

RE-EVALUATION OF MORPH-SPECIFIC VARIATIONS IN PARENTAL BEHAVIOR OF THE WHITE-THROATED SPARROW

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ABSTRACT.—We studied White-throated Sparrows (*Zonotrichia albicollis*) to determine whether morph-specific variations in parental care are typical of this species and whether the influence of neighbors could account for the occurrence of such variations in some samples but not in others. White-striped males made fewer provisioning trips than did tan-striped females. The provisioning rates of tan-striped males and white-striped females were intermediate. Parental care was not affected by the number of neighbors, neighbor singing, local density, or territory size. White-striped male provisioning was positively correlated with the length of their shared territory boundary and their song rates. These effects are likely due to male condition rather than the influence of neighbors. Such variations in the provisioning behavior of white-striped males could account for the lack of morphic variation found in some samples. Received 29 May 1992, accepted 21 Sept. 1992.

During the breeding season, White-throated Sparrows (*Zonotrichia albicollis*), possess a discrete plumage polymorphism (white-striped morph, tan-striped morph; Lowther 1961) that is associated with a chromosomal polymorphism (Thornycroft 1975). This polymorphism is maintained within populations by negative assortative mating. Thus, over 90% of the breeding population consists of two pair types: white-striped males mated with tan-striped females and tan-striped males mated with white-striped females. To understand why polymorphism in the White-throated Sparrow persists, it is necessary to determine what factors promote negative assortative mating.

Knapton and Falls (1983) documented morphic differences in the parental behavior of White-throated Sparrows. They found that white-striped males made fewer provisioning trips to nestlings than did tan-striped females. Tan-striped males and white-striped females had intermediate provisioning rates and did not differ from each other. These results led Knapton and Falls (1983) to suggest that morphic variations in parental care might favor negative assortative mating. Furthermore, because the overall performance of the two pair types was equivalent, negative assortative mating was viewed as a stable strategy in which neither pair type experienced a reproductive advantage (see also Knapton et al. 1984).

A more recent study by Whillans and Falls (1990) failed to find morphic differences in parental care. This latter result casts doubt on the role of

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parental care in promoting negative assortative mating. Therefore, additional data are necessary, first to determine whether parental care does vary with morph and sex, and second, to determine what parameters influence parental care and might be responsible for the different results of the two studies.

Whillans and Falls (1990) suggested that different results could arise from differences between the study areas used. In particular, because white-striped males appear to be more responsive to conspecific song than are tan-striped males (Lowther 1962), they might provide less care to their young in areas of high population density where more birds are singing and interactions between neighbors are more frequent. Under such conditions morphic differences in parental care would be pronounced. On the other hand, where the population density is lower, white-striped males might provide more care toward their young. In this circumstance, morphic differences in parental care might not be evident. Whillans and Falls (1990) noted that their study area had a lower population density than the study area used by Knapton and Falls (1983).

Objectives of the current study were to determine whether morphic differences in parental performance occur among White-throated Sparrows and to test the prediction proposed by Whillans and Falls (1990) that parental performance among morph and sex classes might be influenced by neighboring conspecifics.

METHODS

We observed parental behavior of White-throated Sparrows in Algonquin Provincial Park, Ontario, Canada, from 1986 to 1988. We found nests during the incubation stage by flushing the females from their nests. We then visited each nest daily to determine the date of hatching. On the fourth day post-hatching we set up a blind 3–10 m from the nest in a location that allowed us to identify the adults as they entered to feed the young. Since the normal brood size for this species is three to five young (Knapton et al. 1984) we confined our observations to nests that contained three or more young.

As in the studies of Knapton and Falls (1983) and Whillans and Falls (1990), our observations of parental care were conducted on days 5 to 8 post-hatching. The observation protocol consisted of two 100-min observation periods per day; one during the morning between 07:00 and 12:00 h EST and one during the evening between 17:00 and 21:30 h EST. We divided each 100-min observation period in the following way. During the first 20 min we collected data on the number of provisioning trips made by each parent and the number of times the male and each contiguous neighboring male sang. To collect data on the singing behavior of focal males and their neighbors, we identified the individual song types of each bird when the territories were mapped (see below). During the next 60 min, we concentrated on observing the provisioning behavior of the parents. In 1986, we documented the number of trips made by each parent. In 1987 and 1988, we collected data on the number of provisioning trips made by each parent, the number of items delivered, the length and width of each item delivered, and the types of items delivered (identified to order). Observations conducted during the last 20 min repeated those made during the first

20 min. In this way, each 100-min observation period consisted of 40 min of song and nest observation and 60 min of detailed nest observation.

