A COMPARISON OF BREEDING ECOLOGY AND REPRODUCTIVE SUCCESS BETWEEN MORPHS OF THE WHITE-THROATED SPARROW

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The White-throated Sparrow (*Zonotrichia albicollis*) is polymorphic in plumage and behavior (Lowther 1961, Lowther and Falls 1968, Atkinson and Ralph 1980, pers. obs.) and in karyotype (Thorneycroft 1976), and morphometric differences between morphs have been correlated with karyotype (Rising and Shields 1980). This polymorphism appears to be maintained by negative assortative mating; white-striped (WS) birds of either sex usually pair with tan-striped (TS) birds of the opposite sex (Lowther 1961, Thorneycroft 1976, Knapton and Falls 1983). Furthermore, there are ecological differences between morphs: Knapton and Falls (1982) found that the range of habitat types occupied by WS and TS males was different; WS males defended territories in "open" habitat whereas TS males defended territories in a broader range of habitat, from "open" to "dense." Possible explanations for this difference in habitat occupancy are: (1) WS males dominate TS males in territorial encounters, establish territories in optimal habitat, and force some TS males into suboptimal habitat. (2) WS males arrive on the breeding grounds before TS males, occupy the "best" areas, and force TS males to take territories in suboptimal areas. In either case, some measure of reproductive fitness should be lower in TS males. (3) TS males achieve, over a broad range of habitat types, a reproductive fitness which is equivalent to that of WS males in a narrower range. In this paper, we investigate the arrival dates, breeding ecology, and reproductive success in populations of WS and TS birds to determine if differences occur between morphs.

Aspects of the breeding biology of the White-throated Sparrow have been studied by Lowther (1960, summary in Lowther and Falls 1968) and Wasserman (1980); however, these workers did not examine differences in the breeding ecology of the two morphs. Knapton and Falls (1983) showed differences between morphs in parental contribution to feeding nestlings. Here we compare morphs with the following questions: (1) Does time of arrival on the breeding grounds differ? (2) Are there different degrees of site tenacity? (3) Are there differences in breeding biology—in clutch-size, clutch initiation, growth of nestlings, and number of young fledged per nest?

METHODS

We carried out the study in Algonquin Provincial Park, Nipissing District, Ontario, during the spring and summer of 1979, 1980, and 1981. The following study areas were used: (1) around the periphery of the Lake of Two Rivers airfield (Airfield), (2) at Pog Lake, and (3) near the Pioneer Logging Exhibit (PLE). Distances between study areas ranged from 6 km (Airfield–Pog Lake) to 24 km (Airfield–PLE). We caught birds in mist nets, and banded each one with a unique color combination of plastic bands. Nestlings were banded at 5 days of age with unique plastic band combinations.

Nests were located by searching each study area. Most nests were discovered when the incubating bird was flushed; others were found by following adults carrying food. For each nest, we noted its location on aerial photographs (scale, 1 cm : 40 m), and the identity and morph of each parent. A log was kept for each nest until it was empty: either the young fledged or the nest contents were robbed. Thus, we could determine success rate, and length of incubation and nestling periods, for each of the two main pair types, WS male × TS female and TS male × WS female.

We determined the start of egg-laying from our own data and that of Lowther (1960). We assumed that one egg was laid per day and used day 0 as the start of incubation and day 12 as the day the eggs hatched. In the analysis of clutch intiation, we considered only those nests in which the first egg was laid in May in 1980, and in May and early June in 1981 (see below); thus, these were probably all first nesting attempts. In our comparison of clutch-size between morphs, we used only four and five egg clutches, and only those nests in which clutch-size remained constant for three or more days.

We determined growth rates of young White-throated Sparrows as follows. Each nestling was weighed to the nearest 0.5 g every day until it fledged or disappeared (presumably through predation) from the nest. Each nestling was marked on the tarsus with a felt marker, and therefore we could identify individuals within each nest from one day to the next. In the analyses, we compared growth of the nestlings between parental female morphs and between brood-sizes. Day by day comparisons of nestling weights were made with *t*-tests and two-way analysis of variance (by morph and clutch-size).

