

CORRELATIONAL SELECTION LEADS TO GENETIC INTEGRATION OF BODY SIZE AND AN ATTRACTIVE PLUMAGE TRAIT IN DARK-EYED JUNCOS

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Abstract.—When a trait's effect on fitness depends on its interaction with other traits, the resultant selection is correlational and may lead to the integration of functionally related traits. In relation to sexual selection, when an ornamental trait interacts with phenotypic quality to determine mating success, correlational sexual selection should generate genetic correlations between the ornament and quality, leading to the evolution of honest signals. Despite its potential importance in the evolution of signal honesty, correlational sexual selection has rarely been measured in natural populations. In the dark-eyed junco (*Junco hyemalis*), males with experimentally elevated values of a plumage trait (whiteness in the tail or "tail white") are more attractive to females and dominant in aggressive encounters over resources. We used restricted maximum-likelihood analysis of a long-term dataset to measure the heritability of tail white and two components of body size (wing length and tail length), as well as genetic correlations between pairs of these traits. We then used multiple regression to assess directional, quadratic, and correlational selection as they acted on tail white and body size via four components of lifetime fitness (juvenile and adult survival, mating success, and fecundity). We found a positive genetic correlation between tail white and body size (as measured by wing length), which indicates past correlational selection. Correlational selection, which was largely due to sexual selection on males, was also found to be currently acting on the same pair of traits. Larger males with whiter tails sired young with more females, most likely due to a combination of female choice, which favors males with whiter tails, and male-male competition, which favors both tail white and larger body size. To our knowledge, this is the first study to show both genetic correlations between sexually selected traits and currently acting correlational sexual selection, and we suggest that correlational sexual selection frequently may be an important mechanism for maintaining the honesty of sexual signals.

Key words.—Genetic correlations, heritability, honest signals, *Junco hyemalis*, quantitative genetics, sexual selection, trait integration.

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Sexual selection is one of the strongest evolutionary forces, and it may lead to rapid evolutionary change and striking sexual dimorphism (Andersson 1994; Hoekstra et al. 2001; Kingsolver et al. 2001; Shuster and Wade 2003). Sexually selected traits (ornaments) often function as signals of benefits to a potential mate that are either phenotypic or genetic (reviewed in Andersson 1994; Møller and Alatalo 1999; Møller and Jennions 2001; Kokko et al. 2003). The evolution of such honest signals requires that the optimum value of the trait differs for individuals of differing phenotypic quality (Nur and Hasson 1984; Grafen 1990), which should lead to fitness surfaces that are shaped like rising ridges (Getty 1998). This fitness surface occurs because high-quality males with highly developed ornaments will have the highest fitness. Low-quality males with ornaments that are too large will have lower fitness because of factors such as predation or male-male interactions, and high-quality males with ornaments that are too small will have lower fitness because they attract fewer females.

Such a rising fitness ridge is an example of correlational selection, which occurs when a trait's fitness effect depends on its interaction with another trait (Cheverud 1982, 1984; Lande and Arnold 1983; Phillips and Arnold 1989; Brodie 1992; Schluter and Nychka 1994; Sinervo and Svensson 2002). Positive correlational selection creates linkage disequilibrium and favors covariance due to pleiotropy; over many generations, it can lead to trait integration or the evo-

lution of common inheritance of functionally related traits (Cheverud 1982, 1984; Lande and Arnold 1983; Brodie 1989, 1992; Phillips and Arnold 1989; Schluter and Nychka 1994; Sinervo and Svensson 2002). Correlational sexual selection, in particular, may generate genetic correlations between ornamental traits and traits that reliably predict dominance or condition, leading to the evolution of signal honesty (LeBas et al. 2003). Such sexual selection may arise as the result of interactions between intrasexual competition and intersexual choice. A male ornamental trait, for example, may attract the attention not only of females but also of other males (Berglund et al. 1996; Ligon 1999). Male-male interactions may enforce the relationship of an ornamental trait with a quality-related trait such as body size because males with attractive signals are repeatedly challenged by other males.

Although many studies have demonstrated that sexual selection acts on multiple characters (Andersson 1994; Candolin 2003), we know very little about the importance of correlational sexual selection in natural populations. The regression-based method developed by Lande and Arnold (1983) is a useful way to measure sexual selection on multiple characters, but few studies using this method have reported measurements of the off-diagonal components of gamma (γ_{ij}), known as correlational selection gradients (Moore 1990; Fairbairn and Preziosi 1996; Rodriguez et al. 2002; LeBas et al. 2003, 2004; reviewed in Kingsolver et al. 2001).