We estimated the length and width of prey items by comparing the items to the length of the parent's bill ($\bar{x} = 1.2$ cm, $N = 26$, measures taken from adults during May and June 1989) (for a critique on estimating prey sizes from bill lengths see Goss-Custard et al. 1987). However, we could only collect data on prey size and type when the parents were close enough that the items were clearly visible. This meant that we could not collect data from some, more cryptically behaving, parents. In addition, to improve the accuracy of our estimates, we excluded from the analyses any birds for which data were collected from less than 20 provisioning trips. Lepidoptera larvae appeared to be a preferred item (see also Knapton and Falls 1983). Therefore, we quantified the type of food delivered by estimating the proportion of food items that were Lepidoptera larvae.

Between the first and fourth days post-hatching we mapped the territories using a Uher Report IC stereo tape recorder and the playback method of Falls (1981). The boundaries of the territory were determined from the behavior of the focal birds and their neighbors and were marked with flagging tape. When a boundary was shared between a focal bird and a neighbor, it was marked half-way between the most extreme approaches of the neighbor and the focal bird. Birds that did not approach within 30 m of each other were not considered to be contiguous neighbors, and we defined these boundaries as uncontested. This occurred when the territories were separated by tracts of unsuitable habitat (dense forest, open fields, ponds, rivers). We marked the boundaries using between 10 and 41 flags, depending on the size of the territory, the density of the habitat, and the number of neighbors. Our measurements of distances between markers were made by pacing the straight-line distance between each marker. Repeated trials against known distances indicated that one pace was equivalent to about 0.9 m.

Using the data generated from the mapping procedure, we examined the influence of neighboring White-throated Sparrows on parental care by relating provisioning rates to the number of contiguous neighbors, the song rate of neighbors, and the length of the territory boundary that was shared with neighbors (shared boundary). Since intra-specific competition can influence the size of territories (Krebs 1971, Zimmerman 1971, Myers et al. 1979, Wiens et al. 1985), we also looked for relationships between provisioning rate and the area (m^2) of the territory, the length of the territory perimeter, and the local population density (number of neighbors divided by the area [m^2] of the territory).

Most of our statistical analyses were based on parametric tests (after testing for normality and equal variances) (Neter and Wasserman 1974). However, when comparing groups with sample sizes of less than 19 observations, we used the non-parametric tests described in Pratt and Gibbons (1981). Because of the number of tests involved (see Tables 2 and 3) it was necessary to correct the critical value of P using the Bonferroni method (Rice 1989) or, in the case of the comparisons made in Fig. 1, Duncan's Multiple Comparisons Procedure. Therefore, for the analyses presented in Table 1 we used 0.003 as the critical value of P . For the analyses presented in Tables 2, 3, and 4 we considered a test significant only if the value of P was less than 0.0018. In Table 5, a comparison was considered significant only if the value of P was less than 0.012.

RESULTS

Morph and sex differences in provisioning behavior. — We observed parental behavior at 39 nests (19 white-striped male \times tan-striped female pairs, 20 tan-striped male \times white-striped female pairs). There was a slight tendency among all morphs and sexes for the rate of provisioning