RESULTS

Arrival on breeding grounds.—White-throated Sparrows arrived on the study areas from the last few days of April to mid-May. Males arrived before females in 1980 and 1981 (observations in 1979 started in mid-May, after the males had arrived). Fig. 1 shows cumulative arrival frequencies for males and females of both morphs in 1980; the trends were similar in 1981.

The period of arrival was broad for both WS and TS males (Fig. 1). Cumulative territorial occupancy at 90% was reached in about 15 days by both morphs in 1980 (Fig. 1) and in about 14 days in 1981. Hence the length of the arrival period did not appear to differ between male morphs.

WS males seemed to arrive slightly earlier than TS males. In 1980, 58.7% (27/46) of WS males arrived by 6 May compared to 42.9% (9/21) of TS males, and in 1981, 64.3% (27/42) of WS males arrived by 5 May
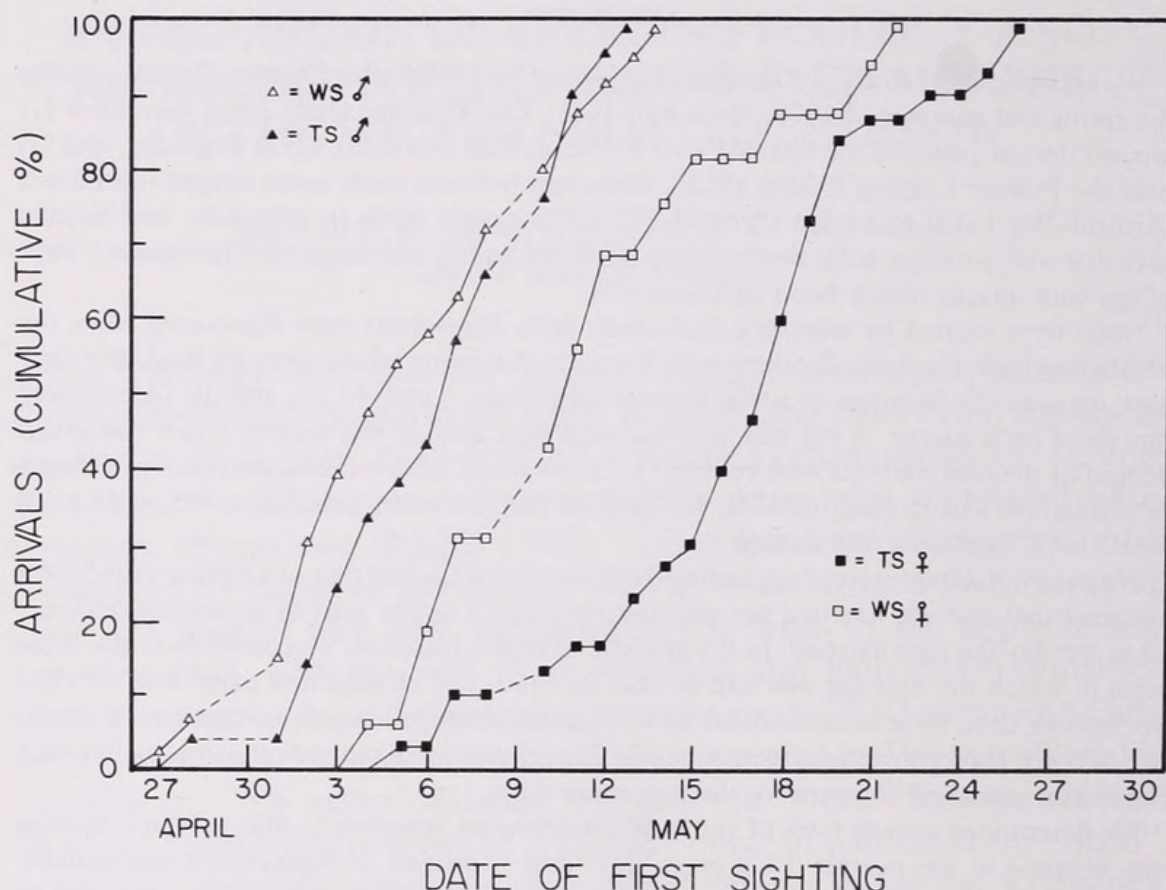
FIG. 1. Cumulative arrival frequencies of WS and TS male and female White-throated Sparrows, 1980 data. Data for 1981 follow similar trends. No mistnetting was done on 29 and 30 April, and 9 May. Numbers for each morph-sex class were 46 WS males, 21 TS males, 30 TS females, and 16 WS females.

