Female ornamentation and male mate choice in dark-eyed juncos

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Traits that enhance attractiveness in one sex may or may not influence attractiveness in the other. In the dark-eyed junco, *Junco hyemalis*, outer tail feathers of males and females are all or partly white and form a sharp contrast with the bird's mostly grey plumage. The amount of white in these feathers ('tail white') is greater in males than in females and, as we report here, is greater in birds that have completed a second prebasic moult than in yearlings. During courtship, male juncos spread their tails, revealing their tail white, and a previous experiment has shown that males with experimentally enhanced tail white are more attractive to females. To determine whether females with experimentally enhanced tail white would be preferred by males, we clipped and replaced tail feathers of females, creating a control group with low to natural levels of tail white and an enhanced group with high levels. We tested preference in a mate choice apparatus like that used previously and found that males courted both control and enhanced females and displayed individual preferences but showed no collective preference for members of either category of females. Because we found neither a preference for trait values that indicate greater age/experience (experimentally enhanced females) nor a preference for less male-like appearance (control females), our results are inconsistent with a role for male mate choice in the maintenance of tail white in females. Female tail white may be subject to selection in another context or persist owing to a genetic correlation between the sexes. Regardless, the sexes apparently prefer different trait values, which suggests that preferences are expressed independently in males and females.

Sexual selection is often cited as a cause of sexual dimorphism, particularly if bright colours or ornaments are involved (Andersson 1994). In birds, males are commonly the more brightly coloured or ornamented sex (Andersson 1982; Hamilton & Zuk 1982) and females have been shown to prefer brighter males in experimental trials of mate choice (Johnson 1988; Zuk et al. 1990; Hill et al. 1999).

In some species, females are also brightly coloured or ornamented (Jones & Hunter 1993; Møller 1993; Irwin 1994; Johnstone et al. 1996), and several explanations have been offered for female brightness including sexual selection (Amundsen 2000) and genetic correlations between the sexes for both preferences and traits (Lande 1980; Hill 1993). If males benefit by mating with females that bear certain indicator traits, then sexual selection by mate choice may act directly on the female phenotype (Potti & Merino 1996; Jones & Hunter 1999; Amundsen 2000). For example, in species with biparental care, male choice of females in good condition may enhance male reproductive success (Searcy 1982; Burley 1986; Hoelzer 1989; Amundsen et al. 1997) and refine male preferences for brightly coloured females. Age in particular may indicate greater parental ability and females of many species brighten as they age (Savalli 1995), predicting that males should prefer brighter, thus older females. However, several efforts to demonstrate greater parental effort or reproductive success on the part of brighter or more ornamented females have proved unsuccessful (Hill 1993; Cuervo et al. 1996; Rohde et al. 1999; Smiseth & Amundsen 2000). Preference for bright females in the absence of a benefit for males may indicate a genetic correlation between the sexes for preference (Hill 1993; Rohde et al. 1999).

Males have also been shown to avoid brightly coloured females, perhaps because they perceive ornamentation as male-like (Burley & Coopersmith 1987; Price & Burley 1994). In other taxa, masculine traits in females may induce uncertainty regarding the sex of a potential mate (Basolo & Delaney 2001) or predict less parental effort (Drickamer et al. 2001).

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Finally, female ornamentation may be neutral with respect to male preference, and persist only as a genetically correlated response to sexual selection on males (Lande 1980, 1987). For example, because tail length does not correlate with reproductive success in female barn swallows, *Hirundo rustica*, the persistence of long tails in female swallows has been attributed to strong sexual selection on tail length in males combined with a genetic correlation between the sexes in trait expression (Cuervo et al. 1996).

The dark-eyed junco, *J. hyemalis carolinensis*, is a weakly sexually dimorphic songbird with biparental care. Both sexes have a patch of white on the outermost rectrices (tail feathers) that contrasts with the dark inner rectrices. The area of white, hereafter tail white, is greater in males than in females (Enstrom et al. 1997; Hill et al. 1999) and is related to age in males (Holberton et al. 1989; Hill et al. 1999). When courting, males spread their tails to display the outer white rectrices (Enstrom et al. 1997; Hill et al. 1999). Female juncos show a preference for older males (D. A. Enstrom, M. Soenksen, C. Ziegenfus, V. Nolan, Jr & E. D. Ketterson, unpublished data) and for males with experimentally enhanced tail white (Hill et al. 1999).

In this study we examined natural variation in tail white in field-caught juncos as it relates to sex and age. We also tested male preference for tail white by allowing males the opportunity to choose between two types of females, one with experimentally enhanced tail white and one (control) with low levels of tail white, both within the natural range of variation. We confirmed that males have more white than females and found that tail white increases with age in females as well as males, leading us to anticipate three possible outcomes of the mate choice trials. First, males might prefer females with enhanced tail white, which would suggest either that female tail white is under direct sexual selection because males prefer older, more experienced, and possibly more fecund females, or, given the already demonstrated female preference for whiter males, that male and female preferences are genetically correlated. Second, males might prefer females with less tail white, thus avoiding females with male-like ornamentation, perhaps because such females would be less effective parents. Third, males might show no preference in relation to tail white, which would suggest that female ornamentation represents a correlated response to sexual selection on this trait in males or functions in contexts other than mate choice.

METHODS

Study Species

The dark-eyed junco, *Junco hyemalis carolinensis*, is a common passerine of the Appalachian Mountains of Virginia, U.S.A., where it breeds at elevations above 1000 m (Chandler et al. 1994; Ketterson et al. 1996). Males are slightly heavier than females and have slightly longer wings and tails (ca. 5%; Nolan et al. 2002). In this population, juncos breed from early May through late July (Ketterson et al. 1992). Females build the nest and incubate, and both sexes care for nestlings and fledglings. Although juncos are socially monogamous, extrapair fertilizations are common (Ketterson et al. 1997; Raouf et al. 1997; Cawthorn et al. 1998).