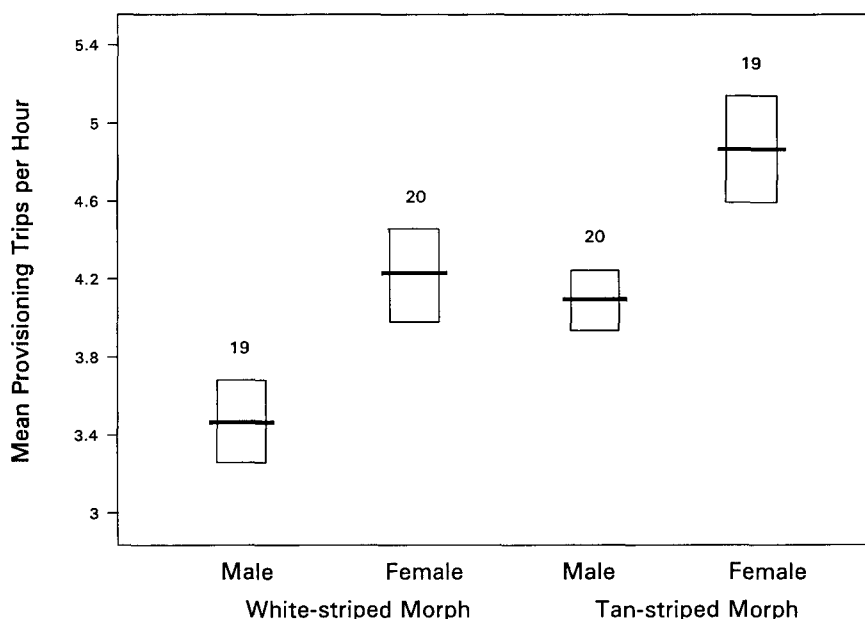


FIG. 1. Mean parental provisioning trips per hour of each morph and sex class. Bars represent ± 1 SE, lines within bars represent means, and numbers over bars are sample sizes.

trips to increase with brood size, but in no case was this effect significant (Kruskal-Wallis Tests, separate tests for each morph and sex class, P all > 0.05). We also found no significant difference in the number of young fledged by each pair type (Wilcoxon's Rank-Sum Test, $S = 377.5$, $P = 0.9519$). For the following analyses, we combined data from different brood sizes.

We found no evidence that male and female provisioning rates were correlated among white-striped male \times tan-striped female pairs (Pearson's Correlation Coefficient; $r = 0.202$, $P = 0.4064$). Among tan-striped male \times white-striped female pairs there was a tendency for male and female provisioning rates to be correlated, but the effect was not statistically significant in this sample ($r = 0.439$, $P = 0.0529$). For subsequent analyses we treated each morph and sex class as if they were independent.

Our data indicated that white-striped male provisioning rates were lower than tan-striped male provisioning rates, tan-striped male provisioning rates did not differ from white-striped female provisioning rates, and white-striped female provisioning rates were lower than tan-striped female provisioning rates (Fig. 1) (Duncan's Multiple Comparisons Procedure, $P < 0.05$). In spite of these differences, there appeared to be no

TABLE 1
THE NUMBER, SIZE, AND TYPE OF FOOD DELIVERED TO NESTLINGS BY EACH MORPH AND SEX CLASS

| | White-striped | | Tan-striped | | χ^2 | df | P^a |
|----------------------------------|---------------|-----------|-------------|-----------|----------|----|--------|
| | Male | Female | Male | Female | | | |
| Number of items per trip | | | | | | | |
| Median | 1.87 | 1.76 | 1.93 | 1.65 | 2.21 | 3 | 0.5309 |
| Range | 1.21–2.24 | 1.14–2.40 | 1.31–2.41 | 1.25–2.71 | | | |
| N | 8 | 15 | 13 | 10 | | | |
| Length of items (cm) | | | | | | | |
| Median | 1.59 | 1.42 | 1.46 | 1.34 | 3.40 | 3 | 0.3341 |
| Range | 1.33–2.37 | 1.02–1.89 | 1.04–2.04 | 0.90–2.59 | | | |
| N | 8 | 15 | 13 | 10 | | | |
| Width of items (cm) | | | | | | | |
| Median | 0.45 | 0.30 | 0.31 | 0.38 | 5.93 | 3 | 0.1150 |
| Range | 0.25–0.51 | 0.26–0.41 | 0.26–0.47 | 0.23–0.50 | | | |
| N | 8 | 15 | 13 | 10 | | | |
| Lepidopteran larvae ^b | | | | | | | |
| Median | 0.54 | 0.67 | 0.62 | 0.54 | 4.59 | 3 | 0.2044 |
| Range | 0.37–0.73 | 0.32–0.98 | 0.36–0.96 | 0.20–0.69 | | | |
| N | 8 | 15 | 13 | 10 | | | |

^a Probability based on Kruskal-Wallis tests (chi-square approximation).

^b The proportion of lepidopteran larvae among items delivered to the young.

difference in the overall provisioning rates of white-striped male \times tan-striped female pairs and tan-striped male \times white-striped female pairs (Wilcoxon's Rank-Sum Test, $S = 408.5$, $P = 0.4232$).

We compared the size and type of food delivered to the young by each morph and sex class (Table 1) and found no evidence that they differed in the number of items brought per trip, the length of food items, the width of food items, or in the proportion of Lepidoptera larvae delivered. Furthermore, within each morph and sex class, we found that none of these measures was correlated with provisioning rate (P all > 0.05).