compared to 52.2% (12/23) of TS males; however, neither difference is significant (1980: $\chi^2 = 0.88$, df = 1, NS; 1981, $\chi^2 = 0.47$, df = 1, NS).

WS females were detected significantly earlier than TS females in both years. Of 46 females (16 WS, 30 TS) identified in May 1980, 12 WS and only eight TS were detected by 14 May ($\chi^2 = 7.97$, df = 1, $P < 0.01$); of 24 females (10 WS, 14 TS) identified in May 1981, nine WS and three TS were detected by 14 May (Fisher's exact test, $P < 0.004$).

Site tenacity.—In total, we banded 340 adults: 176 in 1979, 103 in 1980, and 69 in 1981. We color banded 65 nestlings in 1980.

A comparison of return rates between males of the two morphs revealed no differences for all study areas combined (Table 1). Twenty-three of 46 WS males and 11 of 21 TS males returned in 1980 ($\chi^2 = 0.007$, df = 1, NS), and 20 of 42 WS males and 9 of 23 TS males returned in 1981 ($\chi^2 = 0.55$, df = 1, NS). The number of returning WS males varied from 50.0% (1979–80) to 47.6% (1980–81), and that of TS males from 52.4% (1979–

TABLE 1

RETURN RATES OF MALE WHITE-THROATED SPARROWS OF BOTH MORPHS TO THE STUDY
AREAS

Study area	No. territorial males (1979)	No. returning males (1980)	WS	TS
PLE	31	19 (61.3%)	15/22 (68.2%)	4/9 (44.4%)
Airfield	22	11 (50.0%)	6/14 (43.0%)	5/8 (62.5%)
Pog Lake	14	4 (28.6%)	2/10 (20.0%)	2/4 (50.0%)
Total	67	34 (50.7%)	23/46 (50.0%)	11/21 (52.4%)
	(1980)	(1981)	WS	TS
PLE	30	14 (46.6%)	11/23 (47.8%)	3/7 (42.9%)
Airfield	22	9 (40.9%)	5/12 (41.7%)	4/10 (40.0%)
Pog Lake	13	6 (46.2%)	4/7 (57.1%)	2/6 (33.3%)
Total	65	29 (44.6%)	20/42 (47.6%)	9/23 (39.1%)

80) to 39.1% (1980–81). These return rates are probably conservative, as some males returned to the study areas but not to the same territories occupied the previous year. Thus, a male that returned to take a territory just outside the study areas would have gone undetected.

Return rates of females were very low. Only three females out of 55 banded in 1979 returned in 1980, a return rate of 5.5%. All three were WS, and two returned to the same territories occupied the year before, but to different mates. Four females (three WS, one TS) out of 43 banded in 1980 returned in 1981 (9.3%), two of these females returning to the same territory occupied in 1980. During 1981, we did not see any of the 65 nestlings color-banded in 1980.

The nesting season.—Forty-three nests were found in 1980 and 24 in 1981. Nests were found at various stages of the breeding cycle, and therefore not all nests could be used in each analysis.

