Alternative reproductive strategies in the white-throated sparrow: behavioral and genetic evidence

Elaina M. Tuttle
Department of Life Sciences, Indiana State University, Terre Haute, IN 47809, USA

Organisms exhibiting genetic polymorphism often also exhibit true alternative life-history strategies in which behavioral tactics are genetically fixed. Such systems are ideal for the study of the evolution of life histories because the consequences of selective episodes can be more easily identified. Here I report an interesting and classic example of a species exhibiting true alternative strategies. Due to a chromosomal inversion, male and female white-throated sparrows (Zonotrichia albicollis) occur as two distinct morphs, tan or white. Tan and white morphs mate disassortatively, and this mating pattern maintains the polymorphism in relatively equal proportions within the population. In comparison with tan males, white males are more aggressive, frequently intrude into neighboring territories, spend less time guarding their mates, occasionally attempt polygyny, and provide less parental care. White females are also more aggressive and solicit copulation from their mates twice as often as tan females. Multilocus DNA fingerprinting revealed that 31.8% of nestlings and 56.3% of broods from white male–tan female pairs were the result of extrapair fertilizations, whereas only 4.4% of nestlings and 6.3% of broods from tan male–white female pairs contained extrapair offspring. However, 4.4% of the nestlings (12.5% of broods) from tan male–white female pairs were attributable to conspecific brood parasitism, and brood parasitism was not a factor for white male–tan female pairs. For three excluded extrapair offspring, actual paternity was assigned to territorial white males, suggesting that, although white males are not preferred by females in previous mate choice studies, they do attempt to increase their reproductive success by securing additional matings via extrapair copulations. However, by doing so, white males also lose paternity at home. Behavioral and genetic evidence suggest that the two morphs use alternative tactics and that reproductive trade-offs may serve to maintain a competitive equilibrium between the morphs. Key words: alternative reproductive strategy, extrapair copulations, conspecific brood parasitism, polymorphism, sparrows, Zonotrichia albicollis. [Behav Ecol 14:425–432 (2003)]

Trade-offs are mutually exclusive attributes of an individual that exist when the benefit realized through altering one trait is linked through the cost in change of another trait (Stearns, 1989, 1992). Trade-offs constrain evolution. For example, males cannot simultaneously search for fertile females and feed their chicks, and they must commonly trade-off these two activities (Birkhead, 1987; Trivers, 1972; Westneat et al., 1990). As a direct result of trade-offs, some species have evolved multiple life-history strategies so that different individuals use different tactics in an attempt to maximize their fitness (e.g., Bass, 1993; Cade, 1979, Gross, 1996; Lank et al., 1995; Thompson and Moore, 1992).

Species exhibiting distinct multiple life-history strategies can be classified according to whether the variation is only phenotypic or genotypic (Austad, 1984; Gross, 1996). Two classes, conditional strategies and mixed strategies, are both derived from genetic monomorphism (i.e., are one strategy) in which individuals adopt alternative life-history tactics (or phenotypes) based on their own condition or the strategies of others (Gross, 1996). These phenotypic tactics may be further divided according to whether the average fitnesses of individuals expressing alternative tactics are equal (e.g., an evolutionarily stable strategy; Maynard Smith 1982, 1991; see also Austad, 1984; Dawkins, 1980; Dominey, 1984; Eshel, 1982; Rubenstein, 1980) or unequal (e.g., the best of a bad situation; Davies, 1982; Dawkins, 1980; Dunbar, 1982; Eberhard, 1982; Gross, 1984). A third class, true alternative strategies, are characterized by two or more discrete tactics resulting from genetic polymorphism (Gross, 1996). Only a handful of species fit this category, and, in all, the average fitness of each alternative is equal (Lank et al., 1995; Ryan et al., 1992; Shuster and Wade, 1991; van Rhijn, 1973; Zimmerer and Kallman, 1989). This might be expected since, when fitness is unequal, and there are no evolutionary mechanisms maintaining multiple strategies, selection should cause the extinction of the strategy with the lower fitness (Thompson et al., 1993).

