Mate choice based on static versus dynamic secondary sexual traits in the dark-eyed junco

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Some secondary sexual traits (SSTs) such as structural characteristics are semi-permanent or static, while others, such as courtship display, are more labile or dynamic. In this paper we report results from two experiments designed to test the relative attractiveness to female dark-eyed juncos (Junco hyemalis, Passeriformes, Aves) of a relatively static plumage trait, the amount of white in the tail, and a relatively dynamic behavioral trait, courtship intensity. The experiments derived from a study showing that female juncos prefer males that court more vigorously. We asked whether females also base their preferences on plumage traits and how they respond when presented with a choice between attractive traits that are either static (plumage) or dynamic (courtship) in nature. In the first experiment we presented males to females in paired mate-choice trials and found that males enhanced with more white in their tails were more attractive to females than controls with unenhanced tails. Females spent more time with enhanced males and directed more sexual displays toward them. In the second experiment we tested whether females preferred males with enhanced tails (a static SST) or males with enhanced hormone-mediated courtship behavior (a dynamic SST). In this experiment females did not demonstrate a consensus preference for either the static or the dynamic trait. Instead, some females preferred the male whose courtship performance was enhanced with testosterone, while others preferred the male with an enhanced tail. We conclude that both kinds of traits are important in junco mate choice, but that some females apparently weigh static traits more heavily than dynamic ones, while other females use opposite weightings.

Key words: dark-eyed juncos, Junco hyemalis, lability, mate choice, secondary sexual traits. [Behav Ecol 10:91–96 (1999)]

Secondary sexual traits (SSTs) vary greatly in the lability of their expression. Some are highly dynamic, their expression changing rapidly with ecological, physiological, and/or emotional state; an example is the nuptial coloration of some fish (Lanzing and Brower, 1974). Other SSTs are relatively static, with little or no change in expression after their development for a particular episode of breeding, as in antlers in ungulates or plumage in birds (Payne, 1972). Most SSTs lie somewhere between these two extremes, exhibiting variable potential for shifts in expression as well as variable lag periods between a change in the state of the animal and a change in the expression of the trait.

The significance of variation in lability of expression of SSTs is unclear. Models of intersexual selection based either on Fisherian runaway processes (Fisher, 1958; Lande, 1980) or on preexisting aesthetic preferences and sensory biases (Bassolo, 1990; Burley et al., 1982; Ryan, 1990) make no predictions about expected degree of SST lability. Models positing that SSTs have evolved to facilitate female assessment of variation in male quality (e.g., Hamilton and Zuk, 1982; Kodric-Brown and Brown, 1984; Zahavi, 1975), predict that females should prefer traits that are the most reliable indicators of quality. There are, however, opposing opinions regarding the relationship between reliability of SSTs and lability of expression. On the one hand, highly dynamic SSTs might be the most accurate indicators of male quality because they respond rapidly to changes in male condition (e.g., Fostled and Karter, 1992; Wingfield et al., 1990) and, therefore, provide females with current information regarding the condition of prospective mates. On the other hand, static SSTs may be more reliable indicators because they are less sensitive than dynamic traits to stochastic environmental factors that can affect trait expression (e.g., Möller and Pomiankowski, 1993). Dynamic SSTs may also be less reliable if relatively inferior males are able to sustain deceptively high-quality trait expression for short periods of time.

Traits of differing lability may also convey different information regarding condition or status (Sorenson and Derrickson, 1994). For example, avian plumage development (molt) is an expensive physiological process (e.g., Payne, 1972), and plumage expression (morphology and color) has been shown to be affected by condition during molt (e.g., Johnsen et al., 1996). Thus, plumage expression, by virtue of its physiological cost, may provide an excellent index of the bearer’s genetic quality or long-term viability. However, because molt usually occurs between breeding seasons, plumage may not provide a good measure of current condition at the time of mating. Females that focused solely on plumage might be mislead; whereas females that relied on plumage during mate choice as well as on more dynamic SSTs (such as song or courtship display) might obtain a more complete picture of male quality.