In the dark-eyed junco (*Junco hyemalis*, Passeriformes:

Emberizidae), both males and females vary in the relative size of the area of white found on their otherwise gray outer rectrices ("tail white"; Hill et al. 1999; Wolf et al. 2004; Yeh 2004). Males with experimentally enlarged areas of tail white are more attractive to females (Hill et al. 1999); however, such enhancement of females does not affect their attractiveness to males (Wolf et al. 2004). During courtship, male juncos exhibit their tail feathers to females in a display known as tail spreading (Enstrom et al. 1997; Nolan et al. 2002). Tail white is also displayed in dominance contests, which tend to be won by males with whiter tails (Balph et al. 1979; Holberton et al. 1989). Body size, as measured by wing length, is also a predictor of dominance in juncos (Ketterson 1979). If the interaction between female choice and male-male competition has led to the association of tail white with male quality, we should find evidence of the integration of whiteness with body size.

In this study, we examined the evolution of tail white and two components of body size, wing length and tail length. To determine whether selection favors the integration of tail white with body size, we used data from a long-term field study of a natural population of juncos to estimate the strength of correlational (as well as directional and quadratic) selection. We measured selection using four components of lifetime fitness: juvenile survival, adult survival, mating success, and fecundity, which allowed us to detect the specific episode during which selection for integration occurs and to identify potential conflicting selection pressures (Arnold and Wade 1984a,b; Schluter et al. 1991). Because all three traits are expressed in both sexes, we measured selection separately on males and females; this permitted us to consider whether selection on females might constrain the integration of male traits (Lande and Arnold 1985).

Using a maximum-likelihood pedigree analysis, we estimated the **G** matrix, which includes measurements of additive genetic variance and covariance (Lynch and Walsh 1998) to detect the results of correlational selection (Brodie 1989, 1992, 1993b; Phillips and Arnold 1989; Sinervo and Svensson 2002) and to make evolutionary predictions based on our measurements of selection (Lande 1979; Grant and Grant 1995). We also measured between-sex genetic correlations to examine the potential for further evolution of sexual dimorphism (Lande 1980b; Price and Burley 1993; Merilä et al. 1998).

MATERIALS AND METHODS

Study Species and General Methods

We studied the Carolina subspecies of the dark-eyed junco (*J. h. carolinensis*), which breeds at high elevations in the southern Appalachians (Nolan et al. 2002). Juncos are socially monogamous, but extrapair fertilizations occur commonly (Raouf et al. 1997; Ketterson et al. 1998; Nolan et al. 2002). Females build nests and incubate eggs; both sexes defend eggs and young against predators and feed nestlings and fledglings. The population used in this study breeds at and around Mountain Lake Biological Station in Giles County, Virginia (37°22'N, 80°32'W).

At the beginning of each breeding season (April and May), we censused the population by capturing birds using mist

nets and traps at baited locations that remained the same from year to year. All individuals were marked with aluminum U.S. Fish and Wildlife Service leg bands and a unique combination of plastic color bands. We measured wing length, tail length, and tail white at each capture, and blood samples for DNA parentage analysis were collected once a year. Upon first capture (1987–2000), adult males were implanted subcutaneously with silastic tubes that were either filled with crystalline testosterone (T-males) or left empty (C-males). Effects of testosterone treatment on male juncos are reviewed elsewhere (Ketterson and Nolan 1992, 1999; Ketterson et al. 1996). From April to July, we monitored the nesting attempts of all birds on the study area (usually 50–60 pairs). On day 6 after hatching, we marked nestlings with aluminum and color bands and collected a blood sample for DNA parentage analysis. Juncos in this population may raise two (rarely three) broods each summer in the absence of nest predation and usually attempt to renest after nest loss (Nolan et al. 2002). We censused the population a second time at the end of each summer (July and August), capturing adults and newly independent young that had reached adult size (juveniles). The outer rectrices of juveniles tend to have less white than those of adults, and the two age classes are readily distinguishable by their body plumage (Nolan et al. 2002; Wolf et al. 2004; Yeh 2004). We also removed implants from males caught at the end of the summer.

Trait Measurement

We measured wing length as the distance from the wrist joint to the tip of the longest primary when the wing was flattened with the thumb, and tail length as the distance between the tip of the longest pair of rectrices and their point of insertion on the body (Pyle et al. 1987). Both measurements were taken with a ruler to an accuracy of 0.5 mm. When multiple measurements existed for an individual bird, we selected those taken by more experienced observers and summarized multiple measurements using the mode. In the absence of a clear mode, measurements were averaged.

We measured the tail white value of a rectrix as the percentage of its area that was white; an individual's score was the sum of the tail-white values on the right side of the tail (Fig. 1). Juncos in our population may have white on two, three, or four of the outer pairs of rectrices, and tail-white scores tend to fall between 1 and 3.5 (Wolf et al. 2004). Tail-white values were estimated by eye in increments of 5%; values obtained by this method were highly correlated with values obtained using computer image analysis, a more precise method ($r = 0.96$, $n = 74$; W. L. Wolf, J. M. Casto, E. D. Ketterson, unpubl. data). Multiple measurements were summarized separately for each rectrix, and these values were summed to give the tail-white score for each individual. Again, we used the modal score if available.