Discrete tactics or strategies involved in reproduction are exhibited by a number of animal species. Trivers (1972) suggested that in species where there has been selection for parental care (i.e., monogamous birds), it is likely that males will adopt an alternative or mixed reproductive strategy, which involves helping a single female raise young and simultaneously attempting to mate with other females that he will not aid. Many studies have shown that males actually achieve a selective advantage by adopting such a mixed reproductive strategy that involves the pursuit of extrapair copulations (EPCs; Burke et al., 1989; Gibbs et al., 1990; Røskaft, 1983; Westneat, 1990). Birkhead (1987) discussed four predictions that should hold if EPCs are adaptive: (1) males should direct EPCs toward fertile females, (2) males should adopt patterns that maximize their chances of obtaining EPCs, (3) males should behave in ways that reduce their own chances of being cuckolded, and (4) EPCs should lead to extrapair fertilizations. Likewise, females may adopt alternative reproductive strategies involving not only EPCs, but also conspecific brood parasitism. Both strategies serve to increase the variance in reproductive success, yet it is still relatively unclear as to how they might affect the maintenance of...
Mendelian genetics ensures that half of the brood will be 2m/2m, whereas tan birds are homozygous noncarriers (i.e., 2/2; Thorneycroft, 1966, 1975). Thorneycroft (1975) found only 1 female out of more than 300 birds that was homozygous 2m/2m; no homozygous males were found (but see Falls and Kopachena 1994). The autosomal inversion segregates in a Mendelian fashion so that birds possessing a single 2m pass this chromosome on to one-half of their progeny (Thorneycroft, 1975).

The polymorphism is also correlated with behavioral differences. White birds tend to be more aggressive during the migratory season (Ficken et al., 1978; Hailman, 1975; Watt et al., 1984), and they initiate more aggressive attacks than tan birds (Ficken et al., 1978). White males sing more often than tan males (Falls, 1988; Lowther and Falls, 1968; Tuttle, 1993) and have been reported to attempt polygyny (Knopton and Falls, 1983). Tan birds expend more effort in parental care than white birds (Knopton and Falls, 1983; Kopachena and Falls, 1993; Tuttle, unpublished data).

White-throated sparrows are unusual in that they mate disassortatively with respect to the polymorphism, so that white almost always mates with tan (Lowther, 1961; Thorneycroft, 1975). Disassortative mating ensures that both morphs are maintained in relatively equal proportions in the population because when white (2m/2) mates with tan (2/2), Mendelian genetics ensures that half of the brood will be 2m/2m and the other half will be 2/2. Determining the factors that are responsible for the disassortative mating pattern will give valuable insight into the maintenance of genetic polymorphism in this species. In this study I investigated the behavioral and genetic aspects (via DNA fingerprinting) of mating behavior in the polymorphic white-throated sparrow to determine how they contribute to the maintenance of disassortative mating.

METHODS

Field study

Fieldwork was conducted from 1988–1995 at the Cranberry Lake Biological Station in the Adirondack Mountains, New York, USA. The primary study plot was 30 ha and supported approximately 25–35 breeding pairs of white-throated sparrows each season. White-throated sparrows began arriving in late April and set up breeding territories along either side of a stream that ran through the center of an extensive beaver meadow and into a bog. This species nests on edge habitat (Lowther and Falls, 1968), and so territories at Cranberry Lake consisted of late successional meadow, bog, and mature forest.

I captured 109 adult white-throated sparrows by strategically placing mist nets in areas I knew the birds frequented (e.g., song perches, flyways, nests). Occasionally I used song playback to attract birds to the nets. Birds were banded with U. S. Fish and Wildlife bands and a unique combination of color bands, which allowed me to identify individuals at a distance. I noted sex, morph, and other plumage characteristics according to the criteria described in Tuttle (1993; see also Piper and Wiley, 1989; Watt, 1986). For DNA fingerprinting analysis, I obtained blood samples (approximately 50–200 μl) by venipuncture of the brachial vein with a 26-gauge needle and collecting the blood in microcapillary tubes coated with either EDTA or heparin as an anticoagulant (Hoy yak and Weatherhead, 1991). Blood samples taken from 1988 to 1993 were stored on ice for no more than 4 h, then they were transferred to −80°C until fingerprinting analysis 6 months to 2 years later. Blood samples taken in 1994 and 1995 were immediately transferred to a lysis buffer (Longmire’s solution; Longmire et al. 1992) and stored at 4°C until needed for analysis.