Possible influence of neighboring conspecifics.—We found no evidence among any of the morph and sex classes that provisioning rates were influenced by the number of contiguous neighbors (Table 2). Similarly, we found no evidence that provisioning rates were related to the area of the territory, the local density, or the length of the territory perimeter (Table 3). There was also no evidence that the provisioning rates of tan-striped males, tan-striped females, and white-striped females were related to the length of the territory boundary shared with neighbors (Table 3).

TABLE 2
THE RELATIONSHIP BETWEEN THE NUMBER OF CONTIGUOUS NEIGHBORS AND PARENTAL
PROVISIONING RATE WITHIN EACH MORPH AND SEX CLASS

| Morph/sex class | Number of contiguous neighbors | | | χ^2 | df | P^a |
|----------------------|--------------------------------|---------|---------|----------|----|-------|
| | 2-3 | 4 | 5-7 | | | |
| White-striped male | | | | | | |
| Median | 2.8 | 3.3 | 3.6 | 4.6 | 2 | 0.10 |
| Range | 2.0-3.5 | 2.5-5.7 | 3.2-4.6 | | | |
| N | 6 | 8 | 5 | | | |
| White-striped female | | | | | | |
| Median | 4.2 | 3.8 | 4.0 | 1.5 | 2 | 0.46 |
| Range | 3.4-6.0 | 2.3-5.0 | 3.9-6.8 | | | |
| N | 10 | 7 | 3 | | | |
| Tan-striped male | | | | | | |
| Median | 4.1 | 4.1 | 3.6 | 0.3 | 2 | 0.86 |
| Range | 2.7-5.0 | 3.7-4.7 | 3.2-5.5 | | | |
| N | 10 | 7 | 3 | | | |
| Tan-striped female | | | | | | |
| Median | 4.7 | 4.8 | 6.1 | 1.5 | 2 | 0.48 |
| Range | 3.4-6.2 | 2.9-6.1 | 3.2-6.9 | | | |
| N | 6 | 8 | 5 | | | |

^a Probability based on Kruskal-Wallis tests (chi-square approximation).

However, for white-striped males, there was a positive correlation between provisioning rate and the length of the shared boundary (Table 3).

There appeared to be no systematic variation in the provisioning rates of tan-striped males relative to the rate at which they sang or the combined rate at which all of their neighbors sang (Table 4). Similarly, the provisioning rates of white-striped females and tan-striped females appeared to be unaffected by the rates at which their mates sang or the rate of neighbor singing. For white-striped males, provisioning rates were positively related to their own song rates but not to the song rates of their neighbors (Table 4).

Thus, for white-striped males, both the length of the shared boundary and song rate appeared to predict provisioning rate. However, we found that these variables were correlated to each other (Pearson's Correlation Coefficient; $r = 0.549$, $N = 19$, $P = 0.0150$). Therefore, we conducted multiple regressions and examined the extra sums of squares for each variable (Neter and Wasserman 1974). These analyses indicated that when the length of the shared boundary was accounted for, song rates remained correlated with provisioning rates (Coefficient of Partial Determination,

TABLE 3
CORRELATIONS BETWEEN TERRITORY PARAMETERS AND PARENTAL PROVISIONING RATES
WITHIN EACH MORPH AND SEX CLASS

| Parameter | White-striped | | Tan-striped | |
|-------------------------------|---------------|--------|-------------|--------|
| | Male | Female | Male | Female |
| Size of territory (area) | | | | |
| Pearson's <i>r</i> | -0.026 | -0.203 | -0.168 | -0.012 |
| <i>P</i> | 0.9353 | 0.4042 | 0.4913 | 0.9712 |
| N | 12 | 19 | 19 | 12 |
| Territory perimeter | | | | |
| Pearson's <i>r</i> | 0.185 | 0.204 | -0.043 | -0.128 |
| <i>P</i> | 0.5644 | 0.4012 | 0.8612 | 0.6913 |
| N | 12 | 19 | 19 | 12 |
| Neighbor density ^a | | | | |
| Pearson's <i>r</i> | 0.169 | -0.117 | -0.135 | 0.049 |
| <i>P</i> | 0.4886 | 0.6551 | 0.6053 | 0.8408 |
| N | 19 | 20 | 20 | 19 |
| Shared boundary ^b | | | | |
| Pearson's <i>r</i> | 0.733 | -0.183 | -0.030 | 0.253 |
| <i>P</i> | 0.0004 | 0.4335 | 0.9020 | 0.2963 |
| N | 19 | 20 | 20 | 19 |

^a Number of contiguous neighbors divided by territory size.

