

# FEMALE SITE FIDELITY AND POLYGYNY IN THE BLACKPOLL WARBLER (*DENDROICA STRIATA*)

BONITA C. ELIASON

*James Ford Bell Museum of Natural History, Department of Ecology and Behavioral Biology,  
University of Minnesota, Minneapolis, Minnesota 55455 USA*

**ABSTRACT.**—From 1980 to 1982, 8–30% of male Blackpoll Warblers (*Dendroica striata*) studied on Kent Island, New Brunswick, were bigamous each year ( $\bar{x} = 16.8\%$ ). I tested whether differences in the quality of the breeding situation can give rise to polygynous matings. Five territory parameters and two male parameters were used as measures of quality. Male arrival times were correlated with male mating status and the reproductive success of monogamous females. Territories of bigamous males had more large conifers than did those of monogamous males. Territory parameters did not appear to influence female choices.

Strong site attachment by females may lead them to mate bigamously when few males are available early in the season near the females' former nest sites. The reproductive success of secondary females was not different from that of monogamous females. Any costs of mating bigamously may be offset by increased reproductive success associated with early nest initiation and competitive advantages conferred by site dominance.

Site attachment and return patterns can account for the incidence of polygyny in this population, but probably could not give rise to high levels of polygyny or large harems. More information is needed to evaluate the influence of site fidelity on mating decisions of females in other polygynous passerine species. *Received 5 November 1985, accepted 1 May 1986.*

RESEARCH on the evolution of polygyny in passerine birds has focused on species in which polygyny is common (see Wittenberger 1979, Vehrenkamp and Bradbury 1984 for reviews). Relatively little attention has been directed at understanding the occurrence of polygyny at low levels in primarily monogamous species (Ford 1983). I attempted to identify factors that cause low levels of polygyny in a population of the Blackpoll Warbler (*Dendroica striata*).

Early research on mating systems in territorial passerine birds demonstrated that the number of mates acquired by a male was correlated with the resources he defended. This led to the formulation of the polygyny threshold model, which explains how differences in territory quality can give rise to polygyny in territorial passerine birds (Verner 1964, Verner and Willson 1966, Orians 1969). The model was incorporated into a more general theory on the evolution of mating systems (Emlen and Oring 1977). In the model, female fitness is presumed to be a function of access to resources. Bigamy occurs when differences in territory quality are large enough that a female can have higher fitness if she shares resources on a high-quality territory of a mated male than if she mates monogamously on a low-quality territory.

In the original formulation of the polygyny threshold model, male quality and territory quality were assumed to be highly correlated (Orians 1969). Weatherhead and Robertson (1977, 1979) suggested that when male quality and territory quality are not highly correlated, females might choose mates based on male quality alone. Although the details of their theory have been disputed (Heisler 1981, Searcy and Yasukawa 1981, Wittenberger 1981), their ideas stimulated studies of the role of male characteristics as well as territory parameters in influencing female mate choice.

I evaluated the role of five territory-quality parameters and two male-quality parameters in determining mating status in a population of the Blackpoll Warbler. The mating status of males could be explained by male and territory parameters, but female settling dates could not. The reproductive success of monogamous females was correlated with male arrival dates.

The polygyny threshold model assumes that females are free to mate with any male. This implies that they survey all opportunities available at the time of settling before choosing. In reality, the tendency to return to a familiar site often constrains the choices of both males and females that have bred previously

(Hinde 1956, Greenwood 1980, Oring 1982). Female Blackpoll Warblers tend to breed near their former nest sites. Local sex ratios are sometimes skewed by differential returns of males and females. Given these two factors, the benefits of early nest initiation may cause females to mate with mated males. I assess the costs and benefits to females of mating bigamously under these circumstances. Finally, I suggest that high nest success may make the island a favorable place to breed, enhancing the importance of site tenacity in maintaining a breeding spot there.

#### STUDY AREA AND METHODS

The study was conducted in a 35-ha spruce-fir forest on Kent Island, New Brunswick, during May–August 1979–1982. Kent is an 80-ha island located 20 km southeast of the Maine–New Brunswick border in the Bay of Fundy. The vegetation of the island has been described by McCain (1975). Blackpoll Warblers used only the forested parts of the island.

