

Negative assortative mating in the white-throated sparrow, *Zonotrichia albicollis*: the role of mate choice and intra-sexual competition

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Abstract. White-throated sparrows are dimorphic, mating disassortatively by morph. In laboratory choice trials, females of both morphs preferred tan-striped males when allowed to interact with males (two-way choice), but displayed no preferences when one-way mirrors did not allow stimulus males to interact with them (one-way choice). Males of both morphs displayed significant preferences for white-striped females in one-way choice trials, but not in two-way trials. During within-sex competition trials, white-striped birds were dominant to tan-striped birds of the same sex. These results suggest that negative assortative mating is maintained in part because white-striped females outcompete tan-striped females for access to the preferred tan-striped males. Tan-striped females then pair with the less preferred white-striped males. A three-step process is proposed to account for the high level of negative assortative mating seen in the white-throated sparrow.

Negative assortative mating is extremely rare in nature (cf. Sheppard 1952; Murton et al. 1973; Yamazaki et al. 1982) and the selective forces supporting it are not well understood, emphasizing the need to study the processes involved in its maintenance. Negative assortative mating in a population with two morphs may occur when: (1) both males and females prefer the opposite morph; (2) either males or females display preferences for the opposite morph, with no preferences displayed by the other sex; (3) both types of males prefer one female morph, with one male morph outcompeting the other for access to the preferred female morph; (4) both types of females display preferences for one male morph, with one female morph outcompeting the other for access to the preferred male morph.

White-throated sparrows are dimorphic and mate disassortatively by morph. The white-striped morph has brighter crown stripes, brighter yellow lores and less striping in the throat patch than the tan-striped morph (Lowther 1961; Lowther & Falls 1968; Atkinson & Ralph 1980). White-striped birds are also larger, sing more and are more aggressive than tan-striped birds of the same sex (Lowther 1961; Lowther & Falls 1968;

Atkinson & Ralph 1980; Rising & Shields 1980). A chromosomal inversion separates white-striped from tan-striped birds in both sexes (Thornycroft 1966). Approximately 93–98% of the population mates with an individual of the opposite morph (Thornycroft 1976; Knapton & Falls 1982, 1983). Because white-striped birds are heterozygous for the inversion, while tan-striped birds are homozygous for the presumed ancestral condition, negative assortative mating maintains the dimorphism at 50/50 in the population, regardless of the proportion of pair types on the species' mating grounds (approximately 70% of pairs consist of a white-striped male and a tan-striped female; Thornycroft 1976; Knapton & Falls 1983; unpublished data).

The white-throated sparrow breeding system presents an excellent opportunity to evaluate the processes involved in the maintenance of negative assortative mating, and more generally, the processes involved in sexual selection. Studies of sexual selection have in general been conducted on species in which mating patterns and the associated traits are less obvious than in the white-throated sparrow, where morph is easily identified, bimodally distributed and accounts for over 90% of the variance in mating patterns (Thornycroft 1976; Knapton & Falls 1982, 1983). Because white-throated sparrows are typically already paired when both sexes are located in the

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field, we conducted mate choice and intra-sexual competition trials in the laboratory.

METHODS

Birds were caught on their territories at the beginning of the breeding season at Algonquin Provincial Park, Ontario. In 1990 birds were caught between 14 and 27 May; this group (group 1) included nine tan-striped males, eight white-striped males, 11 tan-striped females and eight white-striped females. A second group of birds (group 2) was captured between 9 and 20 May 1991, and included six tan-striped males, eight white-striped males, seven tan-striped females and five white-striped females. In all cases in which the mate of the bird was captured (and released) or sighted, it was of the opposite morph. All birds captured were adults of unknown age.

Group 1 birds were brought to the Animal Care Facility at the University of Toronto Department of Zoology, where they were maintained in same-sex aviaries (102 × 40 × 94 cm) on a natural light schedule until spring 1991, when choice trials began. Group 2 birds were maintained at the Wildlife Research Station in Algonquin Provincial Park in individual cages (40 × 30 × 44 cm), where choice and competition trials were conducted soon after capture. Birds used in choice trials were determined to be in breeding condition through assessment of sex-specific cloacal development.