Quantifying Natural Variation in Plumage

To assess sex- and age-related variation in tail white, we compiled data collected in the field at Mountain Lake Biological Station, University of Virginia, Giles County, Virginia (37°22′31″N, 80°31′24″W) during the breeding seasons of 1995, 1996 and 1997 as part of a long-term study. Juncos were captured in baited traps and mist nets from early April to mid-August, before their prebasic moult, and sexed according to wing length, plumage coloration and presence of a cloacal protuberance (males) or brood patch (females) (Nolan et al. 2002). Age was measured in two ways. Based on plumage and eye colour, all adults could be classified as adult yearlings (AY) or older adults in at least their second breeding season (AO) (Nolan et al. 2002). A subset of these could be assigned to a specific year class (yearling, 2-year-old, 3-year-old, etc.) based on a known age at banding (for birds initially banded as nestlings, juveniles or yearlings).

We examined each individual's tail, which consists of six pairs of rectrices numbered in the order in which they undergo moult (innermost first, outermost last, referred to as rectrices R1–R6, left and right). R1 and R2 are always entirely grey and R3–R6 vary progressively in the proportion that is white from lowest (R3) to highest (R6). Tails are symmetrical, so by convention we scored only the right side of the tail, noting the proportion of white on R3–R6 to the nearest 0.1. For birds measured repeatedly within one year by the same or different observers, we used the modal score. If measurements for a rectrix were multimodal, we used the mean of the modes.

We used multivariate analysis of variance (MANOVA) to assess the effects of sex and age (AY versus AO) on the proportion of each rectrix (R3–R6) that was white and ANOVA to compare sex and age (AY versus AO) for total tail white (the sum of R3–R6). Having found that AO individuals had greater scores, we used MANOVA to determine whether tail white in R3–R6 continued to increase with age after the transition from the yearling plumage to the first postyearling plumage and ANOVA to compare total tail white by sex and exact age. Post hoc analyses were performed using Tukey highest significant difference (HSD) tests where appropriate; alpha level was set at $P \leq 0.05$.

Mate Choice: Capture and Housing

Subjects for the mate choice study (36 males and 14 females) were captured near Mountain Lake Biological Station and transported to Kent Farm Bird Observatory, Indiana University, Monroe County, Indiana, U.S.A. (39°09′02″N, 86°23′46″W), where they were maintained in mixed-sex groups for at least 9 months before the start of trials. Care consisted of indoor housing, light schedules corresponding to the day lengths of their natural habitat, and a uniform diet including seed (red millet, white millet and sunflower hearts), orange slices, mealworms and a protein-rich mixture of finely chopped dried dog food,

hard-boiled eggs and carrots. Water was treated with vitamins (Quintrex, Aqua-Vite) during 3 weeks of each month and with an antibacterial drug (Sulmet) during the fourth week.

In late April 2000, subjects were separated into single-sex groups. Females were housed in a free-flight aviary (6.40×3.20 m) until the start of trials in early May when they were moved to individual cages ($0.61 \times 0.61 \times 0.90$ m) within the free-flight aviary. Cages provided visual isolation from other females and served to prevent social interactions and possible effects of females' dominance status on their attractiveness to males. Males were housed in a separate free-flight aviary (4.27×6.10 m), except for a period of 48 h just before a trial (see below) when they were isolated in individual cages ($0.61 \times 0.61 \times 0.90$ m) within the free-flight aviary.

Tail White Manipulation

We scored tail white in females as with the natural populations. We also recorded age (AO, AY), mass (g), tail length (of longest rectrix, mm), estimate of body fat (0–5) (Helms et al. 1967) and presence or absence of a brood patch. We lightly anaesthetized the females with metofane, cut rectrices 4 and 5 on each side of the tail to a length of approximately 1.0–1.5 cm from the body, and, using the techniques of Holberton et al. (1989) and Hill et al. (1999), hollowed out the remaining feather-shafts with a sewing needle, and secured new feathers into the hollowed shafts using super glue. New feathers were then trimmed to match the length and overall shape of the original feathers. Blocking for age, females were randomly selected to serve as controls or experimentals. Controls were assigned feathers that produced tail white scores at the low end of the natural range (1.40–1.65) and experimentally enhanced females were assigned feathers that produced tail white scores at the high end of the natural range (2.80–3.00; Fig. 1). Rectrix manipulations were done before the start of trials, and feather repairs were performed as needed throughout the course of the

Figure 1. Frequency distribution of tail white scores in free-living male and female juncos captured during the breeding season near Pembroke, Virginia, U.S.A.

trials. Repairs were made in a similar fashion without anaesthetizing the birds.

Females were presented to males two at a time in dyads, one control and one experimental ($N = 8$ dyads). Seven dyads were unique and the eighth consisted of two females that were tested first as members of other dyads.

Trial Protocol

Trials were conducted in a mate choice apparatus modelled after that used by Enstrom et al. (1997) and Hill et al. (1999) (Fig. 2). Illumination was provided by full-spectrum fluorescent lights (Vita-Lite), and portions of the walls and floor of the apparatus that held the females were lined with UV-reflectant paper to better reveal the appearance of plumage in natural light (Sheldon et al. 1999). The afternoon before testing, members of a dyad of females were placed in individual compartments of the choice aviary at the end distal to the observatory where they were visually isolated from one another (Fig. 2). During the morning hours of the following day, we introduced one male, observed his choice, then did the same for a second male. Afterwards we switched the positions of the females within the apparatus, again allowed them to acclimate overnight, and presented them to another two males the next morning. Hence, each dyad of females was seen by four males, and each male saw no more than one dyad, with one exception: males that failed to make a choice during their initial mate choice trial were tested with a different dyad (see below).

Trials consisted of three phases. During the first or preassessment phase (30 min), we observed female behaviour before introducing the male. We then placed a male in a small, elevated observation cage at the end of the choice aviary proximal to the observatory, from which he could view the females during the assessment phase (20 min; Fig. 2) and we again quantified female behaviour. The male was subsequently released and allowed to express his preference during the choice phase (30 min). Trials began on 29 May and were completed by 29 June 2000.