Birds were netted and marked with unique combinations of three plastic color bands and one numbered aluminum band. Blackpoll Warblers are sexually dichromatic, and therefore males and females were distinguished readily. During the 4 years of the study 41 adults and 173 nestlings were color-banded. For the purpose of analysis, "old" birds are those known to be 2 years old or older. Four males and 1 female that were banded before 1979 provided some known-age birds at the outset. Fourteen birds banded as nestlings returned in subsequent years, providing a group of known-age yearlings.

Arrival dates of both sexes were determined by patrolling the study area daily, looking and listening for birds. I use the term "settling date" for the first day a bird was seen on a territory on which it subsequently bred. Territory boundaries were determined by noting male singing posts and sites of interaction between males. Points were plotted on maps of the study area made from aerial photographs. Each week maps of all territories were drawn by connecting observation points accumulated during the week. After the territory establishment period, I visited each territory at least once every 2 days for a minimum of 1–2 h to determine mating relationships, monitor interactions between mates, and follow reproductive chronology.

A maximum of 15 males held territories on the island in any year. The first field season was devoted to a feasibility study during which the breeding biology of 5 males and their mates was studied. The breeding habitat is dense, and nesting females are secretive. To be reliable, I concentrated on the activities of 8–12 males per year in 1980–1982. A total of

35 male-years of data was obtained. These data represent 25 different males and 22 different females. To distinguish the mates of bigamous males, I term the first female to initiate her nest the "primary" female and the second the "secondary" female.

If differences in the quality of the breeding situation give rise to polygynous matings, variation in measures of quality should explain (1) the division of males into mating-status categories, (2) the settling patterns of the first females on all territories, and (3) the reproductive success of females within mating-status categories (Vehrenkamp and Bradbury 1984). To get sample sizes large enough to test these predictions, it was necessary to pool the information for 1980–1982.

Beginning in 1980, I used the following parameters as measures of territory quality: (1) territory size, (2) conifer density, (3) total conifers, (4) large conifer density, and (5) total large conifers. The birds forage at midcanopy in conifers up to 10 m tall. Microlepidoptera larvae that are inside needles and closed buds are an important part of the diet (Eliason unpubl. data). Because of these factors, direct assessment of food on each territory proved to be beyond the scope of this project. Male age and arrival dates were used as measures of male quality.

I determined territory size by tracing the outlines of the territories with a plane planimeter. For this analysis I used territory maps for the 2-week period when most females settled on territories. In this population, more than 90% of foraging by Blackpoll Warblers was done in conifers (Eliason unpubl. data), so conifer density on the territory was taken as a measure of available foraging space. Tree densities were determined by counting trees (by species and size class) in 10 × 10-m plots. The number of plots used to sample each territory was proportional to the size of the territory, so that sampling intensities were equal (about 6% of territory area). The third parameter, total number of conifers per territory, is the product of territory size and conifer density. Foraging observations also indicated that conifers smaller than 5 m tall and 8 cm in diameter at breast height were used infrequently by the birds. The large conifer parameters were calculated by including only trees above that minimum size.

Male mating-status categories were: bigamous, monogamous, or unmated. Logistic regression was used to construct the best possible model to explain variance in the mating status of males. The five territory-quality parameters and two male-quality parameters were used as potential explanatory variables.

An explanatory regression model was first sought for the response categories of mated vs. unmated. The analysis was then repeated within the mated category for bigamous vs. monogamous. The procedure was performed with the computer program LOGIT (K. Larntz and S. Weisberg, Dept. Applied Statistics,

University of Minnesota). With this method, the statistic being minimized is the deviance (see equation below). The significance of various models is tested by calculating the difference between the deviance values associated with each model. This difference is distributed approximately as  $\chi^2_{(k_1 - k_2) df}$ , where  $k_i$  = the number of explanatory variables in the models being compared (McCullagh and Nelder 1983).