I examined behavioral and ecological traits in males and females to profile their respective reproductive strategies. I observed individuals daily and identified mated pairs by behavior. Paired individuals associated closely. Males often guarded their mates (Birkhead, 1982; Birkhead and Möller, 1992; Möller, 1987), and contact calls between mated individuals were frequent. Most activities of the pair were centered on the territory. I used time-budget analyses of focal-observation (Altman, 1974) to quantify behavior of mated pairs. Observations were conducted between 0500 and 1200 h, began when either member of a pair was spotted, and lasted for either 30 or 60 min. Each pair on my study site was sampled three to four times each week throughout the breeding season, resulting in equal observational effort for all pair types. I chose 5 m as a maximum distance to identify mate-guarding because that was the distance at which individuals generally had unobstructed views of each other. I also noted the identity, sex, morph, and behavior of territorial intruders.

Female white-throated sparrows nest on or near the ground at the base of a small shrub. I found nests either by determining where a female’s activities were centered during nest-building and incubation or by systematically searching a territory. If females were disturbed while brooding, they would suddenly fly off the nest, revealing its location. Once a nest was found, I determined its progress by visiting every other day. Seven or 8 days after hatching, nestlings were banded, measured, and blood samples were taken in the same manner as in adults. Occasionally I would find nestlings dead, and from these, I collected muscle samples to use for genetic analysis. All muscle samples were frozen whole at −80°C.

In birds the fertile period of the female usually begins just before nest building and continues to the end of the laying period (Birkhead and Möller, 1992; Tuttle, personal observation). I estimated the fertile periods of females by extrapolating from the hatching dates of initial clutches. I estimated pair-formation dates by counting back from the hatching dates of initial clutches (see Teather et al., 1988). I assumed that 28 days elapsed from pairing to hatching, based on observations of the duration of the nesting cycle (pairing, nest building, laying the clutch, and incubation to hatching).

DNA fingerprinting

To extract nuclear DNA, approximately 50 μl of whole blood was extracted using a standard phenol-chloroform method (Sambrook and Russell, 2001). For all samples, DNA quality was determined by running 2 μl of a sample on a 1% agarose minigel. Only good quality, undegraded DNA was used in analytical fingerprinting gels. I determined DNA quantity by spectrophotometer.

DNA fingerprinting followed procedures outlined in Westneat (1990). Approximately 5–10 μg of genomic DNA was...
digested to completion with the restriction endonuclease HaeIII (United States Biochemical or Promega, Inc.). Electrophoresis was carried out in 1% agarose gels at a rate of 1.5 volts/cm for 48 h. DNA was transferred to nylon membranes (Boehringer Mannheim) by overnight capillary blotting in the neutralization solution (Southern, 1975). I fixed the DNA to the membranes by first baking them at 80°C for 1 h and later exposing them to UV light.

For 1988 to 1993 samples, approximately 50 ng of M2.5RI (Per) (Georges et al., 1987; Shin et al., 1985) or whole M13 (Ryskov et al., 1988; Vassart et al., 1987) was labeled with [alpha-32P] dCTP using a Random Primed DNA Labeling Kit (Boehringer Mannheim Biochemical). Unincorporated nucleotides were removed by running labeled probes through sephadex G-50 Quick-spin columns (Boehringer Mannheim Biochemical). Prehybridization and hybridization were carried out in a 60°C hybridization oven following procedures outlined in Westneat (1990). Membranes probed with M2.5RI and M13 were washed according to Westneat et al. (1988). All membranes were placed on film and exposed 1–14 days at −80°C with intensifying screens. Filters probed with M2.5RI gave off strong enough signals to be analyzed on a Betagen Scanner (Betagen, Inc.).

DNA samples obtained in 1994 and 1995 were probed with oligonucleotide (GGAT)4 (Ali et al. 1986) that was labeled with DIG-chemiluminescence (Boehringer Mannheim Biochemical). I carried prehybridization and hybridization out in a 55°C oven using generalized protocols prescribed by Boehringer Mannheim Biochemical. Membranes were sprayed with the luminescent substrate, Lumi-phos (Lumigen, Inc., Southfield, Michigan, USA), and then exposed on film for 2–5 h.

**Results**

**Field study**

During the fertile period, tan males spent a higher proportion of their time guarding their mates than white males (mean proportion of time ± SE = 0.67 ± 0.06 for tan males; 0.27 ± 0.07 for white males; Mann-Whitney U = 7.0, N1 = 9, N2 = 11, p < .05). As the nesting stage progressed to incubation and feeding of the offspring, mate-guarding ceased in both pair-types (Figure 1), although tan males did tend to follow their females through incubation (Figure 1b).