Female Behaviour During the Preassessment and Assessment Phases

During the preassessment phase, we noted 12 female behaviours, including preening, bill wiping, flying, climbing, ptiloerection (feather puffing), tail spreading, bowing, wing fluttering and gathering of nest material, and three vocalizations (chipping, trilling and short-range song) (Balph 1977). One observer (W.L.W.) scored the first occurrence of each behaviour during each 30-s interval of the observation period. If a behaviour began in one interval and continued into the next interval, it was scored for both intervals. We later totalled the number of 30-s intervals in which each behaviour occurred. During the assessment phase, while the male viewed both females simultaneously from the observation cage, we again noted each female behaviour according to its first occurrence within each 30-s interval. Preassessment behaviour was quantified once for each dyad of females, and female
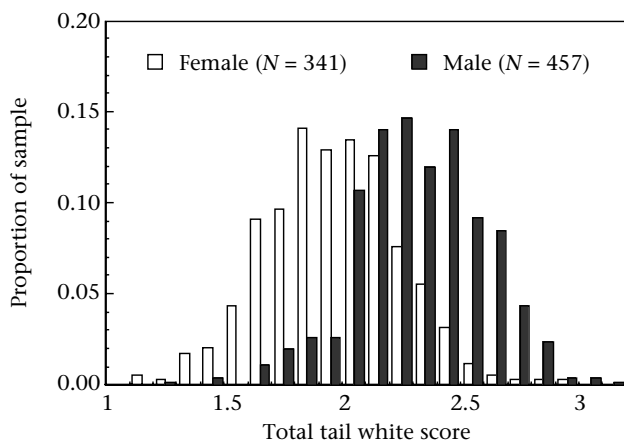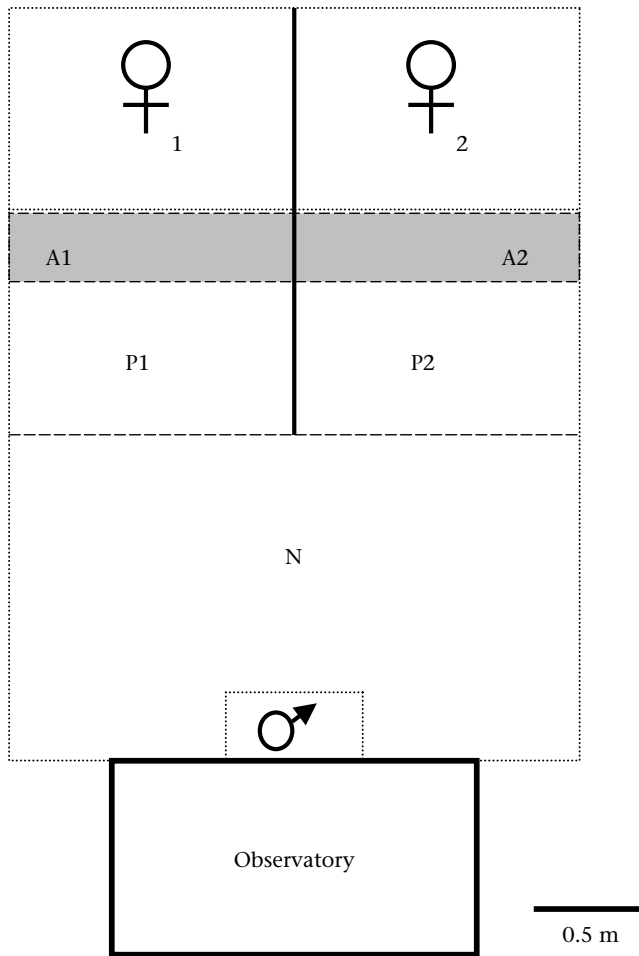
Figure 2. Diagram of mate choice aviary. Zones of male choice designated as N for neutral, P for passive, and A for Active. Human observer sat in observatory. Dotted lines indicate walls of see-through plastic mesh (1.3×1.3 cm). Solid lines indicate opaque walls. Dashed lines indicate virtual boundaries between zones of choice.

behaviour during the assessment phase was quantified for each trial.

Male Behaviour and Male Choice

Courtship displays of male juncos include ptiloerection (puffing of body plumage along the back and flanks), short- and long-range song (Titus 1998), picking up nesting material, and fanning the tail feathers in a display that reveals the white portions of the outer rectrices (Enstrom et al. 1997; Hill et al. 1999). During the choice phase we noted male behaviour, again by scoring the first occurrence of each of the following behaviours in each 30-s interval: bill wiping, ptiloerection, tail spreading, gathering nest material, long-range song and short-range song, classified according to whether they were directed towards the control female or the experimentally enhanced female by noting whether the male was in the active zone of one female or the other (see below).

We noted the location of the male in three zones of the mate choice apparatus, classified according to their proximity to the female: the neutral zone (most distant from the females and nearest the observatory where the male was able to see both females), the passive zone (where the male was closer to one female than the other and his view was restricted to only one female, but his position was not directly adjacent to the female), and the active zone (where the male could see only one female and was in immediate proximity to her; Fig. 2; Enstrom et al. 1997). We computed the number of strong choice intervals that the male spent with each female by counting the number of 30-s intervals in which a male entered the active zone of one female without having spent time (perched) in her passive zone or in the active or passive zone of the other female. All trials were filmed, but some videotapes were not usable, so to validate the method of counting intervals for determining male choice, we scored a subset of the videotapes ($N = 10$) and compared total time (s) spent by males in the females' active zones with the number of strong choice intervals and found them to be strongly correlated (Pearson correlation: $r_8 = 0.977$, $P < 0.001$).