Clutch initiation.—In 1980, we located 14 nests in which the first egg was laid in May, and therefore probably were all first nests. Seven nests were of TS male × WS female pairs, and seven of WS male × TS female pairs. The dates of first eggs laid are as follows: TS male × WS female— 19, 22, 22, 23, 25, 26, 26 May; WS male × TS female—27, 27, 27, 28, 28, 28, 31 May. From this sample, a clear separation in clutch initiation between morphs appeared ($R = 2$, $P < 0.05$ Wald-Wolfowitz runs test). In 1981, the calculated laying date of the first egg was 28 May, 9 days later than in 1980. In 1981, 15 probable first nests were initiated between 28 May and 6 June, as follows: TS male × WS female—29, 31, 31 May,

TABLE 2
COMPARISON OF CLUTCH-SIZE BETWEEN FEMALE MORPHS DURING MAY, JUNE, AND JULY

Clutch-size	May		June		July		Total	
	WS	TS	WS	TS	WS	TS	WS	TS
1980								
4	2	6	4	9	1	2	7	17
5	5	0	2	4	0	0	7	4
1981								
4	0	1	8	7	0	0	8	8
5	0	0	1	3	0	0	1	3

1, 5 June; WS male × TS female—28, 29, 29, 29, 29 May, 3, 3, 4, 5, 6 June. There was no difference between morphs in clutch initiation ($R = 7$, $P > 0.05$, Wald-Wolfowitz runs test).

Clutch initiation of WS male × TS female pairs was similar between years ($R = 6$, $P > 0.05$, Wald-Wolfowitz runs test). On the other hand, clutch initiation of TS male × WS female pairs was much later in 1981 ($R = 2$, $P < 0.05$, Wald-Wolfowitz runs test); there was about a 10-day difference between years.

Clutch-size.—We used a sample of 55 nests (35 in 1980, 20 in 1981) in this analysis. Forty of these were four-egg and 15 were five-egg clutches (Table 2).

Clutch-sizes did not differ between females of the two morphs in either year. In 1980, TS females had 17 four-egg and 4 five-egg clutches whereas WS females had 7 four-egg and 7 five-egg clutches ($P = 0.060$, Fisher's exact test). In 1981, TS females had 8 four-egg and 3 five-egg clutches, and WS females had 8 four-egg and 1 five-egg clutches ($P = 0.932$, Fisher's exact test).

Clutch-sizes did not differ between years for either morph. For WS females, there were 7 four-egg and 7 five-egg clutches in 1980, and 8 four-egg and 1 five-egg clutches in 1981 ($P = 0.069$, Fisher's exact test). For TS females, there were 17 four-egg and 4 five-egg clutches in 1980, and 8 four-egg and 3 five-egg clutches in 1981 ($P = 0.983$, Fisher's exact test). Thus, clutch-size was not affected by the later onset of nesting in 1981.

Success rates.—In this analysis, a successful nest is defined as one from which one or more young fledged. Success rates were 54% for TS females and 50% for WS females in 1980, and 46% for TS females and 45% for WS females in 1981 (Table 3). There were no differences between morphs

TABLE 3
COMPARISON OF SUCCESS RATES OF NESTS BETWEEN WS AND TS FEMALES

Study area (year)	Total no. nests	No. successful nests	Success rates	
			TS female	WS female
1980				
All study areas	38	20 (53%)	13/24 (54%)	7/14 (50%)
1981				
All study areas	24	11 (45%)	6/13 (45%)	5/11 (45%)
1980 + 1981				
PLE	26	18 (69%)	13/21 (62%)	5/5 (100%)
Other areas	36	13 (36%)	6/16 (38%)	7/20 (35%)

in success rates (1980—χ^2=0.06, df = 1, NS; 1981—χ^2 = 0.14, df = 1, NS).

However, there were differences among study areas. Success rate at the PLE was 69% (18 out of 26 nests), whereas that for all other study areas combined was only 36% (13 out of 36 nests) (Table 3, χ^2 = 6.63, df = 1, $P < 0.05$). Observer activity at nests did not vary among study areas, and most nest contents were lost to predation, which accounted for 74% of egg losses and 75% of losses of young. This implies that predation was less intense at PLE than elsewhere. Linings of most robbed nests were disturbed, suggesting mammalian predation. Signs and sightings of two potential mammalian predators, marten (*Martes martes*) and red fox (*Vulpes fulva*), were more frequent at the Airfield than elsewhere, which may help to explain the lowered success rates there.