To establish experimentally the relative importance to mate choice of traits of different labilities, it is necessary to simultaneously manipulate dynamic and static SSTs and then measure their effect on male attractiveness. We investigated the effect of two male secondary sex characteristics, one relatively static and one dynamic, on female mating preferences in the dark-eyed-junco, Junco hyemalis carolinensis. The juncos we study are socially monogamous North American buntings (Emberizinae) that are ideally suited for this investigation for two reasons. First, experimentally manipulated testosterone (T) is known to affect male courtship intensity and attractiveness (Enstrom et al., 1997). Males maintained at peak levels of testosterone (T-males) throughout the breeding season

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court more vigorously (Enstrom et al., 1997) and sing more frequently (Ketterson et al., 1992) than control males with basal breeding season levels of the hormone, and in mate-choice experiments females prefer T-males to controls (Enstrom et al., 1997). Thus, T-mediated courtship behavior can be viewed as a dynamic SST in this species. Second, results from a preliminary set of experiments suggested that females respond to the amount of white color in male tail feathers (rectrices), a relatively static SST (Hill et al., unpublished observations). Courting males spread their tails and exhibit the white in their outer rectrices, and increasing the amount of white by replacing dark feathers with white ones appears to make them more attractive to females. Thus, in juncos, it should be possible to investigate male attractiveness by independently altering both dynamic and static SSTs.

Here we report two experiments. In the first, we manipulated the amount of white in male tail feathers to confirm that this plumage character affects male attractiveness and female mate choice. In the second, we manipulated both the amount of white in the tail and the testosterone level to test the relative importance of both traits to female mate choice.

**METHODS**

**Study species**

*J. h. carolinensis* is a common breeder above 1000 m in the vicinity of Mountain Lake Biological Station (MLBS) of the University of Virginia, Giles County, Virginia, USA, where we work (see Chandler et al., 1994, for a description of the study site). Winter flocks break up and juncos establish territories in April. Pairs form during April and early May. Females build the nests and incubate, and both sexes care for offspring. Juncos are socially monogamous, but extrapair fertilizations are fairly common, and males sire only 60–75% of the offspring they help to rear (Ketterson et al., 1996, 1997; Raouf et al., 1997). Male success at siring young through extrapair copulations varies, indicating that the potential for sexual selection is high (Ketterson et al., 1996, 1997; Raouf et al., 1997).

Male junco courtship displays consist of song, erection of body plumage (pitloeration), pulsatile spreading of tail feathers, and manipulation of nest material (Enstrom et al., 1997; Titus et al., 1997). Performance of these behaviors is at least in part controlled by T (Enstrom et al., 1997) and so can be highly labile, potentially affected by such factors as social status, condition, and age.

In adult juncos of both sexes, prebasic molt occurs in autumn and is complete; thus the wing and tail feathers are replaced. In yearlings these feathers are produced while young are still dependent on their parents and are retained through the following breeding season. The spring prealternate molt in all ages and both sexes is slight and does not involve flight feathers (Pyle et al., 1987; Nolan et al., 1992). Thus, plumage color is static, fixed for the year (except for slight fading) at least 6 months before the onset of breeding.

Junco plumage is gray with sharply contrasting white on the breast and tail. Sex- and age-related dichromatism is detectable by experienced field workers (Balph et al., 1979; Ketter- son, 1979); males are darker than females and have more extensive white in their tail (Figure 1). Among males, adults are darker than yearlings and also have whiter tails. Rectrices (six pairs, the innermost pair numbered 1, the outermost 6) vary in color: the proportion of the feather that is white usually is greatest on pair 6, intermediate on pair 5, and least on pair 4; a trace of white is occasionally found on pair 3. Feathers belonging to pairs 6 and 5 are often entirely or mostly white in males and on some females; pair 4 is usually largely white in adult males, less so in yearling males, and still less so in females.

**Capture and housing**

We captured (at baited mist nets) 30 females and 22 males between 14 and 16 April 1995. Before mate-choice trials, males were housed singly in cages (0.6 × 1.2 × 2.4 m) in an outdoor aviary; females were housed singly or in groups of two in identical cages. Birds were fed mealworms, water, and a variety of seeds ad libitum.

We weighed all birds, measured wing (flattened), tail, and tarsus length, and scored the darkness of the gray of the crown (using the Munsell neutral value scale) and the amount of white in the tail (hereafter “tail white”). We scored tail white by estimating the proportion of white (in 0.1 increments) on rectrices 6–3 on the right side of the tail and summing these proportions. For example, three completely white tail feathers would result in a score of 3, which is higher than occurs in nature (see Figure 1).