Birds were kept in individual cages during and between trials, after which they were transferred to same-sex aviaries. They were given ad libitum birdseed, water, cuttlefish bones and grit, and provided with mealworms, greens and water-soluble vitamins regularly.

Mate Choice Trials

We conducted one- and two-way mate choice trials to separate the effects of physical and behavioural factors on mate preferences. We conducted choice trials in a three-way apparatus (Fig. 1). Birds in the middle chamber (choosing birds) were presented with a simultaneous choice of a white-striped and tan-striped bird of the opposite sex located in two peripheral chambers. All choosing birds were run in two trials, in random order, with different stimulus birds used in each trial. In the first trial (one-way choice trial), we placed

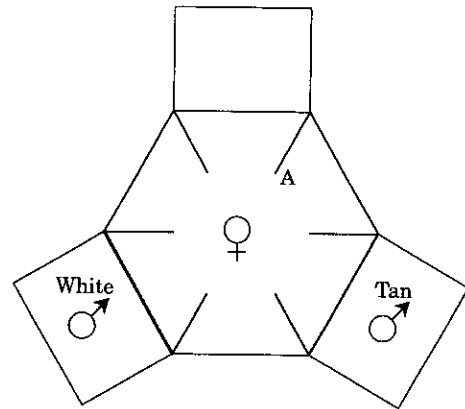


Figure 1. Mate choice apparatus during a female choice trial, with a female in the central chamber and one tan-striped male and one white-striped male in the outer stimulus cage. One stimulus cage remained empty. In male choice trials, a male was placed in the central chamber and one female of each morph was placed in a stimulus cage. The dividers (A) between cages allowed the choosing bird only to see the male it visited, and prevented the stimulus birds from seeing each other. During one-way choice trials, one-way mirrors were placed between the central and outer cages. During two-way choice trials, clear glass panels were placed between the central and outer cages. A choosing bird was considered to be visiting an outer cage when it entered the shaded area (0.12 m²) outside that cage. The central chamber measured 93 cm in diameter and 44 cm high. The dimensions of the stimulus cages were 40 × 30 × 44 cm.

one-way mirrors between the middle chamber and stimulus birds' cages. Thus, a choosing bird could see the stimulus birds, but the stimulus birds were unable to see the choosing bird. In the second trial (two-way choice trial), we placed a clear glass partition between the choosing and stimulus birds' cages, allowing them to interact but not to have physical contact. We conducted the experiments in this order so that one-way trials, in which we were trying to determine morph preferences in the absence of potential behavioural correlates, did not affect behavioural interactions in subsequent two-way trials. No bird ever saw another bird more than once, either as a stimulus bird or a choosing bird.

We conducted choice trials in the following order. Group 1: female one-way choice (1–12 April), male one-way choice (18–24 April), female two-way choice (14–16 May), male two-way

choice (18–19 May); group 2: female one-way choice (22–31 May), male one-way choice (4–14 June), female two-way choice (18–19 June), male two-way choice (20–21 June).

During the 10 days before trials began, we allowed females to acclimatize in random order by leaving them alone in the centre of the mate choice apparatus for 24 h. Food and water were provided in the middle of the centre cage. Males were not acclimatized, as they had already experienced the apparatus during female one-way choice trials.

During a trial, we introduced the choosing bird into the central chamber and videotaped its behaviour for 1 h, using a camera suspended above the apparatus. We later measured the amount of time the choosing bird spent in front of each peripheral cage from the videotape. We calculated preference scores as (time visiting white-striped bird)/(time visiting both birds).

Competition Trials

To determine competitive differences between the morphs and within a sex, we ran competition trials on birds from group 2. To begin a trial, we positioned a white-striped and a tan-striped bird's cage on a table visually isolated from the other cages and clipped them together. We removed the adjacent sides of the cages, creating one larger cage (40 × 60 × 44 cm). This created less stress for the birds than transferring them between cages. We ran trials for 10 min or until the birds' welfare became endangered (one female and one male trial were stopped on this account). All aggressive behaviour patterns were noted, as well as the aggressor and object of aggression. Aggressive behaviour consisted mainly of one bird flying at or chasing the other bird, but also included pecking, a head-forward threat, and trilling and chip-up vocalizations (see Lowther & Falls 1968, for a description of aggressive behaviour in the white-throated sparrow). We scored each trial as won by a white-striped or a tan-striped bird, a tie, or no aggression. The winner was defined as the bird that showed the highest number of aggressive behaviour patterns toward the other. An individual's competitive score was calculated as wins/(wins+losses). We then ranked these scores, with the highest score receiving a rank of 1, the next highest a rank of 2, and so on. All white-striped birds (6 males, 4 females) were tested with all tan-striped birds (5 males, 5 females) of the

same sex. Trials were run from 5 to 21 July 1991, and no bird experienced more than one trial a day.