^b Length of territory boundary shared with contiguous neighbors.

$r^2 = 0.34$, $F = 5.48$, $df = 1, 16$, $P = 0.0325$). Similarly, when we corrected for song rate, we found that the length of the shared boundary remained correlated with provisioning rates (coefficient of partial determination, $r^2 = 0.524$, $F = 8.39$, $df = 1, 16$, $P = 0.0105$).

The relationships between white-striped male provisioning rates, the length of their shared boundaries, and their song rates could influence the interpretation of morphic differences in provisioning the young. Where shared boundaries were short (i.e., less than the median length of shared boundary), or song rates were low (i.e., less than the median song rate), low provisioning rates by white-striped males resulted in significant morphic variations in provisioning behavior (Table 5). On the other hand, where shared boundaries were long (i.e., greater than the median length of shared boundary), or song rates were high (i.e., greater than the median song rate), the provisioning rates of white-striped males were higher, and there was no statistical difference between morph and sex classes in provisioning rates (Table 5).

TABLE 4
CORRELATIONS BETWEEN SONG ACTIVITY AND PROVISIONING RATES WITHIN EACH MORPH AND SEX CLASS

| Parameter | White-striped | | Tan-striped | |
|--------------------------------------|---------------|--------|-------------|--------|
| | Male | Female | Male | Female |
| Male songs per hour | | | | |
| Pearson's <i>r</i> | 0.689 | 0.021 | -0.082 | 0.025 |
| <i>P</i> | 0.0011 | 0.9325 | 0.7385 | 0.9197 |
| N | 19 | 19 | 19 | 19 |
| Neighbor songs per hour ^a | | | | |
| Pearson's <i>r</i> | 0.508 | 0.136 | 0.066 | 0.084 |
| <i>P</i> | 0.0264 | 0.5794 | 0.7893 | 0.7321 |
| N | 19 | 19 | 19 | 19 |

^a Number of songs emitted per hour by all contiguous neighbors.

TABLE 5
THE INFLUENCE OF SHARED BOUNDARY AND FOCAL MALE SONG RATES ON THE DETECTION OF MORPHIC DIFFERENCES IN PARENTAL PROVISIONING RATES

| Context | Parental provisioning rate | | | | χ^2 | df | <i>P</i> ^a |
|------------------------------|----------------------------|---------|-------------|---------|----------|----|-----------------------|
| | White-striped | | Tan-striped | | | | |
| | Male | Female | Male | Female | | | |
| Below median shared boundary | | | | | | | |
| Median | 2.7 | 4.1 | 4.1 | 5.0 | 15.6 | 3 | 0.001 |
| Range | 2.0–3.5 | 2.3–6.0 | 2.7–4.9 | 3.4–6.2 | | | |
| N | 7 | 12 | 12 | 7 | | | |
| Above median shared boundary | | | | | | | |
| Median | 3.5 | 4.1 | 4.2 | 4.8 | 4.2 | 3 | 0.241 |
| Range | 2.8–5.7 | 2.3–6.8 | 3.6–5.5 | 2.9–6.9 | | | |
| N | 12 | 7 | 7 | 12 | | | |
| Below median song rate | | | | | | | |
| Median | 3.0 | 4.2 | 4.1 | 5.1 | 13.4 | 3 | 0.004 |
| Range | 2.0–4.0 | 2.3–6.0 | 2.7–5.0 | 3.4–6.2 | | | |
| N | 9 | 9 | 9 | 9 | | | |
| Above median song rate | | | | | | | |
| Median | 3.5 | 4.1 | 4.1 | 4.7 | 3.6 | 3 | 0.314 |
| Range | 2.8–5.7 | 3.4–6.8 | 3.2–5.5 | 2.9–6.9 | | | |
| N | 10 | 10 | 10 | 10 | | | |

^a Probability based on Kruskal-Wallis tests (chi-square approximation).