**Hormonal treatment of females**

We implanted females subcutaneously with one 8-mm length (1.47 mm i.d., 1.96 mm o.d.) of silastic tubing containing crystalline β-17-estradiol to stimulate expression of unambiguous precopulatory displays. In previous experiments Enstrom et al. (1997) showed that this treatment increases the tendency of female juncos to give precopulatory displays, but has no influence on their preferences for males in mate choice trials.

**General experimental protocol**

Each mate-choice experiment consisted of trials in which a single female was allowed to choose between two simultaneously presented males of different phenotypes. Males were presented to females in a Y-shaped aviary described and depicted in Enstrom et al. (1997). On the afternoon before their presentation to females, males were placed in enclosures in the arms of the Yaviary and allowed to acclimate. The following morning, the preferences of three females, one at a time, were tested with this male pair. Each female was first held in a small assessment cage (0.31 × 0.31 × 0.62 m), from which she could view both males, and then released into the larger aviary and allowed to express her preference as described below. After the third trial male positions were switched from one arm of the Y to the other in preparation for the next day,
when three more females were tested. In experiment 1, four male dyads were presented to six females each, and two dyads were presented to three females each. In experiment 2, each of five different male dyads was presented to six females. We tested potential effects of dyad and male position on female attendance time (see below) and found no effect of either variable in either experiment (ANOVA; experiment 1: $F_{6,8} = 1.87, p = .14$; experiment 2: $F_{5,7} = 0.74, p = .67$).

In both experiments 1 and 2, each trial consisted of two parts: a 20-min period of assessment by the female and a 30-min period of active female choice. Males courted females both during the assessment period and during the period of active choice. During the assessment period, the female could see and hear both males from a distance of 1.6 m (0.5 m closer than described in Enstrom et al., 1997). Following the assessment period, the female was released into the Y for the period of active choice. During this period, the female could approach and interact with one or the other male through the hardware-cloth front walls of his cage. When a female was within 0.9 m of the wall of either male's cage, a wooden barrier prevented her from seeing the other male; and time spent by the female within 0.6 m of a male cage was scored as attendance time in the choice area of that male (see Enstrom et al., 1997).

We evaluated each female's preference on the basis of two a priori criteria. The first criterion was attendance time with each male. The second was the number of precopulatory displays given to each male from within his choice area. Behavior and time spent in other parts of the cage were considered neutral. We treated a trial as successful (i.e., indicative of a preference) if the female spent at least 7.5 min (one quarter of her active choice time) in either of the male choice areas (combined). Females that failed to meet this criterion were retested after at least 3 days had elapsed. Females were tested as many as three times; an individual that still showed no choice was removed from the experiment. We considered a trial as ending in a tie if the difference in attendance time with each male was less than 10% of the total time spent associating with both males (e.g., if a female spent 6 min with one male and 5 min with the other, the difference in time spent, 1 min, would be less than 10% of the total 11 min of attendance time; trial declared a tie). Although the results including ties were similar, the criterion for ties was established a priori, and ties are not reported in the results.

We compared the behavior of the two male treatment groups by quantifying song rates and the extent of ptiloerection, an index of courtship intensity (Enstrom et al., 1997). The most exaggerated ptiloerection in each minute of the period was ranked on a scale of 1 (lowest) to 3. Scores were averaged over the entire period to determine a mean ptiloerection score. Male behavior was recorded during a 30-min observation period at the start of each day before the introduction of the first female and during the assessment period of each trial. We did not quantify male behavior during the period of active choice because the proximity of the female largely determines male behavior at that time (see Enstrom et al., 1997).

**Experiment 1: Increased tail white and male attractiveness**

In experiment 1 (29 April–19 May 1995) we tested female preference for males with experimentally increased tail-white compared to control males whose tail white was within the normal adult male range. Male dyads were matched for age (yearling or older), size, and body mass (within 2.2 mm wing length and within 2.3 g mass).

We manipulated tail white according to the methods described by Holberton et al. (1989). We cut rectrices 3 and 4 approximately 1 cm from the pygostyle, hollowed out the remaining feather shaft with a needle, and inserted and glued (super glue) a new feather (trimmed at its distal end to match the size and shape of the natural feather). Before manipulation the mean male tail-white score was 2.45 (Figure 1). In experimental males, we replaced rectrices 3 and 4 on each side with four white feathers, producing tail white scores of about 4. In control males we replaced rectrices 3 and 4 with feathers similar in color to those that were removed, producing a mean score of 2.4 (i.e., unchanged).