RESULTS

Choice Trials

Group 1 and group 2 data were combined for analyses, as we could see no differences in behaviour between the groups. Birds spent on average half of the 1-h trial visiting stimulus birds (1849 ± 98.3 s); the average individual visit (\pm SE) was $137 (\pm 32.7)$ s. During trials, choosing birds typically began to move back and forth between the stimulus birds' cages less than 10 min after trials began ($\bar{X} \pm$ SE latency to begin visiting: 539 ± 133.0 s). During the two-way choice trials, both the choosing bird and stimulus birds displayed interest in the other bird(s): the stimulus birds moved to the front of their cages when they spotted the choosing bird and would begin hopping back and forth when it approached. In one of the female one-way choice trials and one of the female two-way choice trials, a female visited one male exclusively. Because we could not be sure that she had seen both males, and was therefore making an active choice, these trials were excluded from the analyses. Very few birds vocalized during trials (12 times in 80 trials), and the few times in which stimulus birds did vocalize, it did not appear to affect the behaviour of the choosing bird. However, in four of the male two-way choice trials (two tan-striped and two white-striped males), one of the stimulus females displayed extreme aggression (head-forward display and chip-ups) whenever the male approached her cage. These trials were excluded from the analyses, as the male avoided the female and therefore did not display mate choice.

No differences were found between white-striped and tan-striped females or white-striped and tan-striped males in their mate-choice preferences (Table 1; two-factor repeated-measures ANOVA on proportion of time spent with white-striped bird: females: morph: $F_{1,7}=0.4956$, $P=0.5$, trial: $F_{1,7}=3.201$, $P=0.09$; males: morph: $F_{1,5}=0.5328$, $P=0.5$, trial: $F_{1,5}=0.3566$, $P=0.6$), so the results were combined for further analysis.

Females showed no significant preference for either morph in one-way choice trials, but displayed a significant preference for tan-striped

Table I. Results of mate choice trials: comparisons between morphs

| Choosing bird morph: | Average (\pm SE) proportion of time spent with white-striped stimulus birds | |
|----------------------|--|---------------|
| | Tan | White |
| Female choice | | |
| One-way | 0.600 (0.102) | 0.466 (0.096) |
| Two-way | 0.195 (0.067) | 0.353 (0.109) |
| Male choice | | |
| One-way | 0.616 (0.098) | 0.741 (0.074) |
| Two-way | 0.595 (0.107) | 0.620 (0.087) |

Table II. Results of mate choice trials. The proportion of time a choosing bird spent with the white-striped stimulus bird compared with random visitation (0.50)

| | Average (\pm SE) proportion of time spent with white stimulus bird | t^* | N | P |
|----------------------|---|--------|-----|-------|
| Female choice | | | | |
| One-way | 0.529 (0.070) | 0.563 | 19 | 0.6 |
| Two-way | 0.319 (0.073) | -2.653 | 19 | 0.016 |
| Male choice | | | | |
| One-way | 0.684 (0.058) | 3.036 | 20 | 0.007 |
| Two-way | 0.608 (0.067) | 1.655 | 16 | 0.1 |

* t -tests were performed on arcsine square-root transformed proportional data.

males in two-way trials. Males only showed a strong preference for white-striped females in one-way trials (Table II).

Competition Trials

No aggression was displayed by either bird in five of the female- and six of the male-competition trials. Of the remaining trials, white-striped females won 12 trials, tan-striped females won two trials and one trial was tied. White-striped males won 21 trials, tan-striped males won two trials, and one trial was tied. When the competitive ranks of individual white-striped and tan-striped birds were compared, white-striped birds had significantly higher ranks than tan-striped birds of the same sex (Table III; Mann-Whitney U -test: males: $z=2.8723$, $N=11$, $P<0.004$; females: $z=2.3875$, $N=9$, $P<0.02$).