Successful trials were defined as those in which males accumulated at least 15 strong choice intervals on both sides combined (one quarter of the total intervals possible) and spent at least 10% more intervals with one female than the other. If a male failed to meet these criteria he was retested at a later date with a different female dyad. If a male failed to perform after two trials, he was removed from the experiment. We tested 36 males, 32 of which led to successful trials. Twenty-six males met the criteria during their first opportunity to choose, six met the criteria in their second attempt, and four males failed after two trials.

Analyses

Behavioural data could not be transformed to meet criteria for parametric tests, so we used Wilcoxon matched-pairs signed-ranks tests to compare female behaviour during the preassessment and assessment phases and male behaviour during the choice phase. To assess male choice, we first asked whether preference (the percentage of strong choice intervals that were spent with the experimental female) varied with female dyad, and when it did not (Kruskal–Wallis test: $\chi^2_7 = 3.224$, $P = 0.864$), we treated each trial as a datum. During the assessment phase control females were more active (flew more) than experimental females, so to control for this behavioural difference, we combined observations across treatments, regressed number of strong choice intervals on number of intervals flown, and compared the residuals by treatment (Wilcoxon matched-pairs signed-ranks test), treating the residuals as variation in preference not explained by variation in flight. We also assessed preference with a binomial test, asking whether the proportion of males preferring control or experimental females deviated from an expected value of 0.5. We assessed significance using two-tailed tests and where necessary

corrected for multiple comparisons with a modified Bonferroni procedure (Sokal & Rohlf 1995), using 0.05 as the criterion for significance, but commenting on results for which $P < 0.1$. All tests were run using SPSS 10.0 for Macintosh.

RESULTS

Sex- and Age-related Variation in Plumage Characteristics in Natural Populations

A comparison of the frequency distributions of total tail white scores from males and females, year classes combined (Fig. 1), was bimodal. Total tail white scores ranged from 1.10 to 3.13 and the distributions of males and females were highly overlapping ($\overline{X}\pm$SE male: 2.29 ± 0.013, $N = 457$; female: 1.94 ± 0.016, $N = 341$).

A multivariate ANOVA simultaneously considering tail white scores for R3–R6 revealed a significant age difference in R4 between yearlings and older adults (AO versus AY), significant sex differences in all four feathers, and no significant interactions (R4–R6 in Fig. 3, Table 1). There were also significant differences in total tail white between the sexes and between yearlings and older adults (Fig. 3).

Samples of known-age birds were smaller and failed to show increasing tail white with age beyond the transition from the yearling plumage (Table 2, R4 depicted in Fig. 4). With respect to total tail white, we found significant effects of both age ($P = 0.0039$) and sex ($P = 0.0111$), with males having greater tail white scores than females and yearlings having lower total tail white scores than birds in

their second, third, fourth, fifth or sixth breeding seasons (which could not be distinguished from one another). Of the four feathers analysed (R3–R6), variation in the MANOVA model was most affected by R4 ($r^2 = 0.244$).

Female Behaviour During the Preassessment and Assessment Phases

Treatment did not significantly affect female behaviour during the preassessment phase (Table 3). Experimentally enhanced females tended to wing-flutter more than control females (Wilcoxon matched-pairs signed-ranks test: NS), but not significantly so. During the assessment phase control females flew during significantly more intervals ($\overline{X}\pm$SE = 25.16 ± 2.59) than experimentally enhanced females (13.34 ± 2.04; Wilcoxon matched-pairs signed-ranks test: $P = 0.003$), but did not differ from enhanced females in any other behaviour (Table 4).

Male Preference and Behaviour

Males did not behave differently when courting control or enhanced females (Table 5) and did not court one group more than the other (Fig. 5). The average number of strong choice intervals males spent with enhanced females ($\overline{X}\pm$SE = 17.00 ± 2.79) did not differ significantly from the number spent with control females (14.09 ± 2.06; Wilcoxon matched-pairs signed-ranks test: $Z = 0.337$, $N = 32$, $P = 0.736$). To control for the difference in the number of flights taken by females in each treatment, we regressed the number of strong choice intervals directed
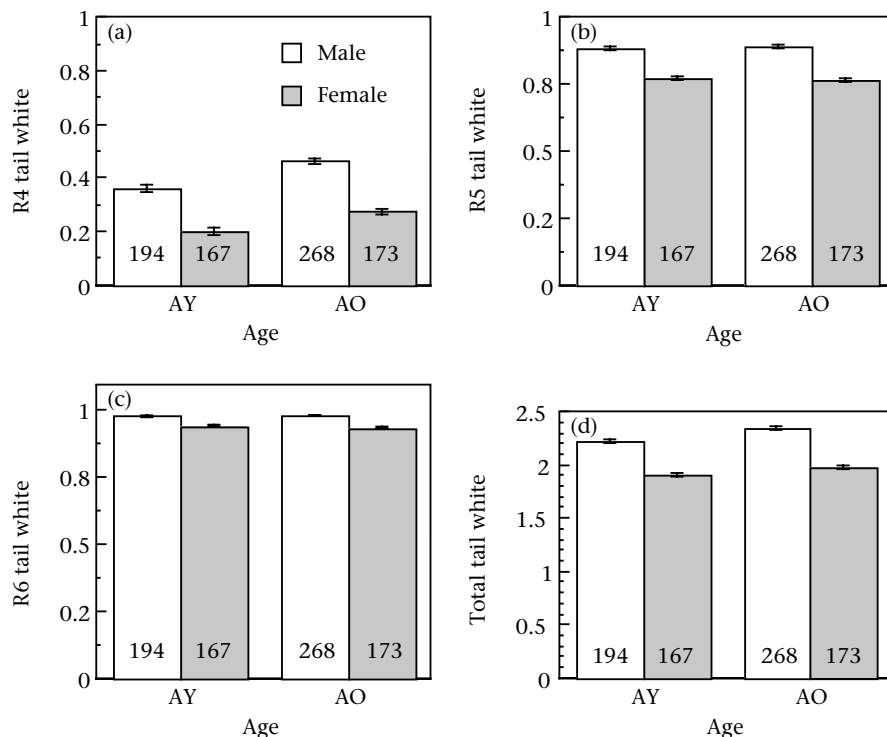

Figure 3. Effect of sex and age class (AY, AO) on the proportion of white in rectrices R4–R6 (a–c) and total tail white (sum of R3–R6; d).