A step-up method of analysis was used in which models with one explanatory variable were compared with the baseline deviance of a model with no variables (baseline deviance =  $2n_i \log_e(n_i + n_0)/n_i + 2n_0 \log_e[(n_i + n_0)/n_0]$ , where  $n_i$  = the number of individuals in a response category). Additional variables then were added to the best single-variable model to see if a better fit could be obtained. Multiple-variable models were deemed better than single-variable models only if they produced significantly smaller deviance values than the best model with one fewer variable.

Nests were located by following females during building and incubation. Nests were checked daily to determine the date of first laying, number of eggs laid, hatching date, and number hatched. The day the first egg of a clutch hatched was designated day 1. Nestlings were weighed and measured daily from hatching through day 8. Young were banded at day 6. After day 8 nests were checked three times daily to determine the number of young fledged, which was used as a measure of female reproductive success. I did not anticipate second broods and did not seek them in 1979 and 1980. In 1981 and 1982 territories were monitored closely throughout the re-nesting period. Season-long reproductive success comparisons refer to 1981–1982 only.

Because females do not sing, they are less conspicuous than males. Female settling dates are thus more difficult to determine. I was confident of the accuracy of settling dates for females that were engaged in the early stages of courtship when first seen ( $n = 11$ ). Eight of these 11 females were the first females to settle on their territories. I performed a correlation analysis on this sample to test the prediction that female settling dates are correlated with territory quality. I had a larger sample of females with known first-egg dates than of females with known settling dates, and settling dates and first-egg dates were positively correlated for the 11 females whose settling dates were known with confidence ( $r = 0.58$ ,  $t_s = 2.15$ ,  $P = 0.06$ ). I performed a multiple regression analysis using first-egg dates as the dependent variable and the five territory-quality parameters plus male arrival dates as potential explanatory variables. Male age was not included in this or the fitness analysis described below because too few yearling males were mated.

I also used multiple regression analysis to explore whether some combination of the territory- and male-

quality parameters could explain the variance in female reproductive success (prediction 3). The polygyny threshold model allows one to make predictions about the relationship of territory quality and female fitness only within mating-status categories (Vehrenkamp and Bradbury 1984). I did this analysis for monogamous females only because sample sizes of non-monogamous females were too small.

Multiple regression analyses were performed using the program MULTREG (Weisberg 1982). All other statistical analyses were performed using SPSS 6000, version 8.3 on the University of Minnesota computer system.

As part of the assessment of possible costs to females of their mating choices, the number of feeding trips of both sexes to the nest were counted during three 30-min periods each day throughout the nestling period. Means of feeding rates for days 5–8 post-hatching were used to compare the attentiveness of birds of different mating status.

## RESULTS

### MATING SYSTEM

Bigamy occurred in all years, ranging in frequency from 8 to 40% ( $\bar{x} = 22.6\%$ ) of males of known mating status (Table 1). Territory parameters were not measured in 1979. The mean level of bigamy for the 3 years for which I have territory-quality information was 16.7%. Bigamy occurred in first broods only; no bigamous pair bonds lasted beyond the first brood. No monogamous females switched mates between broods. Two females switched after mating with bigamous males for their first broods to mate with previously unmated males for a second brood. The frequency of known unmated males at the time females were involved in their first broods ranged from 0 to 40% ( $\bar{x} = 17\%$ ) over the 4 years. I saw no unmated females at the time females were involved in their first broods. This population exhibits "facultative polygyny" (Ford 1983) because polygyny occurs regularly, but less than 20% of males have more than one mate.

### TERRITORY AND MALE QUALITY

*Male mating status.*—The best explanation of the fit of males into mated vs. unmated categories was provided by a regression model with arrival time as the only explanatory variable. The addition of territory-quality measures did not improve the fit (Table 2). A regression

TABLE 1. Male mating status. Percentages of males in each mating-status category in each year and the mean percentages for the 4 years are shown. The 35 male-years shown represent the histories of 25 different males.

Year	<i>n</i>	Monogamous	Bigamous	Unmated
1979	5	60	40	0
1980	8	75	12.5	12.5
1981	12	75	8	17
1982	10	30	30	40
Mean		60	22.6	17.4

model with total large conifers plus arrival time as explanatory variables provided the best explanation for the monogamous/bigamous dichotomy (Table 2).