The number of nests found in 1980 was 38 (Table 3). Six pairs renested, one pair was double-brooded (see below), therefore we have success rates of 31 males. Twenty of these males were successful, and of these 20, eight (six WS, two TS) returned in 1980. Of the 11 unsuccessful males, six (four WS, two TS) returned. Thus, successful males are no more likely to return the next year than unsuccessful ones (χ^2 = 0.17, df = 1, NS). Only one female (WS) of the 31 pairs returned in 1981; she had successfully raised young in 1980.

Nesting mortality.—There was no consistent difference in number of fledged young between WS and TS females during 1980 and 1981 (Table 4). TS females fledged proportionately more young than WS females in 1980 (50%:43%) but fewer young in 1981 (37%:49%). Differences were not significant in either year (1980—χ^2 = 0.48, df = 1, NS; 1981—χ^2 =

TABLE 4

COMPARISON OF HATCHING AND FLEDGING SUCCESS BETWEEN FEMALE MORPHS

	1980		1981		1980 + 1981	
	TS	WS	TS	WS	TS	WS
No. eggs laid	84	63	57	41	141	104
No. eggs hatched	63 (75%)	44 (70%)	36 (63%)	28 (68%)	99 (70%)	72 (69%)
No. young fledged	42 (50%)	27 (43%)	21 (37%)	20 (49%)	63 (44%)	47 (45%)

0.95, df =1, NS) or for both years combined (1980 + 1981, χ^2 = 0.003, df = 1, NS).

There was no relationship between age of young and risk of predation (Table 5). Eggs hatched in 23 nests, hence we could estimate the age of nestlings in these nests to within a day. Young fledged from 11 of these nests, and the rate of predation on the other 12 nests was relatively uniform. Thus, predation rates did not increase with age of young or increased parental activity at the nest.

Length of nestling period.—We used day 0 as the day on which the eggs hatched, and recorded the days when young were in the nest. Table 5 shows that young fledged at day 9 from 9 of the 11 nests that were followed from hatching to fledging. Young from the remaining two nests left at day 8 and day 10 respectively. Six of the female parents were TS, five were WS, and there were no differences between morphs in the length of nestling period.

Second broods.—The information on double-broodedness refers to the PLE study area. Eleven pairs fledged young before 7 July; of these 11, six (54.5%) attempted second broods (four WS × TS and two TS × WS pairs). A breakdown of these six is as follows: a second nest, later robbed, was found for one pair, three pairs were found with young barely able to fly in late July and August, and two pairs were seen carrying food and giving distraction displays (approach within 1 m of observer, high rate of alarm calls, "broken wing" display) in early August. Loncke and Falls (1973) related double-broodedness to high populations of spruce budworm (*Choristoneura fumiferana*). This was probably not a factor in 1980 as budworm populations were not particularly high (Howse et al. 1981). White-throated Sparrows are probably frequently double-brooded provided that they raise one brood early enough to allow them sufficient time to attempt a second brood. As in other studies of White-throated Sparrows (e.g., Lowther 1960), we found renesting to be common.

TABLE 5
AGE OF NESTLINGS AND RATE OF PREDATION

	Day										
	0	1	2	3	4	5	6	7	8	9	10
No. active nests	23	22	21	18	15	14	13	11	10	1	0
No. empty nests	0	1	1	3	3	1	1	2	0	0	0
No. successful nests[a]	—	—	—	—	—	—	—	—	1	9	1

[a] Nest empty; young out of the nest nearby.

Growth rates of nestlings. — We found no significant differences in nestling weight at any age (from hatching to fledging) between female morphs, and furthermore there were no significant differences in nestling weight between brood-sizes of three and four (*t*-tests, $P > 0.05$, Fig. 2 and Appendix). Finally, we found no significant differences in nestling weight when female morph and brood-size are considered together (two way analysis of variance, $P > 0.05$).

DISCUSSION

As mentioned earlier, Knapton and Falls (1982) found that WS males defended territories in a narrower range of habitat types than did TS males. To reiterate two possible explanations: (1) WS males dominate TS males in territorial encounters and thus come to occupy the optimal habitat, forcing some TS males into suboptimal habitat; and (2) WS males arrive on the breeding grounds before TS males, occupy the "best" areas, and in this way cause TS males to take territories in suboptimal areas. In either case, some measure of reproductive fitness should be lower in TS males than in WS males.