**Table 1.** MANOVA of tail white scores in AO and AY males and females

Factor	F	df	P
Sex			
Wilks' $\lambda = 0.73$	75.06	4, 795	<0.001
Rectrix 3	27.55	1, 798	<0.001
Rectrix 4	190.95	1, 798	<0.001
Rectrix 5	233.33	1, 798	<0.001
Rectrix 6	106.10	1, 798	<0.001
Age class			
Wilks' $\lambda = 0.93$	14.98	4, 795	<0.001
Rectrix 3	1.91	1, 798	0.168
Rectrix 4	49.35	1, 798	<0.001
Rectrix 5	0.08	1, 798	0.772
Rectrix 6	0.21	1, 798	0.644

towards each female on the number of intervals she spent flying ($r = -0.34$) and found no effect of treatment on the magnitude of the residuals of this regression (Wilcoxon matched-pairs signed-ranks test: $Z = 0.365$, $N = 32$, $P = 0.715$) and thus no evidence for an effect of treatment on preference.

Analysed in another way, of the 32 males that made a choice, 18 males preferred experimentally enhanced females and 14 males preferred controls (sign test: $P = 1.0$). To assess the power of this comparison we assumed a null hypothesis of equal preference (50:50) and used tables from Cohen (1988) to compute the power to detect deviations from 50:50 based on a sample of 32 males and an alpha of 0.05. Our power to distinguish a ratio of 45:55 as different from 50:50 (Cohen's small effect size of 0.05) was 0.15. Our powers to distinguish ratios of 25:75 (effect size 0.25; Cohen's large effect) and 20:80 (effect size of 0.30) were 0.92 and 0.98, respectively. We selected an effect size based on that reported in Hill et al. (1999) for male juncos of 0.29 (19 of 24 females preferred the male with enhanced white). Interpolating between effect sizes and related powers of 0.25 (power = 0.92) and 0.30 (0.98) for a sample of 32 and an alpha of 0.05 provides a power estimate of 0.97. Had males shown a preference of the same magni-

Table 2. MANOVA of tail white scores in known-age males and females

Factor	F	df	P
Sex			
Wilks' $\lambda = 0.98$	2.29	4, 576	0.059
Rectrix 3	1.41	1, 579	0.236
Rectrix 4	5.30	1, 579	0.022
Rectrix 5	6.62	1, 579	0.010
Rectrix 6	4.30	1, 579	0.039
Known age			
Wilks' $\lambda = 0.92$	2.61	20, 1911	<0.001
Rectrix 3	0.45	5, 579	0.814
Rectrix 4	7.68	5, 579	<0.001
Rectrix 5	0.47	5, 579	0.799
Rectrix 6	0.27	5, 579	0.930
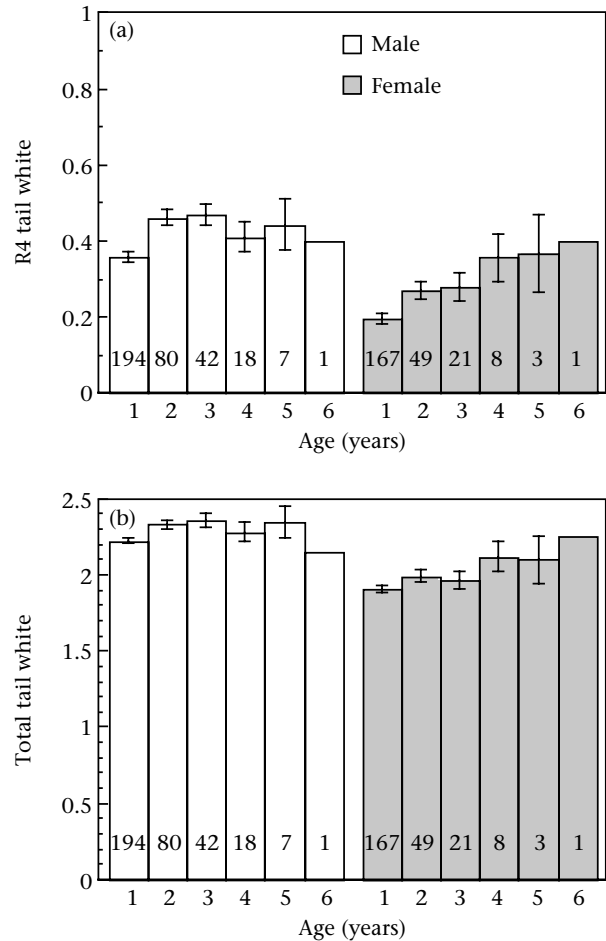
Figure 4. (a) Relationship between exact age and sex in rectrix R4 and (b) the sum of R3–R6, total tail white.

tude as females, our samples would have been adequate to detect it.

DISCUSSION

Tail white scores were greater in males than in females and increased with age. In both sexes, tail feathers grown by nestlings in the nest and maintained during the first year of breeding in the yearling plumage had less white than feathers grown in subsequent moults, but tail white did not continue to increase after the transition from the yearling plumage. By using an experimental manipulation to create individuals with trait values that exist but are uncommon in nature, we were able to ask how such values affected mate choice. Although females had earlier been shown to prefer males whose tail white was experimentally enhanced (Hill et al. 1999), we did not find the reverse to be true for males. Males approached females of both treatments, sang to them and made choices, but choice was independent of treatment.