**Experiment 2: Female preference for extent of tail white and intensity of courtship behavior**

In this experiment we tested (31 May–15 June 1995) whether females preferred males with increased tail white or males with enhanced hormone-mediated courtship behavior. One treatment group, which we refer to as ES for enhanced static trait, consisted of males with increased tail white that had participated in experiment 1; these males were implanted for the purposes of experiment 2 with two empty 10-mm silastic tubes. The other group, which we refer to as the enhanced dynamic trait (ED) group, was composed of control males (normal tail-white scores) from experiment 1, now implanted with two 10-mm lengths of silastic tubing packed with crystalline testosterone (for implanting details, see Keterson et al., 1992, 1996). As stated earlier, these treatments created two classes of males: (1) those with T levels similar to free-living males after the spring peak (empty implants) and with increased white in their tails (ES males), and (2) those with elevated T levels resembling the spring peak (T implants) and with naturally colored tails (ED males). Males remained in the same dyads they had belonged to in experiment 1; however, no female saw the same dyad in experiment 2 that she had seen in experiment 1.

**Analysis**

We compared central tendency in attendance time using Wilcoxon paired-sample tests; numbers of females preferring one or the other type in each experiment were compared using binomial tests. $P$ values are two-tailed for all tests except those in which we made a priori predictions, which are indicated.

**RESULTS**

**Experiment 1**

**Male behavior**

In the absence of females, the behavior of males did not differ according to treatment. Males did not engage in courtship behaviors before the introduction of females, and song rates of experimental (increased tail white) males (mean = 0.01 songs/min) and control males (mean = 0.02) did not differ significantly (Wilcoxon paired-sample test: $Z = -1.0, n = 6, p = .37$).

During the period of female assessment, male ptiloerection did not vary significantly with treatment (experimental males, $mean = 22.12$; control males, $mean = 19.53$; $Z = -0.74, n = 6, p > .46$). There was also no significant difference in song rate between experimental ($mean = 0.01$) and control males ($mean = 0.37; Z = 1.54, n = 6, p = .15$).

**Female behavior**

During the 30-min active choice period, females spent significantly more time with experimental males ($mean = 11.42$ min) than with control males ($mean = 5.19; Z = -2.40, n = 24, one-tailed $p < .01$). Nineteen of 24 females preferred experimental males (binomial test: $n = 24, p < .01$; Figure 2).
Nine of the 24 females tested gave 39 precopulatory displays during experiment 1. The rate of display toward experimental males (mean = 1.33 displays/trial) was significantly greater than that toward controls (mean = 0.46; Wilcoxon paired-sample test: Z = -1.93, n = 24, one-tailed p = .03). Seven females displayed only to the experimental male; two displayed to both the experimental male and the control.

**Experiment 2**

**Male behavior**

In the absence of females, ED males sang at a significantly higher rate (mean = 0.19 songs/min) than ES males (mean = 0.01; Z = -1.60, n = 5, one-tailed p = .05).

During the period of female assessment, ED males again sang at a significantly higher rate (mean = 0.83 songs/min) than ES males (mean = 0.25; Z = 1.83, n = 5, one-tailed p = .03), and they had higher average piloerection scores (mean ED males = 7.9) than ES males (mean = 4.8; n = 5, one-tailed p = .04).

**Female behavior**

Females spent similar amounts of time with ED males (mean = 7.16 min) and ES males (mean = 9.67 min) during active-choice (Z = -1.15, n = 20, two-tailed p = .2; power = 0.43 at \( \alpha = 0.05 \)). Fourteen of the 20 females spent more time with the ES males than with the ED males (binomial: n = 20, \( \hat{p} = .06 \); Figure 3).

Five of the 20 females tested gave 15 precopulatory displays during experiment 2; 10 of the displays were given to the ES males and 5 to the ED males. Two females displayed only to the ES male, one displayed only to the ED male, and two displayed to both males.

**DISCUSSION**

Female juncos appear to rely on both static (plumage) and dynamic (courtship intensity) SSTs to assess potential mates. In our first experiment, females demonstrated a significant preference for males with whiter tails, suggesting that evaluation of plumage may be sufficient to influence the assessment of male attractiveness. Enstrom et al. (1997) had previously established that female juncos can base their choice of mate on a dynamic SST, courtship intensity. Together, these results provide further support for the possibility that female preference for male SSTs can drive sexual selection in socially monogamous, relatively dimorphic species (Ketterson et al., 1997; Johnson and Burley, 1997). Consistent with this view, genetic paternity analysis of this study population suggests that the potential for sexual selection is high (Ketterson et al., 1997).

