1819-1828.
- BEST, L. B., AND N. L. RODENHOUSE. 1984. Territory preference of Vesper Sparrows in cropland. *Wilson Bull.* 96:72-82.
- BROWN, J. L. 1969. Territorial behavior and population regulation in birds. A review and re-evaluation. *Wilson Bull.* 81:293-329.
- CAREY, M., AND V. NOLAN, JR. 1979. Population dynamics of Indigo Buntings and the evolution of avian polygyny. *Evolution* 33:1180-1192.
- COLE, L. C. 1954. The population consequences of life history phenomena. *Q. Rev. Biol.* 29:103-137.
- DWIGHT, J., JR. 1900. The sequence of plumages and moults of the passerine birds of New York. *Ann. N. Y. Acad. Sci.* 13:73-360.
- FRETWELL, S. D. 1972. Populations in a seasonal environment. *Monogr. Popul. Biol.* 5. Princeton Univ. Press, Princeton, NJ.
- HILDÉN, O. 1965. Habitat selection in birds: a review. *Ann. Zool. Fenn.* 2:53-75.
- HINDE, R. A. 1956. The biological significance of the territories of birds. *Ibis* 98:340-369.
- KREBS, J. R. 1982. Territorial defence in the Great Tit (*Parus major*): do residents always win? *Behav. Ecol. Sociobiol.* 11:185-194.
- LANYON, S. M., AND C. F. THOMPSON. 1984. Visual displays and their context in the Painted Bunting. *Wilson Bull.* 96:396-407.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithol. Monogr.*, No. 26.
- ORIAN, G. H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.* 103:589-603.
- ORING, L. W. 1982. Avian mating systems, p. 1-92. In D. S. Farner and J. R. King [eds.], *Avian biology*, Vol. 6. Academic Press, New York.
- PLESZCZYNSKA, W. K. 1978. Microgeographic prediction of polygyny in the Lark Bunting. *Science* 201:935-937.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51:3-47.
- THOMPSON, C. F., AND S. M. LANYON. 1979. Reverse mounting in the Painted Bunting. *Auk* 96:417-418.
- VERNER, J., AND M. F. WILLSON. 1966. The influence of habitats on mating systems of North American passerine birds. *Ecology* 47:143-147.