Static Versus Dynamic Traits

Static traits that are constant over time, such as plumage coloration or size, have been compared to dynamic,

Table 3. Female behaviour during the preassessment phase

Behaviour	Control females		Enhanced females	
	$\overline{X}$	SE	$\overline{X}$	SE
Bill wiping	4.88	2.05	6.25	1.74
Chipping	0.00	0.00	1.88	1.88
Climbing	2.75	2.47	1.00	0.73
Flying	32.75	9.77	27.25	8.37
Gathering nest material	2.88	2.95	1.13	1.13
Preening	3.38	2.73	0.63	0.50
Ptiloerection	28.38	9.69	18.00	6.22
Short-range song	7.13	5.94	2.00	1.15
Wing fluttering	0.50	0.19	1.63	0.53

Mean number of intervals in a trial in which a behaviour occurred at least once. Wilcoxon matched-pairs signed-ranks: $N = 8$, all comparisons NS.

changeable traits such as display or song, and several authors have considered which kind of trait should be more important in mate choice (Hill et al. 1999; Kodric-Brown 2001). To the extent that traits reflect condition, dynamic traits are more likely to reflect current circumstances, whereas static traits are more likely to reflect circumstances at an earlier time, for example when moult occurred (Hill et al. 1999). We considered the possibility that females of one group might have behaved in ways that were more attractive to males, while females of the other group were more attractive in appearance. We found that control females flew significantly more often than experimentally enhanced females during the assessment phase when males were observing them. Greater activity enhances attractiveness in males of this species (Enstrom et al. 1997; Hill et al. 1999), but in this study we found that males tended to avoid active females. However, when we removed the effect of activity statistically by regressing preference on flying, we found no treatment difference in the residuals and thus no indication that tail white affects attractiveness.

Implications for Persistence of Tail White in Females, Role of Male Mate Choice

When the sexes experience different selective pressures, sexual or otherwise, they tend to diverge in morphology, behaviour and physiology. If sexual selection is strong only on males, and if traits that enhance success in sexual competition among males are of little value when possessed by females and are otherwise disadvantageous, we expect selection to produce large sex differences and to favour mechanisms that lead to sex-limited expression (Cuervo & Møller 2000). Small sex differences (weak dimorphism), on the other hand, are the expected result of similar selective pressures on males and females and mechanisms of expression that may be sex-biased but are not sex-limited (Lynch & Walsh 1998; Chippindale et al. 2001). The challenge in any particular case is to determine why a trait that is more prominent in males also persists in females. Is persistence the direct result of sexual or natural selection on females, or is it the result of a genetic correlation with males in the absence of direct selection on females (Amundsen 2000)?

In some cases, bright coloration in female birds indicates female condition or quality (Ruusila et al. 2001). For example, brighter females may be less subject to parasitic infections, as has been shown for pied flycatchers, *Ficedula hypoleuca* (Potti & Merino 1996), bar-tailed godwits, *Limosa lapponica taymyrensis* (Piersma et al. 2001) and barn owls, *Tyto alba* (Roulin et al. 2001b). More male-like female bluethroats, *Luscinia s. svecica*, are in better condition (greater body mass and tarsus length) and are more attractive to males (Amundsen et al. 1997). These observations suggest that males may benefit from mating with brighter females and act as directional selective agents on indicator traits (but see Rohde et al. 1999). In contrast, males are sometimes less attracted to bright females, perhaps because they are more male-like in appearance or less disposed to provide parental care (Drickamer et al. 2001).

The other frequently cited explanation for brightness in females is a genetic correlation between the sexes. Cross-fostering has demonstrated a genetic correlation for

Table 4. Female behaviour during the assessment phase

Behaviour	Control females		Enhanced females		Z	P
	$\overline{X}$	SE	$\overline{X}$	SE		
Bowing	0.13	0.06	0.38	0.21	−0.877	0.380
Bill wiping	8.38	0.87	9.44	1.07	−0.921	0.357
Chipping	0.50	0.47	0.00	0.00	−1.342	0.180
Climbing	4.69	1.17	6.00	1.72	−0.382	0.703
Flying	25.16	2.59	13.34	2.04	−2.973	0.003
Gathering nest material	3.47	1.29	1.50	0.51	−1.356	0.175
Preening	4.78	1.48	5.53	1.23	−0.533	0.581
Ptiloerection	16.34	2.38	21.06	1.73	−1.533	0.125
Short-range song	2.44	1.24	1.50	0.73	−0.357	0.721
Trilling	0.25	0.12	0.66	0.33	−0.986	0.324
Tail spreading	0.13	0.10	0.13	0.10	0.000	1.000
Wing fluttering	1.31	0.29	2.00	0.43	−1.202	0.229

Mean number of intervals in a trial in which a behaviour occurred at least once. Wilcoxon matched-pairs signed-ranks: $N = 32$.

Table 5. Male behaviour during choice phase

Behaviour	Control females		Enhanced females		
	$\overline{X}$	SE	$\overline{X}$	SE	$P*$
Bill wiping	1.38	0.80	1.34	0.45	0.971
Long-range song	0.72	0.37	1.31	1.28	0.664
Gathering nest material	1.25	1.03	0.06	0.06	0.261
Ptiloerection	5.69	1.52	10.16	2.39	0.111
Short-range song	4.13	1.17	7.31	2.24	0.215
Tail spreading	1.00	0.54	1.59	0.81	0.455

Mean number of intervals in a trial in which the behaviour occurred at least once.
*Binomial test.

plumage traits in male and female barn owls (Roulin et al. 2001a), as have selection experiments on bill colour in zebra finches, *Taeniopygia guttata* (Price & Burley 1994). When, as in zebra finches, traits are correlated across the sexes but preferences are not (females prefer redder bills, males do not), evolution in one sex can be constrained by the effects of trait expression in the other sex (Price & Burley 1993, 1994).