DISCUSSION

Among the White-throated Sparrows we observed in this study, white-striped males provided fewer provisioning trips to nestlings than did tan-striped females. Tan-striped males and white-striped females were found to have provisioning rates that were intermediate to those of white-striped males and tan-striped females. The combined rates of food delivery by white-striped male \times tan-striped female pairs and by tan-striped male \times white-striped female pairs were equivalent. These results are consistent with the results obtained by Knapton and Falls (1983). As was found in their study, we found no evidence that differences in the number of delivery trips to nestlings were compensated for by differences in the size, number, or types of food delivered. This suggested that morphic variations in parental performance were limited to differences in provisioning rate that, in turn, corresponded to differences in the amount of food delivered to the young.

Whillans and Falls (1990) found no differences in provisioning among morph and sex classes of White-throated Sparrows. This result, in part, could be due to the small samples used in their study ($N = 10$ for each morph and sex class). Whillans and Falls (1990) also suggested that the difference between the results of their study and that of Knapton and Falls (1983) might be attributable to differences in population density. The results of our study indicated that local population density, the number of neighbors, and the song rates of neighbors had no important effect on provisioning behavior.

The provisioning rates of white-striped males were positively related to the length of their shared territory boundary and with the rate at which these males sang. As a result, under conditions where territories had short shared boundaries and focal male song rates were low, differences in provisioning behavior between the morph and sex classes were more pronounced. Where shared boundaries were long and song rates were high, these differences were not statistically significant. If many of the pairs examined by Knapton and Falls (1983) possessed territories with short shared boundaries and many of the pairs examined by Whillans and Falls (1990) possessed long shared boundaries, the observed discrepancy between the results of the two studies would be expected.

Uncontested boundaries differed from shared boundaries in that these portions of the boundary generally occurred in areas where the habitat was unsuitable. Conversely, shared boundaries appeared to occur in areas where the habitat was suitable. In these latter areas, it is likely that, in the absence of defensive effort by the territory owner, either a neighbor or another bird would attempt to occupy that portion of the territory.

Consequently, long shared boundaries should require more effort to defend than short shared boundaries. Therefore, the length of the shared boundary incorporates attributes of both the quality of the area defended and the level of effort needed to defend it.

For white-striped males, we found that the length of their shared boundary was positively related to their song rates. Since song rates may be associated with male condition (Reid 1987), it is possible that for white-striped males, song rate, and consequently the length of the shared boundary, is also related to physical condition.

This latter suggestion may be supported by the observation that provisioning rates and song rates by white-striped males were positively correlated. In many species, there is a negative relationship between male aggressive performance (such as singing behavior) and parental care (Wingfield et al. 1990, but see also Greig-Smith 1982). This effect may be due to either the antagonistic influences of hormones on reproductive behavior (Balthazart 1983) or to energetic trade-offs of reproductive investment (Williams 1966, Cody 1966). A positive relationship among white-striped males between provisioning behavior and song rate implies that these males differed from each other, not in the activity of hormones, but in the total amount of energy being devoted to current reproduction. Greater levels of reproductive investment imply better physical condition.

Unlike in white-striped males, there was no evidence of systematic relationships between provisioning behavior, male song rate, and the length of the shared boundary among white-striped females, tan-striped males, and tan-striped females. For these birds we found no evidence that the length of the shared boundary might be related to physical condition.

Knapton and Falls (1983) observed the parental behavior of two white-striped male \times white-striped female pairs. They found no evidence that either sex compensated for the behavior of their mates, suggesting that differences in provisioning behavior may be relatively fixed within the morph and sex classes. Such variations in parental care should influence the reproductive success of pairs and might have implications for promoting negative assortative mating and the maintenance of polymorphism in White-throated Sparrows. Plumage color, song rates, and the length of the shared boundary could be assessed by females and might be useful if they used expected parental performance as a criterion in choosing mates. Similarly, since female provisioning behavior varies according to morph, males might exercise choices among females, using plumage color as a signal of expected parental performance. If so, then in general, tan-striped males and tan-striped females should preferentially pair together because such pairs should exhibit the greatest parental performance. The exception should occur for that half of the male population that occupy

territories with longer than the median shared boundary. In this case, preferences for morph may not be as important. The preceding scenario would predict the occurrence of a large number of tan-striped male \times tan-striped female pairs among the breeding population. However, this prediction is not borne out by the low frequency (1.0%) of these pairs actually observed in the population (Kopachena 1992).