Male arrival dates were correlated inversely with total large conifers ( $r = -0.47, P = 0.01$ ), consistent with the idea that males that arrive first settle on the best territories. The mean values of all territory parameters were smallest for unmated males and largest for bigamous males, with the values for territories of monogamous males intermediate (Table 3). The mean values for large conifer density and total large conifers were significantly different among the territories of males of different mating status. Ter-

TABLE 2. Deviance values from logistic regression analysis. Values for models containing each of the seven explanatory variables alone, plus the two best multiple-variable models, are shown, along with the baseline deviance values for the response categories of mated vs. unmated and bigamous vs. monogamous. Asterisks indicate best models.

Explanatory variables	Response variables	
	Mated vs. unmated	Bigamous vs. monogamous
Baseline	26.4	15.8
Territory size (TS)	24.2	15.1
Conifer density (CD)	24.0	15.5
Total conifers (TC)	23.0	10.8
Large conifer density (LCD)	22.7	13.8
Total large conifers (TLC)	21.8	5.1
Male arrival dates (ARR)	5.4*	13.8
Male age (AGE)	11.5	14.6
ARR + AGE	5.4	13.6
ARR + TLC	5.3	0.50 × 10 <sup>-5*</sup>

TABLE 3. Mean values of territory parameters for males in three mating-status categories: unmated (U), monogamous (M), and bigamous (B). Parameter abbreviations are defined in Table 2.

Parameter	Mating status			Mean
	U	M	B	
<i>n</i>	6	16	5	
TS (ha)	0.8	1.1	1.2	1.1
CD (trees/100 m <sup>2</sup> )	23.9	37.3	48.2	36.3
LCD (trees/100 m <sup>2</sup> ) <sup>a</sup>	14.5	22.8	37.9	23.7
TC (trees/territory)	2,200	3,480	5,150	3,510
TLC (trees/territory) <sup>b</sup>	1,310	2,150	4,040	2,320

<sup>a</sup> One-way ANOVA,  $F_{2,24} = 3.83, P = 0.04$ .

<sup>b</sup> One-way ANOVA,  $F_{2,24} = 9.46, P < 0.001$ .

ritories of bigamous males had significantly more total large conifers (Student-Newman-Keuls test,  $P < 0.01$ ) than those of other males, but there was no difference between the territories of unmated and monogamous males. Thus, there appeared to be differences between the territories of bigamous males and other males.

*Female settling dates.*—There was no significant correlation between female settling dates and any of the six breeding-quality parameters. No significant regression model could be constructed to explain the variance in first-egg dates using the six breeding-quality parameters as potential explanatory variables.

*Female reproductive success.*—The only significant regression model to explain the variance in the season-long reproductive success of monogamous females was one with male arrival dates alone ( $r = 0.68, t_{10} = 2.91, P = 0.02$ ). The addition of the territory parameters did not improve the fit.

SITE FIDELITY AND ARRIVAL SCHEDULES

In all 12 cases where males with known breeding histories returned, the territories they defended in their second year included part of the territories they had defended in the previous year. In 11 of 12 cases where females with known breeding histories returned, they settled on or immediately adjacent to the territory on which they had nested the year before. In 4 cases the mate returned, but in 7 he did not.

Members of different age and sex classes re-

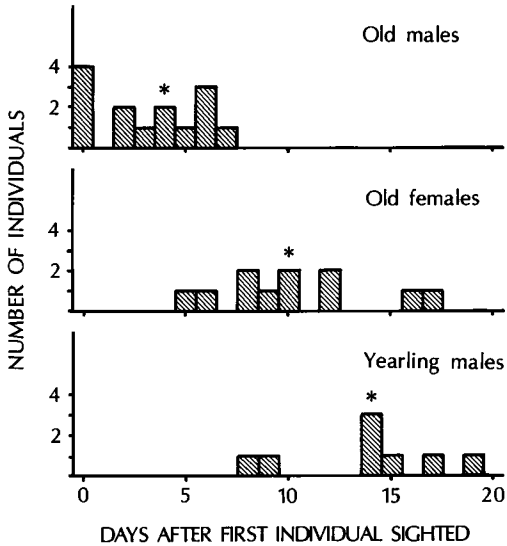


Fig. 1. First sighting dates of birds in three age and sex classes for 1981 and 1982. "Old" refers to birds 2 years old and older. Dates were ordered by using the date the first individual was sighted as day 0 and then numbering days consecutively. Asterisks indicate medians.

turned at different times (Fig. 1). Old males arrived first and yearling males latest, with no overlap in the dates they began advertising on territories. Females arrived over a longer period. Some old females arrived before any yearling males. The median date of old female arrival was earlier than that of yearling males (Fig. 1).