Our analyses support neither explanation. There was no obvious dichotomy of arrival between male morphs. Total arrival periods for males were equally broad for each morph, and birds of both morphs returning from the previous year appeared on the study areas throughout the arrival period, not necessarily at the beginning. Although WS males arrived slightly earlier, the differences between morphs were not significant. Furthermore, TS males are more cryptic in behavior than WS males (pers. obs.), and hence are more likely to be overlooked. WS females were detected earlier than TS females; however, not only are TS females more cryptic than WS females, but a female tends to be detected when she is already associating with a male, hence the actual arrival dates of all females may be earlier than indicated. Possibly, these results indicate that pair for-
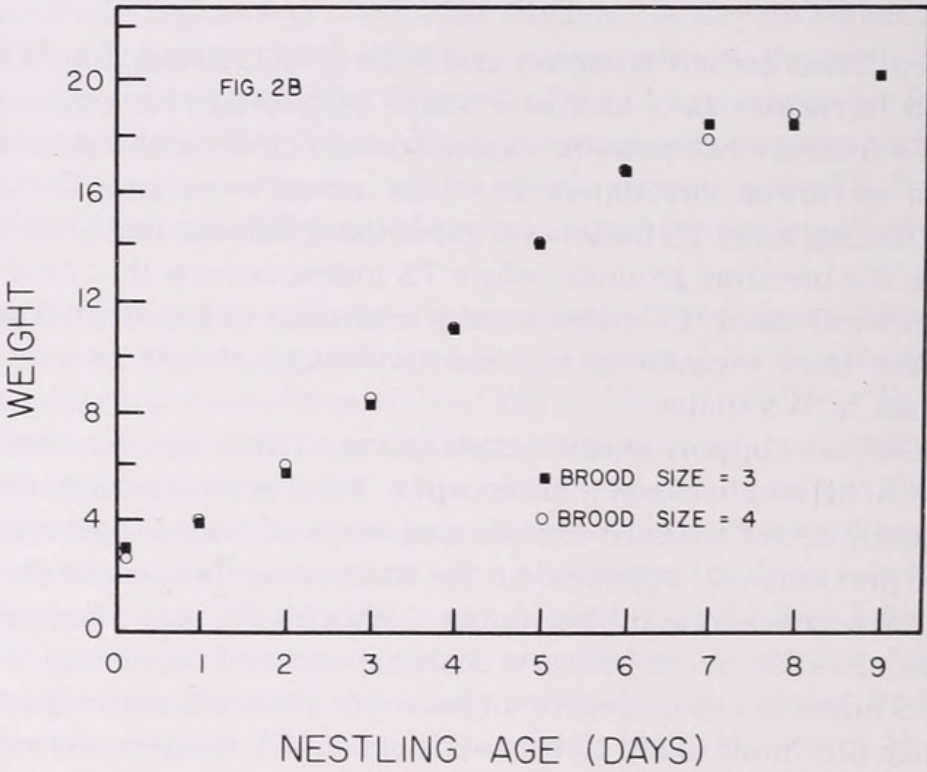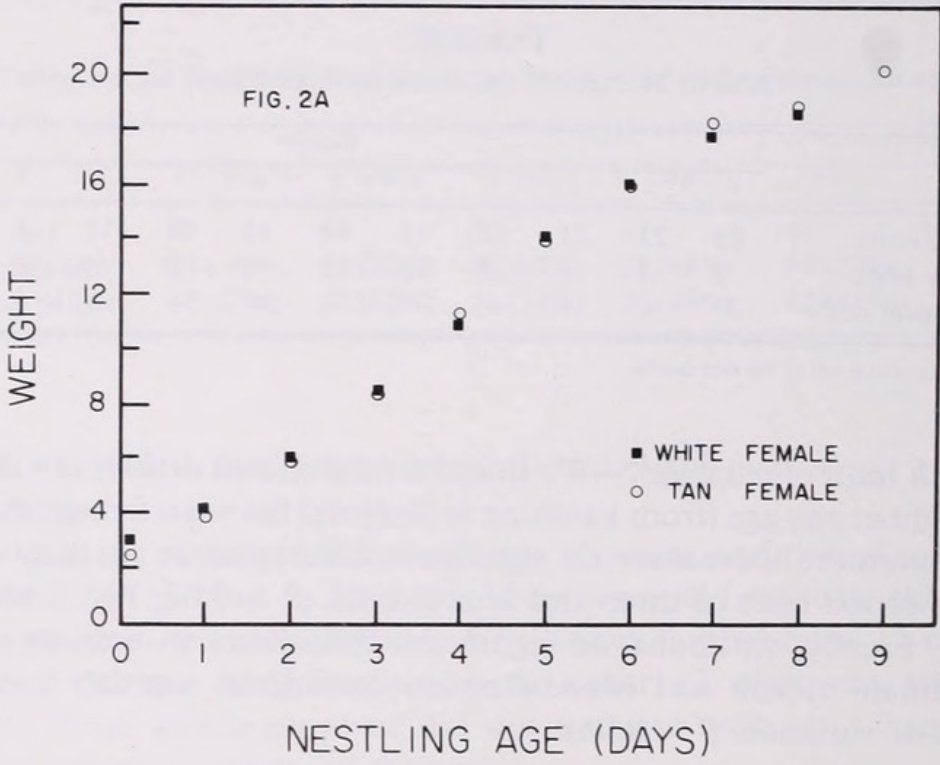
FIG. 2. Comparisons of nestling age with weight (g) between female morphs (2A) and between brood-size (2B).