Females frequently solicited copulation from their mates. Solicitations (as defined in Andrew 1961) were sometimes given in response to song by males, but more frequently, the female initiated the behavior in absence of any cue from the male. White females solicited their mates significantly more often than tan females (white females, mean ± SE = 4.45 ± 0.35 solicitations/30 min; tan females, 2.18 ± 0.81 solicitations/30 min; t = 2.74, df = 20, p < .001). Even though females spent a large portion of their time soliciting copulations (12%), they spent only 2% of their time copulating. The high solicitation rate of white females had no observable effects on the copulation rate as both tan and white males seemed to be less responsive to their females’ demands. Only 12% of tan males approached their mates when the females solicited, whereas 35% of white males responded by approaching their mates after solicitation (nT = 16 and nW = 20; χ2 = 1.35, df = 1, p > .05).

Because EPCs were difficult to observe and because territorial intrusion is a necessary prelude to an EPC attempt, I quantified the number of intrusions and used these data as indirect indicators of EPC frequency. Tan males experienced more territorial intrusions than white males. The probability of intrusion into a tan male’s territory was 0.68, and the probability of intrusion into a white male’s territory was 0.32 (n = 64). White birds were responsible for most territorial intrusions; 79% of intruders were white and 21% were tan (n = 64; χ2 = 18.54, df = 1, p < .05). Furthermore, 73% of all intrusions occurred during the resident female’s fertile period. Most territorial intrusions did not involve song (81%; n = 64) and were therefore not obvious. Behavioral responses to intrusions did not differ significantly; 78% of white males and 85% of tan males responded to intrusion by aggressive chases (nW = 11; nT = 13; χ2 = 0.044, df = 1, p > .05). Tan males drove out intruders alone (without their mates’ help) 62% of the time, whereas white males chased by themselves in only 27% of encounters (χ2 = 1.61, df = 1, p > .05). Females of the two morphs also did not respond differently to territorial intruders. Approximately 64% of tan females chased intruding birds (n = 11); 18% of these drive intruders out of their territories without assistance from their mates. Only 31% of white females were involved in intruder chases (n = 13), and only 8% of these...
Figure 1
(a) Proportion of time white and tan males spent guarding their mates according to nesting stage (means ± SE). Shaded bars represent means for tan males; white bars represent means for white males. Data includes clutches 1 and 2. There were significant effects of nesting stage \((F = 67.17, \text{df} = 2, \ p < .0001)\), male morph \((F = 11.08, \text{df} = 1, \ p = .002)\), and the interaction of stage and morph \((F = 10.68, \text{df} = 2, \ p = .0001)\) on guarding. Proportion of time spent guarding during the females’ fertile period was significantly different from proportions for the other two stages (Tukey-Kramer HSD, \(p < .05\)). *Means for tan and white males were significantly different (Tukey-Kramer HSD, \(p < .05\)). (b) The probability that a male would follow his mate, given that his mate initiated a move (means ± SE). Shaded bars represent means for tan males; white bars represent means for white males. Data includes clutches 1 and 2. Nesting stage and male morph significantly affected \((F = 8.72, \text{df} = 2, \ p = .0009 \text{ and } F = 9.65, \text{df} = 1, \ p = .004, \text{ respectively})\) male behavior. There was no effect of an interaction between stage and male morph \((F = 0.98, \text{df} = 2, \ p = .39)\). *Significantly different (Tukey-Kramer HSD, \(p < .05\)).

chased while unaccompanied by their mates (females involved in intruder chases: \(\chi^2 = 1.44, \text{df} = 1, \ p > .05\); females chasing alone: \(\chi^2 = 0.001, \text{df} = 1, \ p > .05\)).

White males were polygynous in 2% of all breeding attempts. In addition to occasionally exhibiting polygyny, white-throated sparrows also copulated outside the pair-bond. I observed 12 attempted EPCs. During these instances, males flew quickly toward the female and knocked her into the shrubs, where a struggle ensued. In 9 of the 12 observed EPCs, I identified the intruder as a neighboring white male; in the other 3 EPCs, the intruder was unidentified. In six cases, a white female was the recipient, and in three cases a tan female was the recipient. Males seeking EPCs would sometimes disrupt within-pair copulations (5 of the 12 attempted EPCs; 42%). All attempted EPCs appeared unsolicited, as the female always responded aggressively toward the intruding male.