DISCUSSION

Of the possible routes to negative assortative mating outlined earlier, the hypothesis best

supported by the experiments presented here is that all females prefer one male morph (tan-striped), and one female morph (white-striped) outcompetes the other for access to the preferred males. The mate choice experiments were not consistent with preferences for the opposite morph by either one or both sexes, as females of both morphs preferred tan-striped males in mate choice trials and males of both morphs did not show a strong morph preference. Results of the competition experiments did not support the hypothesis that male choice and male-male competition determine the mating pattern, because (1) males do not appear to have a morph preference and (2) white-striped males are dominant to tan-striped males and should be able to outcompete them for access to white-striped females if they are preferred.

Females did not display a preference for either male morph until they were able to interact with them (two-way choice trials), whereas during two-way trials males appeared to lose the preference for white-striped females displayed in one-way choice trials. One possible explanation for this difference is that white-throated sparrows

Table III. Competitive scores and ranks of white- and tan-striped birds in group 2

| | White morph | | Tan morph | | |
|----------------|--------------------|------------|--------------------|--------|------------|
| | Wins/(wins+losses) | Rank | Wins/(wins+losses) | Rank | |
| Males | | | | | |
| GRO1 | 4 of 4 | 2.5 | GRO8 | 2 of 5 | 7.0 |
| AIR4 | 2 of 2 | 2.5 | CAM1 | 0 of 4 | 9.5 |
| CAM2 | 4 of 4 | 2.5 | POG1 | 0 of 4 | 9.5 |
| GRO10 | 4 of 4 | 2.5 | GRO7 | 0 of 6 | 9.5 |
| POG2 | 4 of 5 | 5 | GRO4 | 0 of 4 | 9.5 |
| GROB | 3 of 4 | 6 | | | |
| | Average rank: | 3.5 (0.65) | | | 9.0 (0.50) |
| Females | | | | | |
| PLE2 | 4 of 4 | 2 | PLE4 | 1 of 2 | 5.5 |
| AIR7 | 1 of 1 | 2 | CAM6 | 1 of 4 | 7.0 |
| CAM8 | 3 of 3 | 2 | CAD2 | 0 of 5 | 8.5 |
| KEA1 | 3 of 4 | 4 | AIR3 | 0 of 3 | 8.5 |
| PLE1 | 1 of 2 | 5.5 | | | |
| | Average rank: | 2.6 (0.63) | | | 6.9 (0.71) |

require behavioural cues to identify the sex of conspecifics. Thus, females showed no differential attraction to birds of unknown sex, but preferred tan-striped to white-striped males. Males, however, appeared to be attracted to white-striped birds of unknown sex, but displayed no clear preference for either female morph. Although all one-way trials were run before all two-way trials, the difference in results between the one- and two-way trials does not appear to be due to birds needing to become accustomed to the mate choice apparatus. If this were the case, we would predict that choosing birds would spend more time visiting stimulus birds during two-way trials. However, there was no significant difference in the amount of time choosing birds visited stimulus birds in one- and two-way trials (total visiting time: one-way trials: 1989 ± 129.8 s; two-way trials: 1812 ± 162.6 s; repeated-measures ANOVA: trials: $F_{73}=1.1316$, $P=0.3$; subjects: $F_{73}=2.1236$, $P=0.01$). It is possible that males showing a 'preference' for white-striped birds of unknown sex were displaying aggressive rather than sexual behaviour. White-striped models placed on white-throated sparrow territories are attacked at higher rates than tan-striped models (Jones 1987; Kopachena 1992). It is also possible that males approached white-striped females more than tan-striped females in one-way trials because the white-striped morph is an aggressive stimulus.

Tuttle (1993) also found that both female morphs of the white-throated sparrow prefer tan-striped males in laboratory mate choice experiments. Her females received oestradiol implants prior to the experiments and choice was determined by copulation solicitations directed at males. She also found that males of both morphs spent more time with white-striped females in two-way choice trials.