More old females than old males returned in some years, although the return rates of old birds were similar for males (48%) and females (49%) when averaged over the 4 years of the study. Depending on the settling patterns of early males, this could mean that no unmated males were available near the areas where returning females formerly nested.

This is evidently what happened in 1982 (Fig. 2), when 7 old females and only 3 old males returned. The territories of the 3 returning males contained portions of what had been multiple territories in 1981, but there were many unoccupied areas. All 6 females whose nest sites are shown in Fig. 2 returned in 1982. Each mated with the male that held the territory closest to her old nest site. This resulted in 3 bigamous matings.

Site fidelity appeared to influence mating

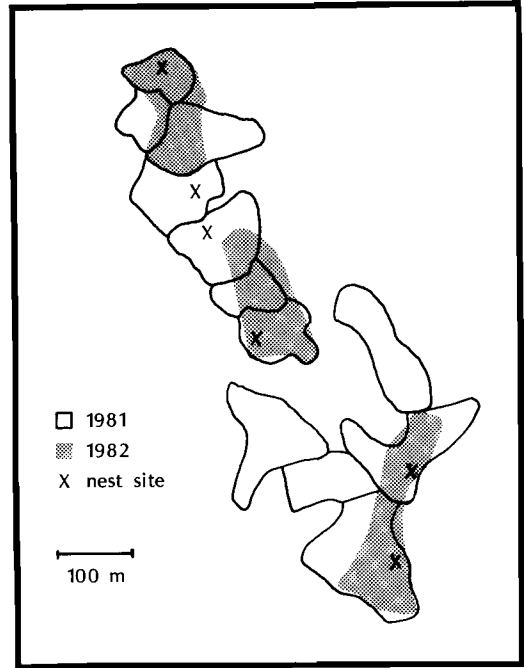


Fig. 2. Territories (stippled) of the first 3 males to settle in 1982 superimposed on 12 territories (solid lines) and 6 nest sites (X's) for 1981.

choices in 1981 as well. There was one case of bigamy that involved a female (O/B) that had nested on the same territory in 1980, and a yearling female (M/Y). Although O/B arrived after M/Y, she initiated her nest first. The male made more feeding trips to her nest than to that of M/Y ( $3.2$  vs.  $2.7$  trips  $\cdot$  nestling $^{-1} \cdot$  h $^{-1}$ ), and the male fed her fledglings but not those of M/Y. In the bigamous mating described

TABLE 4. Reproductive output of females in relation to their mating status.\* Values shown are means  $\pm$  SD, with sample sizes in parentheses.

Mating status	Number fledged (first brood)** 1979-1982	Number fledged (season-long)* 1981-1982
Primary	$4.8 \pm 0.39$ (6)	$8.3 \pm 0.96$ (4)
Secondary	$2.9 \pm 1.30$ (5)	$4.8 \pm 1.70$ (4)
Monogamous	$3.5 \pm 1.05$ (15)	$4.8 \pm 1.06$ (10)

\* \* =  $P < 0.05$ , \*\* =  $P < 0.01$ ; Kruskal-Wallis test.

TABLE 5. Male feeding rates on days 5-8 post-hatch.

Female status	<i>n</i>	Trips· nestling <sup>-1</sup> ·h <sup>-1</sup> by male <sup>a</sup> ( $\bar{x} \pm SD$ )	Percent- age of total trips made by male
Secondary	5	0.53 $\pm$ 0.53	16.1
Monogamous	14	1.89 $\pm$ 0.62	52.5

<sup>a</sup>  $U = 2$ ,  $P < 0.05$ ; two-tailed Mann-Whitney  $U$ -test.

above, only the primary female (O/B) returned to a site on which she had bred previously, but she settled there even though another female was already present.