I saw no behavioral evidence of intraspecific (or conspecific) brood parasitism in white-throated sparrows. Females usually remained within the boundaries of the territory and occasionally wandered off on foraging forays. I did find physical evidence, however, of two suspected cases of brood parasitism when I banded the nestlings. Both cases occurred in the same tan male × white female pair in 2 consecutive years. In the first case, one chick was considerably larger than the other two, and I estimated from its growth pattern that it was 2–3 days older than the others. In the other case, one chick was smaller than the other three and was approximately 2 days younger than the rest. These nests did not contain an unusually high number of eggs, which is commonly used as a sign of CBP.

Females nested synchronously at the start of the breeding season but became less synchronous during subsequent clutches. The synchrony index (Björklund and Westman, 1986) for the first clutch was 44.4%, whereas the synchrony index for second clutch was 23.8%. The overall synchrony index for the entire breeding season was 24.5%.

Parentage analyses

Band-sharing probabilities of related and unrelated individuals at Cranberry Lake were bimodal with the two distributions being distinct at the 0.95 confidence limits. The average (± SE) band-sharing probability between unrelated individuals at Cranberry Lake was 0.191 ± 0.006; the average band-sharing probability of related individuals (i.e., parent–offspring and full sibs) was 0.515 ± 0.008. Means were significantly different for related and unrelated individuals (one-tailed t test, \(t = 32.73, \text{df} = 196, \ p < .001\)).

Ten of 32 broods (31.3%) contained at least one excluded offspring (Table 1). Most broods contained only one excluded offspring; however, I did find one white male that had two nestlings from the same clutch that were not his own. Of the 89 offspring in which both putative parents were known and sampled, I found 18 exclusions; 14 nestlings were excluded in white male–tan female pairs (31.8%) and 4 nestlings were excluded in tan male–white female pairs (8.9%). Fingerprinting of excluded offspring averaged 5.52 ± 0.96 novel fragments that could not be found in the fingerprints of the putative parents \((n = 16)\). The average band-sharing probability between excluded offspring and putative parents was 0.187.

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<th>Table 1</th>
<th>DNA fingerprinting results</th>
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Exclusions in the two disassortative pair types were attributable to different sources (Table 1). All cases of extrapair parentage (31.8%) in white male–tan female pairs occurred through EPFs (i.e., the excluded parent was the territorial male). However, in tan male–white female pairs, two of the four exclusions (4.4%) were attributable to CBP; only two exclusions (4.4%) were attributable to EPFs.

I was able to assign paternity to three excluded offspring: neighboring white males were determined to be the actual fathers of these EPC nestlings. The males had fingerprint patterns that explained all the novel fragments seen in the chicks’ fingerprints and high band-sharing probabilities (mean = 0.465) with those chicks. I was unable to assign parentage for the two CBP chicks.

**DISCUSSION**

**Evidence of alternative reproductive strategies**

Behavioral and genetic evidence suggest that white and tan males practice different reproductive strategies based on the trade-off between securing additional matings and parental effort (Table 2). Tan males invest heavily in parental care (Knapton and Falls, 1983; Kopachena and Falls, 1993) and mate guarding; white males invest heavily in advertisement though song, intrusion into neighboring territories, and the pursuit of additional matings. Evidence suggests that white males are adopting mixed reproductive tactics; they occasionally attempt polygyny but more commonly pair monogamously with females, with whom they aid in raising broods, while simultaneously pursuing EPCs with neighboring females. In addition to the polygynous male that I found, Knapton and Falls (1983) also reported a small percentage of white males that had secondary females nesting on their territories. Furthermore, Thorneycroft (1975) reported two tan–tan pairs that each hatched an offspring that possessed a 2n chromosome, even though neither parent could have contributed that chromosome. Although this was the first direct evidence of extrapair parentage or CBP, the present study is the first to determine the actual frequencies of each behavior.