In experiment 2 we found that females did not show a significant consensus preference for either the ED (testosterone-enhanced courtship) or the ES (increased tail white) male. Power was low in this experiment, however, and more females did prefer the ES male (14) over the ED male (6). Furthermore, the choice we presented was between an enhanced dynamic trait within the range of natural variation (our T manipulation mimicked natural peak levels, see Enstrom et al., 1997) and an enhanced static trait that was exaggerated beyond the range of natural variation (our manipulation increased the amount of white in the tail by at least one third; Figure 1). It is therefore possible that our ES treatment acted as a supernormal stimulus and that our result does not reflect the relative appeal of these two SSTs during normal mate choice. However, individual females did express a clear preference for one or the other treatment, and we conclude that both behavior and plumage are important during mate choice in this species.

The apparent tendency for some females to focus on plumage while others focus on behavior is consistent with a result from experiments investigating age-based mate choice in juncos (Enstrom et al., in preparation). In that study we found that females overwhelmingly preferred older males to yearlings (older males naturally court more vigorously and have “brighter” plumage than yearlings, including whiter tails).
However, when yearlings were implanted with T and older males received empty implants (causing the yearlings to court more vigorously than the older males), some females preferred the yearlings (11), while others preferred the older males (14). Here again, some individuals appeared to favor the bright plumage, while others evidently favored the behavioral effects produced by enhanced T.

In general, female birds appear to base their choice of mates on a variety of SSTs. Numerous studies have demonstrated female preferences for static traits, such as tail length (Andersson, 1982; Saino et al., 1997) and plumage coloration (e.g., Hill, 1990), for moderately labile traits, such as comb color and morphology (e.g., Zuk et al., 1990, 1992) and song repertoires (e.g., Scarry and Brenowitz, 1988), and for highly dynamic behavioral traits, such as courtship performance and bower decoration (e.g., Borgia, 1993; Enstrom et al., 1997; Houtman, 1992). In addition, suites of SSTs of differing labilities appear to be involved in mate choice in several species (e.g., Gibson and Bradbury, 1985; Zuk et al., 1992). For example, male jungle fowl (Gallus gallus) have relatively static SSTs (plumage color and morphology), somewhat dynamic SSTs (comb color and morphology), and highly dynamic SSTs (courtship behavior) (Zuk et al., 1990). That more than one SST may affect mate choice is shown by studies demonstrating choice based on multiple criteria, which can include both static and dynamic SSTs (Burley, 1981; Gibson and Bradbury, 1985; Johns and Zuk, 1996; Sorenson and Derrickson, 1994; Zuk et al., 1992).

Choice based on several traits of differing labilities might evolve if these traits convey information about different aspects of a male’s quality (Møller et al., 1998; Sorenson and Derrickson, 1994). For example, courtship intensity may provide accurate information regarding a male’s current condition, whereas plumage expression may better reflect long-term condition or viability. Females may also use plumage to determine the age of potential mates (e.g., Enstrom, 1993; Enstrom et al., in preparation) but use courtship intensity to assess health or viability. It is also possible that individual female condition or experience affects which traits are salient for her during mate choice. These questions call for experiments that quantify variation in mating preferences (Arnold, 1983) in relation to changing female condition (e.g., age, previous mating success, hormonal state).

Our results are also consistent with models of intersexual selection that do not predict particular patterns of lability in SST expression. Indeed, our finding that females prefer tail white exaggerated beyond the range of natural variation supports the hypothesis that female preferences originate before, and subsequently drive, the evolution of male SSTs (Basolo, 1990; Burley et al., 1982; Ryan, 1990). This preference for supernormal tail-white expression is not consistent with the view that females discriminate against phenotypic extremes and implies that females are not the selective factor that limits tail-white expression in males.

Our results suggest that female mating decisions may be based on simultaneous assessment of two or more SSTs of differing labilities and reveal that female juncos have no strong preference for either the static or the dynamic trait. Current understanding of how selection might affect lability of expression of SSTs is poor. Continued research into the decisions females make when faced with both dynamic and static SSTs and the forces that shape those decisions is needed. This will require focusing not only on variation in relevant male traits, but also on variation among females in their preferences for these traits.

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