mation is quicker in TS male × WS female pairs, rather than an earlier arrival of WS females.

If WS males dominated or arrived before TS males, then one might predict that WS males would show a higher rate of return than TS males in subsequent years. We detected no such difference in rate of return between males of the two morphs to the study areas.

Clutch intiation in 1980 was significantly earlier in TS × WS pairs than in WS male × TS female pairs, but was similar between pair types in 1981. The difference in 1980 could be explained either by an earlier arrival of WS females or by quicker pair formation in TS male × WS female pairs. Cumulative arrival data show a broad overlap in time of arrival of females of both morphs. Thus, we are left with the argument that pair formation is quicker in TS male × WS female pairs, and, under certain environmental conditions, this can result in an earlier onset of clutch initiation.

Success rates of nests, number of young fledged per nest, length of nestling period and growth rates of nestlings did not differ between morphs. Therefore the argument that TS males suffer reduced reproductive fitness because they are in suboptimal habitat does not seem convincing. We cannot compare contributions to future gene pools between morphs as no banded nestlings returned to breed on the study areas in subsequent years. Young of WS and TS females fledged at similar weights, however, and if weight at fledging reflects future survival, then there is no indication that the young of one morph differed from those of the other. Thus, the argument that TS males suffer a reproductive cost by occupying "suboptimal" habitat is not supported.

TS males sing less (Lowther and Falls 1968), are less responsive to song playback than WS males on the breeding grounds (J. Jones, pers. comm.), and initiate fewer aggressive encounters (Ficken et al. 1978), while their level of contribution to feeding young is significantly greater (Knapton and Falls 1983), than that of WS males. These behavioral differences suggest that if TS males are indeed forced into suboptimal habitats, they maximize their fitness by apportioning more time and energy into parental care and less into territory defense and advertisement.

SUMMARY

We compared breeding ecology and reproductive success between morphs of the White-throated Sparrow (*Zonotrichia albicollis*). Total arrival time was equally broad for both white-striped (WS) and tan-striped (TS) males, and no difference was found in time of arrival on the breeding grounds between male morphs. WS females were detected significantly earlier than TS females; this is possibly a result of quicker pair formation in TS male × WS female pairs as clutch initiation was earlier in this pair type in one year than in WS male ×

TS female pairs. Return rates of males to the study areas in successive years did not differ between morphs; return rates of females were very low in all years.