Tan and white morphs of the white-throated sparrow provide an intraspecific comparison of reproductive trade-offs at multiple levels (Table 2). The most obvious trade-off occurs in males between investment in a monogamous pair-bond and mate guarding versus the pursuit of additional matings. Tan males spent a large proportion of their time guarding their mates and protecting them from the threat of EPCs, whereas white males mated polygynously (see also Knapton and Falls, 1983; Thorneycroft, 1975) and pursued EPCs (intruded frequently, etc.). A strategy of mate guarding seems to be successful, as tan males were rarely cuckolded, despite the frequent intrusions into their territories by EPC-seeking white males. In addition, both males and females may show a trade-off between investment in parental effort and investment in reproductive effort. Tan morphs invested a great deal in parental effort (Knapton and Falls, 1983; Kopachena and Falls, 1993), whereas white morphs invested in securing additional matings (through song display, solicitation, etc.).

The alternative strategies of females, if any, are less clear (Table 2). Behavioral observations of white-throated sparrows did not reveal the occurrence of brood parasitism, although DNA fingerprinting showed that it did occur twice in tan male × white female pairs, and so a few females in the Cranberry Lake population were increasing their reproductive success via this strategy. As female floaters are rare, territorial females are probably responsible for all cases of egg dumping. It is interesting to note that both cases of CBP occurred in the same tan–white pair in 2 consecutive years. This may indicate that certain pairs are highly susceptible to CBP and the probability of CBP in a given year may not be independent of the probability in previous years. CBP may be a mixed reproductive strategy adopted by females to increase their reproductive success. The fact that the same pair was victimized twice also seems to indicate that the parasitic female may have been a neighboring territorial female who had access to this pair’s nest 2 years in a row. In short, female morphs may parallel males in their behavioral tactics. Tan females invest more heavily in parental care than white females (Knapton and Falls, 1983; Kopachena and Falls, 1993). White females seem to be investing greatly in mate advertisement by frequently soliciting for copulation, and, because white morphs intrude more frequently than tan morphs, it is possible that white females are adopting an alternative strategy that involves brood parasitism. More data are needed to determine female reproductive strategies.

**Evolution of alternative reproductive strategies**

Alternative strategies will be adaptive only if the benefits outweigh the costs (Westneat et al., 1990). For example, a male must commonly trade-off pursuit of additional matings and parental investment, and EPFs will only increase fitness if the loss of male parental care does not decrease survivorship of his own offspring (Trivers, 1972; Westneat et al., 1990). Maynard Smith (1977) developed a cost–benefit model for individuals that adopt mixed reproductive strategies that involve both monogamy and the pursuit of EPCs. The strategy that a male will choose depends on the cost, reduction in survival of his young due to his reduced parental effort, and the benefit, the extra young he is able to father. The importance of parental contribution of males may be different for the two morphs. Since white females do not provide as much parental care as tan females (Knapton and Falls, 1983; Kopachena and Falls, 1993), tan males may be caught in a “cruel bind” (Trivers, 1972). That is, if they desert
to secure additional matings, the costs may greatly exceed the benefits of additional matings because their white female may not be able to substantially increase her parental effort to compensate for the loss of his, resulting in loss of the brood (but see Whillans and Falls, 1990). In contrast, white males may be able to lower their parental effort to pursue additional matings because their tan females invest heavily in care of the brood. Recent studies suggest that male parental care may be most critical during the period of offspring fledging to independence (Whillans and Falls, 1990; Wolf et al., 1988). If white males confine their extrapair activities to the period before fledging of their own young, then an early reduction in paternal care may not be detrimental.

Paternal care is generally negatively correlated with the frequency of extrapair paternity (Møller and Birkhead, 1993), and males may withhold parental investment if assurance of paternity is low (Westneat et al., 1990; Whittingham et al., 1992; Xia, 1992). Even though evidence suggests that only white males are pursuing EPCs, DNA fingerprinting suggests that these males are also losing a higher proportion of their paternity to EPFs than tan males. White males may lower parental investment for this reason, whereas parental investment of tan males remains high because they are relatively more certain of paternity.