Persistence of Tail White in Female Dark-eyed Juncos, Role of Male Mate Choice

As shown, tail white in juncos is expressed by both sexes, but more so in males and at greater levels in older individuals of both sexes. Female juncos prefer older males (Enstrom et al., unpublished data) and males with experimentally enhanced tail white (Hill et al. 1999). Since male juncos did not base their preferences on tail white, we can reject two hypotheses. Unlike females, male juncos are not attracted by a signal of greater age in females. Neither are they repulsed by a trait that can be considered masculine. Instead, because female tail white had no detectable effect on mate choice, we may reason that the trait persists in females because (1) its expression in females reflects a genetic correlation combined with no selection against tail white in females (Lynch & Walsh 1998), or (2) tail white benefits females in some context other than mate attraction (West-Eberhard 1983), such as in attaining social status. It would be interesting to know more about the mechanisms that act on the moult process and that account for differential expression of tail white, and especially whether they act similarly in males and females. Studies underway are assessing the strength of genetic correlations (J. W. McGlothlin, P. G. Parker, V. Nolan, Jr & E. D. Ketterson, unpublished data), the relationship between condition and tail white, and the roles of natural selection and reproductive competition among females in accounting for female tail white.

Figure 5. Male attendance time (number of strong choice intervals) with enhanced and control females. Points above the diagonal line represent males that spent more time with enhanced females; points below the line represent males that spent more time with control females. The point within the circle represents three overlapping data points.

References

Amundsen, T. 2000. Why are female birds ornamented? *Trends in Ecology and Evolution*, **15,** 149–155.

Amundsen, T., Forsgren, E. & Hansen, L. T. T. 1997. On the function of female ornaments: male bluethroats prefer colourful females. *Proceedings of the Royal Society of London, Series B*, **264,** 1579–1586.
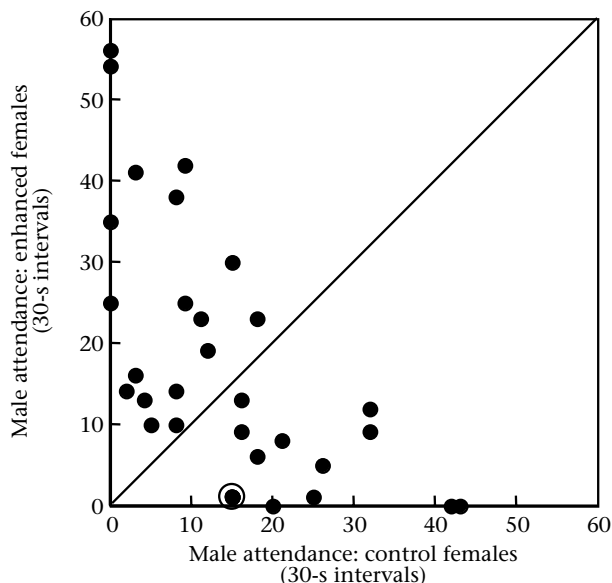
Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature*, **299**, 818–820.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Balph, M. H. 1977. Winter social behaviour of dark-eyed juncos: communication, social organization, and ecological implications. *Animal Behaviour*, **25**, 859–884.

Basolo, A. & Delaney, K. 2001. Male biases for male characteristics in females in *Priapella olmecae* and *Xiphophorus helleri* (family Poeciliidae). *Ethology*, **107**, 431–438.

Burley, N. & Coopersmith, C. B. 1987. Bill colour preferences of zebra finches. *Ethology*, **76**, 133–151.

Burley, N. T. 1986. Sexual selection for aesthetic traits in species with biparental care. *American Naturalist*, **127**, 415–445.

Cawthorn, J. M., Morris, D. L., Ketterson, E. D. & Nolan, V., Jr. 1998. Influence of experimentally elevated testosterone on nest defence in dark-eyed juncos. *Animal Behaviour*, **56**, 617–621.

Chandler, C. R., Ketterson, E. D., Nolan, V., Jr & Ziegenfus, C. 1994. Effects of testosterone on spatial activity in free-ranging male dark-eyed juncos, *Junco hyemalis*. *Animal Behaviour*, **47**, 1445–1455.

Chippindale, A. K., Gibson, J. R. & Rice, W. R. 2001. Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in *Drosophila*. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 1671–1675.

Cohen, J. 1988. *Statistical Power Analysis for the Behavioral Sciences*. New York: Academic Press.

Cuervo, J. & Møller, A. 2000. Sex-limited expression of ornamental feathers in birds. *Behavioral Ecology*, **11**, 246–259.

Cuervo, J. J., de Lope, F. & Møller, A. P. 1996. The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study. *Behavioral Ecology*, **7**, 132–136.

Drickamer, L., Robinson, A. & Mossman, C. 2001. Differential responses to same and opposite sex odors by adult house mice are associated with anogenital distance. *Ethology*, **107**, 509–519.

Enstrom, D. E., Ketterson, E. D. & Nolan, V., Jr. 1997. Testosterone and mate choice in the dark-eyed junco. *Animal Behaviour*, **54**, 1135–1146.

Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science*, **213**, 384–387.

Helms, C., Aussiker, W., Bower, E. & Fretwell, S. D. 1967. A biometric study of major body components of the slate-colored junco, *Junco hyemalis*. *Condor*, **69**, 560–578.

Hill, G. E. 1993. Male mate choice and the evolution of female plumage coloration in the house finch. *Evolution*, **47**, 1515–1525.

Hill, J. A., Enstrom, D. E., Ketterson, E. D., Nolan, V., Jr & Ziegenfus, C. 1999. Mate choice based on static vs. dynamic secondary sexual traits in the dark-eyed junco. *Behavioral Ecology*, **10**, 91–96.

Hoelzer, G. A. 1989. The good parent process of sexual selection. *Animal Behaviour*, **38**, 1067–1078.

Holberton, R., Able, K. & Wingfield, J. 1989. Status signaling in dark-eyed juncos, *Junco hyemalis*: plumage manipulations and hormonal correlates of dominance. *Animal Behaviour*, **37**, 681–689.

Irwin, R. E. 1994. The evolution of plumage dichromatism in the new world blackbirds: social selection on female brightness? *American Naturalist*, **144**, 890–907.

Johnson, K. 1988. Sexual selection in pinyon jays II: Male choice and female–female competition. *Animal Behaviour*, **36**, 1048–1053.