Success rates of nests, number of young fledged per nest, length of nestling period, growth rates of nestlings, and weight of nestlings at fledging did not differ between morphs. Thus, the argument that TS males suffer a reproductive cost by occupying "suboptimal" habitat is not supported.

ACKNOWLEDGMENTS

LITERATURE CITED

ATKINSON, C. T. AND C. J. RALPH. 1980. Acquisition of plumage polymorphism in White-throated Sparrows. Auk 97:245–252.

FICKEN, R. W., M. S. FICKEN, AND J. P. HAILMAN. 1978. Differential aggression in genetically different morphs of the White-throated Sparrow (*Zonotrichia albicollis*). Z. Tierpsychol. 46:43–57.

HOWSE, G. M., P. D. SYME, H. L. GROSS, D. T. MYREN, AND M. J. APPLEJOHN. 1981. Insect and disease conditions in Ontario, Summer 1980. Survey Bull. 4. Great Lakes Forest Research Centre, Environment Canada, Sault Saint Marie, Canada.

KNAPTON, R. W. AND J. B. FALLS. 1982. Polymorphism in the White-throated Sparrow: habitat occupancy and nest-site selection. Can. J. Zool. 60:452–459.

——— AND ———. 1983. Differences in parental contribution among pair types in the polymorphic White-throated Sparrow. Can. J. Zool. 61:1288–1292.

LONCKE, D. J. AND J. B. FALLS. 1973. An attempted third brood in the White-throated Sparrow. Auk 90:904.

LOWTHER, J. K. 1960. Some aspects of the breeding biology of the White-throated Sparrow, *Zonotrichia albicollis* (GMELIN). M.A. thesis, Univ. Toronto, Toronto, Ontario.

———. 1961. Polymorphism in the White-throated Sparrow, *Zonotrichia albicollis*. Can. J. Zool. 39:281–292.

——— AND J. B. FALLS. 1968. White-throated Sparrow. Pp. 1364–1392 *in* Life histories of North American cardinals, buntings, towhees, finches, sparrows and allies. Pt. 3 (O. L. Austin, Jr., ed.). U.S. Natl. Mus. Bull. 337.

RISING, J. D. AND G. F. SHIELDS. 1980. Chromosomal and morphological correlates in two New World sparrows (Emberizidae). Evolution 34:354–662.

THORNEYCROFT, H. B. 1976. A cytogenetic study of the White-throated Sparrow, *Zonotrichia albicollis*. Evolution 29:611–621.

WASSERMAN, F. E. 1980. Territorial behavior in a pair of White-throated Sparrows. Wilson Bull. 92:74–87.

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APPENDIX

GROWTH RATES (WGT. IN G) OF NESTLING WHITE-THROATED SPARROWS WITH RESPECT TO MORPH OF FEMALE AND BROOD-SIZE

	TS female			WS female		
Age	N	$\bar{x}$	±SD	N	$\bar{x}$	±SD
0	23	2.6	0.5	26	3.0	0.9
1	32	3.8	0.7	34	4.2	1.2
2	32	6.0	1.3	30	6.0	1.5
3	28	8.4	1.4	27	8.6	1.7
4	25	11.2	1.6	22	10.8	2.0
5	22	14.0	1.5	22	14.1	1.9
6	15	16.0	1.6	22	15.9	1.7
7	16	18.3	1.8	19	17.7	1.7
8	9	18.8	1.2	10	18.5	1.7
9	2	20.3	0.2			
	Brood-size 3			Brood-size 4		
Age	N	$\bar{x}$	±SD	N	$\bar{x}$	±SD
0	15	2.9	0.7	28	2.6	0.6
1	21	3.8	0.9	40	4.0	1.0
2	21	5.7	1.6	36	6.1	1.3
3	18	8.3	1.6	32	8.6	1.5
4	15	11.0	2.1	32	11.0	1.7
5	12	14.1	1.6	32	14.0	1.7
6	9	16.6	1.2	28	15.7	1.7
7	3	18.4	1.6	32	17.9	1.8
8	1	18.4	—	18	18.7	1.4