Birkhead (1987) suggested that if EPCs are adaptive, males should direct EPC attempts toward fertilizable females. White-throated sparrows may be able to judge the reproductive state of a female by copulations between the mated pair, by the stage of nest construction, or by mate-guarding behavior (Birkhead, 1987). Determining when most EPCs, within-pair copulations, and intrusions occur is one method that can be used to indirectly estimate the peak fertility period (Emlen and Wrege, 1986; Roskaft, 1983; Westneat, 1987). I used a similar approach of extrapolating fertility period from the hatching date of the first clutch and found that 75% of all intrusions occurred during the female’s fertile period. Furthermore, tan males guarded their females only when they were fertile, further suggesting that males can predict the fertile period of a female and alter their behavior accordingly. To maximize fitness and opportunities for EPCs, a male should monitor the reproductive state of females while keeping a close eye on his own female to prevent cuckoldry. This can best be done by confining activities to the territories in the immediate vicinity of his own territory (Björklund and Westman, 1983; Westneat, 1987). In white-throated sparrows, white neighboring territorial males accounted for most intrusions, and, furthermore, white males fathered offspring through EPCs with the neighboring females from adjacent territories.

Female behavior during attempted EPCs will affect a male’s likelihood of success (Westneat et al., 1990). In white-throated sparrows, although specific avoidance behaviors vary between the morphs, all females appeared to violently oppose EPC attempts. During intrusions white females chased intruders less than tan females, perhaps in an attempt to avoid possible encounters with males seeking EPCs. Avoidance may be adaptive if there are fitness consequences for females bearing EPF offspring. Homozygotes for the inversion may be less able to substantially increase her parental effort to compensate for the loss of his, resulting in loss of the brood; however, white females risk the loss of one-quarter of their progeny. If the genetic costs of EPCs are higher, white females may be better at avoiding EPCs than tan females. It is less clear how tan females should react toward EPC attempts. They may either avoid or passively accept an EPC attempt depending on whether their mates will withhold parental effort.

If males witness an EPC, they may adjust their parental effort. In one unusual case, a white male that copulated with a white female after her tan mate had disappeared never provided any parental care for the chicks. DNA fingerprinting showed that this male did not father any of the chicks, and so it may be possible for white-throated sparrows to adjust their parental effort accordingly. In fact, this pattern may cause the parental care differences in the morphs; if white males are always cuckolded by EPFs, then it may be adaptive to always provide less parental care.

Males should behave in ways that reduce their risk of cuckoldry (Birkhead, 1987). The best way to avoid cuckoldry is to mate guard during peak fertility (Emlen and Wrege, 1986; Møller, 1987), thereby lowering the probability that a given EPC will be successful (Björklund and Westman, 1986; Westneat, 1987a). I found that tan males spent more time guarding their mates than white males, which may mean that they are more effective in deterring EPC attempts on their mates. This may explain why EPC rates were low in tan male × white female pairs.

Solicitation by females may function for purposes other than copulation because it was often performed during and after aggressive interactions with intruding birds, in response to song, or if the male wandered too far from the female. Frequent solicitation may be adaptive if the mates of white females (tan males) need more behavioral stimulation from their mates in order to copulate, mate guard, or maintain the pair-bond. Solicitation may also serve to incite males into male–male competition (Cox and LeBeouf, 1977).

Reproductive strategies and the maintenance of polymorphism

White-throated sparrows exhibit true alternative strategies. When true genetic alternatives are maintained in a population, fitness of the alternatives should be equal. White-throated sparrows may be an exception to this rule because, regardless of fitness effects, the genetic alternatives are present in both sexes, there is likely to be evolutionary mechanisms maintaining multiple strategies, and the disassortative mating system results in equal production of the two morphs in the population. Long-term data on survivorship are needed to determine if overall fitness is equal in white and tan morphs; however, the present study suggests that reproductive success may indeed be the same. Although white males experience a fitness advantage away from the nest by engaging in EPCs, they are also losing paternity at home by presumably investing less in mate guarding. If white and tan fitness are unequal, then selection should cause extinction of the strategy with the lower fitness. However, it is possible that an advantage in one component of fitness may be balanced by a disadvantage in another. Even if fitness is unequal in the two morphs, disassortative mating functions as an evolutionary mechanism maintaining multiple strategies. By mating disassortatively, both morphs have an equal probability of producing tan and white offspring, thereby allowing each parental type to benefit equally from the fitness advantages associated with the alternative strategies exhibited by their offspring. Disassortative mating could give rise to an evolutionary compromise in which the variance in fitness between the morphs is decreased and the stability of the polymorphism is maintained. Mating preferences and the evolutionary forces influencing these preferences may ultimately be responsible for maintaining this genetic polymorphism. Analysis of long-term data and cycles of survivorship and reproductive success in males and females.
of the two morphs will reveal much about how selection has shaped life-history strategies.

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