#### COSTS AND BENEFITS OF SECONDARY STATUS

*Costs of secondary over monogamous status.*—I found no evidence of a significant cost to secondary females compared with monogamous females in terms of either number of young produced or adult survival. Primary females produced significantly more fledglings than did monogamous or secondary females, but there was no significant difference between the success of the monogamous and secondary females (Table 4). This was true for comparisons of first-brood and season-long success.

In terms of the number of young produced, secondary females were no worse off than the average monogamous female. However, secondary females received significantly less help from their mates in feeding nestlings relative to monogamous females (Table 5). Secondary females responded to reduced male aid by increasing nestling feeding rates compared with monogamous females. Secondary females made as many trips as were made by both members of 14 monogamous pairs (3.6 vs. 3.5 trips·nestling<sup>-1</sup>·h<sup>-1</sup>). There might be a cost to secondary females because of this extra effort. For example, secondary females might suffer higher overwinter mortality than monogamous females. I found no evidence for this, but the sample sizes were small. The average return rate for adult females was 49%, whereas 50% of secondary females ( $n = 4$ ) from 1979-1981 returned in subsequent years.

*Benefits: early nest initiation.*—Females that had second broods initiated their first nests significantly earlier than those that did not have second broods (Table 6). In fact, no female that

TABLE 6. Laying dates and reproductive success of females in relation to the number of broods they produced. Egg 1 dates were recorded by making the date the first egg of the season was laid equal to 1 and numbering days sequentially.<sup>a</sup>

No. of broods	<i>n</i>	Date egg 1 laid* ( $\bar{x} \pm SD$ )	Fledglings produced** ( $\bar{x} \pm SD$ )
1	6	9.8 $\pm$ 5.3	3.7 $\pm$ 0.82
2	13	4.7 $\pm$ 2.46	6.6 $\pm$ 1.76

<sup>a</sup> \* $U = 14.5$ ,  $P = 0.03$ ; \*\* $U = 6.5$ ,  $P < 0.01$ ; two-tailed Mann-Whitney  $U$ -test.

initiated her first brood more than 10 days after the first egg of the season was laid had a second brood. Females that attempted two broods fledged significantly more young than those that did not (Table 6).

Early nest initiation allows, but does not guarantee, an opportunity for a second brood. Only secondary females that switched mates after their first broods and mated with previously unmated males had second broods. These previously unmated males were not present when the females initiated their first nests.

#### DISCUSSION

One measure of territory quality, the number of large conifers on the territory, was correlated with male mating status. Female settlement choices were better explained by site fidelity than by variations in territory quality. Bigamous matings resulted when no unmated males were available near the former nest sites of returning females. The cost of bigamous matings appeared to be low. Secondary females did not have lower reproductive success or survival than did monogamous females. Mating with already-mated males allowed females to initiate their nests early enough to have second broods.

The correlation of male arrival time with male mating status and female reproductive success is consistent with the idea that the mating choices of female Blackpoll Warblers on Kent Island are influenced by the benefits of early nest initiation. I found the influence of territory quality to be equivocal in female settlement choices. In particular, territories of bigamous and monogamous males differed in the numbers of total large conifers (TLC), but TLC was not correlated with female settling pat-

terns, nor did it explain the variance in reproductive success among monogamous females.

The difference in the number of large conifers between the territories of bigamous males and other males may be an artifact of small sample sizes and differences in male return patterns due to chance alone. Four of the 5 instances of bigamy occurred in the part of the study area with the highest tree density. The low return rates of males in that area resulted in reduced competition among the males. As a result, males claimed territories with large numbers of conifers. If bigamy arose as I have suggested, however, females mated with those males, not because the males' territories had large numbers of conifers, but because the females preferred to nest near where they had nested formerly.

Territory quality may limit the number of females that can breed on a territory. No male had more than two mates. In one case 5 females returned that had bred on adjacent territories in the previous year. Two males returned and established territories that included the territories on which the 5 females had bred. Two bigamous matings resulted that involved 4 females. The fifth female mated monogamously on a territory more than 3 territories away from her former breeding spot. This was the only one of 12 returning females that did not settle near her former breeding spot.