Thus, negative assortative mating among White-throated Sparrows cannot be explained simply on the basis of mate choices among males and females attempting to maximize parental care toward the young. While parental care may be important, a satisfactory explanation of why negative assortative mating persists in the White-throated Sparrow requires the incorporation of additional factors. Previous studies (Lowther 1962; Kopachena 1992; Loncke, unpubl. data) have indicated that there are also morphic variations in aggressive performance. It is possible that these differences, in conjunction with morphic variations in parental care, represent a suite of reproductive strategies that favor a negative assortative mating system.

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LITERATURE CITED

- BALTHAZART, J. 1983. Hormonal correlates of behavior. *Avian Biol.* 7:221–365.
- CODY, M. L. 1966. A general theory of clutch size. *Evolution* 20:174–184.
- FALLS, J. B. 1981. Mapping territories with playback: An accurate census method for songbirds. *Studies in Avian Biol.* 6:86–91.
- GOSS-CUSTARD, J. D., J. T. CAYFORD, J. S. BOATES, AND S. E. A. LE V. DIT DURRELL. 1987. Field tests of the accuracy of estimating prey size from bill length in oystercatchers, *Haematopus ostralegus*, eating mussels, *Mytilus edulis*. *Anim. Behav.* 35:1078–1083.
- GREIG-SMITH, P. W. 1982. Song-rates and parental care by individual male stonechats (*Saxicola torquata*). *Anim. Behav.* 30:245–252.
- KNAPTON, R. W. AND J. B. FALLS. Differences in parental contribution among pair types in the polymorphic white-throated sparrow. *Can. J. Zool.* 61:1288–1292.
- , R. V. CARTER, AND J. B. FALLS. 1984. A comparison of breeding ecology and reproductive success between morphs of the White-throated Sparrow. *Wilson Bull.* 96: 60–71.
- KOPACHENA, J. G. 1992. Behavioral correlates of plumage polymorphism and post-fledging parental care in the White-throated Sparrow (*Zonotrichia albicollis*). Ph.D. diss., Univ. of Toronto, Toronto, Ontario.

- KREBS, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. Ecology 52:2-22.
- LOWTHER, J. K. 1961. Polymorphism in the White-throated Sparrow, *Zonotrichia albicollis* (Gmelin). Can. J. Zool. 39:281-292.
- . 1962. Colour and behavioral polymorphism in the White-throated Sparrow, *Zonotrichia albicollis* (Gmelin). Ph.D. diss., Univ. of Toronto, Toronto, Ontario.
- MYERS, J. P., P. G. CONNORS, AND F. A. PITELKA. 1979. Territory size in wintering sanderlings: the effects of prey abundance and intruder density. Auk 96:551-561.
- NETER, J. AND W. WASSERMAN. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, Illinois.
- PRATT, J. W. AND J. D. GIBBONS. 1981. Concepts of nonparametric theory. Springer-Verlag, New York, New York.
- RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.
- REID, M. L. 1987. Costliness and reliability in the singing vigour of Ipswich sparrows. Anim. Behav. 35:1735-1743.
- THORNEYCROFT, H. B. 1975. A cytogenetic study of the White-throated Sparrow, *Zonotrichia albicollis* (Gmelin). Evolution 29:611-621.
- WHILLANS, K. V. AND J. B. FALLS. 1990. Effects of male removal on parental care of female white-throated sparrows *Zonotrichia albicollis*. Anim. Behav. 39:869-878.
- WIENS, J. A., J. T. ROTENBERRY, AND B. VAN HORNE. 1985. Territory size variation in shrubsteppe birds. Auk 102:500-505.
- WILLIAMS, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100:687-690.
- WINGFIELD, J. C., R. E. HEGNER, A. M. DUFTY, JR., AND G. F. BALL. 1990. The "Challenge Hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. Am. Nat. 136:829-846.
- ZIMMERMAN, J. L. 1971. The territory and its density dependent effect in *Spiza americana*. Auk 88:591-612.

WILSON ORNITHOLOGICAL SOCIETY MEETINGS

The Wilson Ornithological Society will meet at the University of Guelph, Guelph, Ontario, 29 April-1 May 1993. Questions concerning the meeting can be directed either to Alex Middleton (Chair, Local Committee), Zoology Department, University of Guelph, Guelph, Ontario, N1G 2W1, or Keith L. Bildstein (Chair, Scientific Program Committee), Hawk Mountain Sanctuary, R.D. 2, Kempton, Pennsylvania 19529.