Johnstone, R., Reynolds, J. D. & Deutsch, J. 1996. Mutual mate choice and sex differences in choosiness. *Evolution*, **50**, 1382–1391.

Jones, I. & Hunter, F. 1999. Experimental evidence for mutual inter- and intrasexual selection favouring a crested auklet ornament. *Animal Behaviour*, **57**, 521–528.

Jones, I. L. & Hunter, F. M. 1993. Mutual sexual selection in a monogamous seabird. *Nature*, **362**, 238–239.

Ketterson, E. D., Nolan, V., Jr, Wolf, L. & Ziegenfus, C. 1992. Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). *American Naturalist*, **140**, 980–999.

Ketterson, E. D., Nolan, V., Jr, Cawthorn, M. J., Parker, P. G. & Ziegenfus, C. 1996. Phenotypic engineering: using hormones to explore the mechanistic and functional bases of phenotypic variation in nature. *Ibis*, **138**, 70–86.

Ketterson, E. D., Parker, P. G., Raouf, S. A., Nolan, V., Jr, Ziegenfus, C. & Chandler, C. R. 1997. The relative impact of extra-pair fertilizations on variation in male and female reproductive success in dark-eyed juncos (*Junco hyemalis*). In: *Avian Reproductive Tactics: Female and Male Perspectives* (Ed. by N. T. Burley), pp. 81–101. Lawrence, Kansas: Allen Press.

Kodric-Brown, A. 2001. Female choice in the guppy (*Poecilia reticulata*): the interaction between male color and display. *Behavioral Ecology and Sociobiology*, **50**, 346–351.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, **34**, 292–305.

Lande, R. 1987. Genetic correlations between the sexes in the evolution of sexual dimorphism and mating preferences. In: *Sexual Selection: Testing the Alternatives* (Ed. by M. B. Andersson), pp. 83–95. Chichester: J. Wiley.

Lynch, M. & Walsh, B. 1998. *Genetics and Analysis of Quantitative Traits*. Sunderland, Massachusetts: Sinauer.

Møller, A. P. 1993. Sexual selection in the barn swallow, *Hirundo rustica* III. Female tail ornaments. *Evolution*, **47**, 417–431.

Nolan, V., Jr, Ketterson, E. D., Cristol, D. A., Rogers, C. M., Clotfelter, E. D., Titus, R. C., Schoech, S. J. & Snajdr, E. 2002. Dark-eyed junco (*Junco hyemalis*). In: *The Birds of North America. No. 716* (Ed. by A. Poole & F. Gills). Philadelphia: The Birds of North America.

Piersma, T., Mendes, L., Hennekens, J., Ratiarison, S., Groenewold, S. & Jukema, J. 2001. Breeding plumage honestly signals likelihood of tapeworm infestation in females of a long-distance migrating shorebird, the bar-tailed godwit. *Zoology—Analysis of Complex Systems*, **104**, 41–48.

Potti, J. & Merino, S. 1996. Decreased levels of blood trypanosome infection correlate with female expression of a male secondary sexual trait: implications for sexual selection. *Proceedings of the Royal Society of London, Series B*, **263**, 1199–1204.

Price, D. & Burley, N. 1993. Constraints on the evolution of attractive traits: genetic (co) variation of zebra finch bill color. *Heredity*, **71**, 405–412.

Price, D. K. & Burley, N. T. 1994. Constraints on the evolution of attractive traits: selection in male and female zebra finches. *American Naturalist*, **144**, 908–934.

Raouf, S. A., Parker, P. G., Ketterson, E. D., Nolan, V., Jr & Ziegenfus, C. 1997. Testosterone affects reproductive success by influencing extra-pair fertilizations in male dark-eyed juncos (Aves: *Junco hyemalis*). *Proceedings of the Royal Society of London, Series B*, **264**, 1599–1603.

Rohde, P. A., Johnsen, A. & Lifjeld, J. T. 1999. Female plumage coloration in the bluethroat: no evidence of an indicator of maternal quality. *Condor*, **101**, 96–104.

Roulin, A., Dijkstra, C., Riols, C. & Ducrest, A. 2001a. Female- and male-specific signals of quality in the barn owl. *Journal of Evolutionary Biology*, **14**, 255–266.

Roulin, A., Riols, C., Dijkstra, C. & Ducrest, A. 2001b. Female plumage spottiness signals parasite resistance in the barn owl (*Tyto alba*). *Behavioral Ecology*, **12**, 103–110.

Ruusila, V., Poysa, H. & Runko, P. 2001. Female wing plumage reflects reproductive success in common goldeneye *Bucephala clangula*. *Journal of Avian Biology*, **32**, 1–5.

Savalli, U. M. 1995. The evolution of bird coloration and plumage elaboration: a review of hypotheses. In: *Current Ornithology* (Ed. by D. M. Power), pp. 141–190. New York: Plenum.

Searcy, W. 1982. The evolutionary effects of mate selection. *Annual Review of Ecology and Systematics*, **13**, 151–157.

Sheldon, B. C., Andersson, S., Griffith, S. C., Ornborg, J. & Sendecka, J. 1999. Ultraviolet colour variation influences blue tit sex ratios. *Nature*, **402**, 874–877.

Smiseth, P. & Amundsen, T. 2000. Does female plumage coloration signal parental quality? A male removal experiment with the bluethroat (*Luscinia s. svecica*). *Behavioral Ecology and Sociobiology*, **47**, 205–212.

Sokal, R. R. & Rohlf, F. J. 1995. *Biometry*. New York: W. H. Freeman.

Titus, R. 1998. Short-range and long-range songs: use of two acoustically distinct song classes by dark-eyed juncos. *Auk*, **115**, 386–393.

West-Eberhard, M. J. 1983. Sexual selection, social competition and speciation. *Quarterly Review of Biology*, **58**, 155–183.

Zuk, M., Johnson, K., Thornhill, R. & Ligon, J. D. 1990. Parasites and male ornaments in free-ranging and captive red jungle fowl. *Behaviour*, **114**, 232–248.