Further support for the hypothesis that female choice and female-female competition are important in determining the white-throated sparrow's negative assortative mating pattern comes from field studies of the species. White-striped females and tan-striped males pair earlier than white-striped males and tan-striped females, even though there is no difference in arrival time at the breeding grounds between morphs within a sex (Knapton et al. 1984). This is consistent with white-striped females outcompeting tan-striped females for access to tan-striped males as mates, and tan-striped females then accepting the less preferred white-striped males as mates.

Results of the competition experiments are supported by earlier studies of dominance and aggression in white-throated sparrows. Although tan-striped females may be dominant to white-striped females in winter feeding flocks (Watt et al. 1984), white-striped birds of both sexes appear to be dominant to tan-striped birds at all other times. White-striped males are dominant to

tan-striped males in winter flocks (Watt et al. 1984). White-striped birds are dominant to tan-striped birds during migration (Hailman 1975; Ficken et al. 1978) and are more aggressive on the breeding grounds (cf. Lowther & Falls 1968).

It is surprising that disassortative mating in over 90% of the population can be explained by anything other than preferences for the opposite morph by both sexes, unless there are nearly identical numbers of tan-striped males and white-striped females. If there were an excess of tan-striped males, then tan-striped females should pair with them rather than the less preferred white-striped males. If there were more white-striped females, any remaining white-striped females should outcompete tan-striped females for access to white-striped males, assuming that a second-choice mate is better than none at all. In either case we would expect to see a higher proportion of same-morph matings on the breeding grounds than we do. There is some evidence that there are similar numbers of tan-striped males and white-striped females in the adult population. Watt et al. (1984) found that 36% of males were tan-striped and 38% of females were white-striped on white-throated sparrow wintering grounds in Pennsylvania. Similar values have been found during spring migration through Long Point, Ontario, and Chicago, Illinois, suggesting morph-specific differences in post-fledging losses (unpublished data).

What are the reproductive consequences of negative assortative mating in white-throated sparrows? White-striped males are the most aggressive, sing the most and spend the most time in territory defence of the morph/sex types (Lowther & Falls 1968; Kopachena 1992). Tan-striped males and white-striped females display intermediate levels of aggressive, song and territorial behaviour, while tan-striped females show little such behaviour (Kopachena 1992). In contrast, chick feeding rates are highest for tan-striped females; intermediate for tan-striped males and white-striped females, and lowest for white-striped males (Knapton & Falls 1983; Kopachena 1992). When the behaviour patterns of the pair types are compared, i.e. white-striped males/tan-striped females and white-striped females/tan-striped males, the total amount of time each pair type spends in territory defence, chick feeding and the number of offspring fledged do not differ (Knapton & Falls 1983; Kopachena 1992). Thus,

the pair types offer alternative patterns of parental investment leading to identical levels of reproductive success. It is possible that monomorphic pairs would either spend too little effort in chick feeding, in the case of white-white pairs, or too little effort in territory defence, in the case of tan-tan pairs (Kopachena 1992). This could create strong selection pressure for disassortative mating.

We suggest that maintenance of negative assortative mating, and thus a balanced polymorphism, in the white-throated sparrow is a three-step process. The first step is mate choice and sexual competition, as assessed in our study: females of both morphs preferred to pair with tan-striped males and white-striped females can outcompete tan-striped females for access to these preferred males. Tan-striped females should then pair with white-striped males. The second step is during the establishment of a pair bond, as shown by J. Kopachena (unpublished data) in a study in which he introduced white-striped males into aviaries with either white- or tan-striped females. Although the males initially displayed high levels of aggression towards both types of females, within a few weeks, aggression levels towards tan-striped females were significantly lower than those towards white-striped females. Thus, any white-striped birds that managed to pair monomorphically in step 1 would have difficulty establishing a pair bond due to high levels of male aggression toward the female. The final step would be during nesting and reproduction. Tan-striped monomorphic pairs would have difficulty in holding territories, due to their low level of territorial behaviour in relation to dimorphic pairs, while white-striped monomorphic pairs would have difficulty in fledging chicks, due to their relatively low level of chick feeding. These three steps together may explain the uniquely high level of negative assortative mating seen in the white-throated sparrow.

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