Several factors may have obscured relationships between the quality of the breeding situation and female settling patterns and reproductive success. First, females may have chosen where to settle based on characteristics that I did not measure. Second, pooling among years may have obscured the actual relationship between the number of large conifers on the territory and female settling patterns or reproductive success. Third, the number of young fledged annually may not be a reliable indicator of lifetime reproductive success. There may be differential postfledging or overwinter mortality, or a lack of congruence between seasonal and lifetime reproductive success. Finally, even if females base their choices of where to settle on territory quality, unpredictable nestling mortality factors such as weather may obscure relationships in a small sample.

Site fidelity by males has been recognized as a complicating factor in determining the relationship among male quality, territory quality,

and mating status in other species (Searcy 1979, Oring 1982). There have been few studies of the effects of female site fidelity on female mate choices in polygynous species. Although the role of territory quality in mate choice by females in this population remains equivocal, site fidelity was a sufficient explanation for the occurrence of polygyny.

Kent Island may be a favorable place to breed for reasons independent of territory quality. Ricklefs (1969) found that predation was the most important mortality factor of eggs and young for most birds. Predation on eggs and nestlings was very low on Kent Island because there are no mammalian and few avian predators. The minimum number of fledglings produced by any female in a season was 2 ( $n = 34$ ). Ninety-eight percent of clutches ( $n = 48$ ) produced at least one fledgling (Eliason 1986). This compares with 52.5% for 35 altricial passerine species (Nice 1957). A female Blackpoll Warbler breeding on Kent Island has a high probability of producing some young no matter what her mating status.

High nest success may explain the tendency of females to breed near where they formerly bred. Birds that nest successfully have been shown to disperse shorter distances between breeding attempts than those that are unsuccessful (Catchpole 1972, Harvey et al. 1979, Blockstein 1986). If female Blackpoll Warblers use the simple rule of returning to a site where they were successful, then 98% of them should return to their former sites (92% of them did so).

A female Blackpoll Warbler has several options if she returns to her former territory and finds no unmated males nearby. If she pairs with a mated male and initiates her nest immediately, she almost certainly can raise some young, and may be able to have a second brood. Also, a female that maintains her position on a site by becoming a secondary female may have an advantage in competing for breeding opportunities on the site in subsequent years. In fact, two secondary females that returned to the same site the next year became primary females. Primary females had significantly higher annual reproductive success than either secondary or monogamous females (Table 4), received as much male aid as monogamous females, and received significantly more aid than secondary females (Eliason 1986). A female that

does not mate with a mated male when no unmated males are present near where she formerly nested faces the possibilities of not mating or not having a second brood. If she decides to leave the island, the same uncertainties exist, plus the likelihood of higher predation rates.

Assuming the sample of birds I studied was typical of the population as a whole, the overall sex ratio once all birds had arrived was slightly biased toward males in years when it deviated from equality (Table 1). Female-biased sex ratios existed early in the season because yearling males returned later than older males. Yearlings return later in a number of species (e.g. Martin 1970, Nolan 1978, Oring and Lank 1982). Oring and Lank (1982) suggested that because yearlings could not compete successfully with more experienced birds for territories, they delayed their arrival until older males were involved in breeding activities and less committed to territory defense. An alternative explanation for the later arrival of yearlings is that yearlings are less successful in competing for resources in wintering areas, take longer to build up reserves for migration, and are not ready to migrate as soon as older birds are (Rohwer and Butler unpubl. ms.).

Site attachment and return patterns can account for the incidence of polygyny in this population, but data are not available to evaluate the role of these factors in determining mating status in other populations of Blackpoll Warblers. The combination of site fidelity and return patterns that led to polygyny in this population probably could not give rise to high levels of polygyny or large harems. Long-term data on breeding locations and mating relationships of marked individuals are needed to determine the influence of site fidelity in other species that exhibit low levels of polygyny.

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#### LITERATURE CITED

- BLOCKSTEIN, D. E. 1986. Reproductive behavior and parental investment of Mourning Doves (*Zenaida macroura*). Unpublished Ph.D. dissertation, Minneapolis, Univ. Minnesota.
- CATCHPOLE, C. 1972. A comparative study of territory in the Reed Warbler (*Acrocephalus scirpaceus*) and Sedge Warbler (*A. schoenbaenus*). *J. Zool.* (London) 166: 213-231.
- ELIASON, B. C. 1986. Mating system, parental care, and reproductive success in the Blackpoll Warbler (*Dendroica striata*). Unpublished Ph.D. dissertation, Minneapolis, Univ. Minnesota.
- EMLEN, S., & L. ORING. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215-223.
- FORD, N. 1983. Variation in mate fidelity in monogamous birds. Pp. 329-356 in *Current ornithology*, vol. 1 (R. Johnston, Ed.). New York, Plenum Publ. Corp.
- GREENWOOD, P. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.* 28: 1140-1162.
- HARVEY, P., P. GREENWOOD, & C. PERRINS. 1979. Breeding area fidelity of the Great Tit (*Parus major*). *J. Anim. Ecol.* 48: 305-313.
- HEISLER, I. 1981. Offspring quality and the polygyny threshold: a new model for the sexy son hypothesis. *Amer. Natur.* 117: 316-328.
- HINDE, R. 1956. The biological significance of the territories of birds. *Ibis* 98: 340-369.
- MARTIN, S. 1970. Polygyny in the bobolink: habitat quality and the adaptive complex. Unpublished Ph.D. dissertation, Corvallis, Oregon State Univ.
- MCCAIN, J. 1975. A vegetational survey of the vascular flora of the Kent Island group, Grand Manan, New Brunswick. *Rhodora* 77: 196-209.
- MCCULLAGH, P., & J. NELDER. 1983. Generalized linear models. New York, Chapman & Hall.
- NICE, M. M. 1957. Nesting success of altricial birds. *Auk* 74: 305-321.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler, *Dendroica discolor*. *Ornithol. Monogr.* No. 26.
- ORIANI, G. 1969. On the evolution of mating systems in birds and mammals. *Amer. Natur.* 103: 589-603.
- ORING, L. 1982. Avian mating systems. Pp. 1-79 in *Avian biology*, vol. 6 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- , & D. LANK. 1982. Sexual selection, arrival



- times, philopatry, and site fidelity in the polyandrous Spotted Sandpiper. *Behav. Ecol. Sociobiol.* 10(3): 185-192.
- RICKLEFS, R. 1969. An analysis of nesting mortality in birds. *Smithsonian Contr. Zool.* 9: 1-48.
- SEARCY, W. 1979. Male characteristics and pairing success in Red-winged Blackbirds. *Auk* 96: 353-363.
- , & K. YASUKAWA. 1981. Does the "sexy son" hypothesis apply to mate choice in Red-winged Blackbirds? *Amer. Natur.* 117: 343-348.
- VEHRENKAMP, S., & J. BRADBURY. 1984. Mating systems and ecology. Pp. 251-278 in *Behavioral ecology: an evolutionary approach*, 2nd ed. (J. Krebs and N. Davies, Eds.). Sunderland, Massachusetts, Sinauer Assoc.
- VERNER, J. 1964. Evolution of polygamy in the Long-billed Marsh Wren. *Evolution* 18: 252-261.
- , & M. WILLSON. 1966. The influence of habitats on mating system of North American passerine birds. *Ecology* 47: 143-147.
- WEATHERHEAD, P., & R. ROBERTSON. 1977. Harem size, territory quality, and reproductive success in the Red-winged Blackbird (*Agelaius phoeniceus*). *Can. J. Zool.* 5: 1261-1267.
- , & ———. 1979. Offspring quality and the polygyny threshold: "the sexy son hypothesis." *Amer. Natur.* 113: 201-208.
- WEISBERG, S. 1982. *Multreg users manual*, version 4.1. Technical Rept. #298, Sch. Statistics, Univ. Minnesota.
- WITTENBERGER, J. 1979. The evolution of mating systems in birds and mammals. Pp. 271-349 in *Handbook of behavioral neurobiology: social behavior and communication* (P. Marler and J. Vandenberg, Eds.). New York, Plenum Press.
- . 1981. Male quality and polygyny: the "sexy son" hypothesis revisited. *Amer. Natur.* 117: 329-342.