Because each of the three focal traits may change with age (Table 1, see also Nolan et al. 2002; Wolf et al. 2004; Yeh 2004), our analysis was based on measurements taken from the juvenile plumage, unless otherwise noted. The wings and tail of the juvenile plumage are retained until the end of the individual's second summer (its first breeding season; Nolan et al. 2002). Therefore, when measurements from juveniles

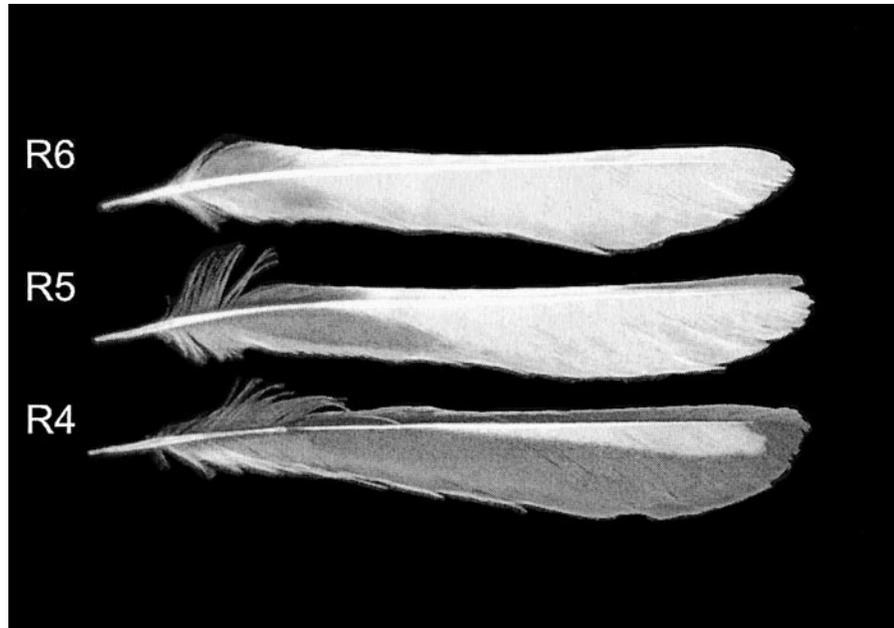


FIG. 1. Three outer right rectrices (R6 is the outermost) of a male junco. Tail white values for these feathers are R6 = 0.85, R5 = 0.65, and R4 = 0.15, giving this individual a tail white score of 1.65.

were unavailable, we used tail-white measurements from first-year adults. However, we did not use wing-length and tail-length measurements from first-year adults because feathers will have been shortened by a year's abrasion. Individual differences remain consistent across age classes for each trait in both males and females (J. W. McGlothlin, P. G. Parker, V. Nolan, Jr., and E. D. Ketterson, unpubl. data), which is a requirement for making evolutionary predictions for traits that change with age (Brodie 1993a).

Wing length, tail length, and tail white all show modest sexual dimorphism in juncos (Table 1, see also Nolan et al. 2002; Wolf et al. 2004; Yeh 2004). Wing length had the highest loading (0.91) on the first principal component in an analysis that included four components of body size (wing length, tail length, mass, and tarsus length), so wing length was used as a correlate for overall size (J. W. McGlothlin, unpubl. data).

Identification of the Sexes

The sex of juvenile juncos cannot be reliably determined in the field using a single diagnostic measurement, and during

TABLE 1. Descriptive statistics for wing length, tail length, and tail white (see Materials and Methods for definitions). Values are calculated from measurements taken from 258 females and 313 males, measured as juveniles. All traits are significantly sexually dimorphic (MANOVA, $P < 0.001$). A sexual dimorphism index (SDI) for each trait was calculated by dividing the male mean by the female mean.

	Males		Females		SDI
	Mean	SD	Mean	SD	
Wing length (mm)	82.2	1.50	77.7	1.42	1.06
Tail length (mm)	71.3	1.91	67.9	2.18	1.05
Tail white	2.18	0.26	1.82	0.25	1.18

the period of this study we did not collect blood samples from juveniles, hence we cannot use genetic markers to assign sex. However, adults caught during breeding may be sexed by the presence of a brood patch (females) or a cloacal protuberance (males), so juveniles caught as adults could be sexed retroactively. To assign sex to juveniles that were not recaptured as adults, we created a discriminant function using 571 juveniles (258 females, 313 males) that survived to adulthood. The function

$$Y = 111.1 \log(\text{wing length}) + 6.3 \log(\text{tail length}) + 1.5(\text{tail white}) - 226.3, \quad (1)$$

which correctly classified 95.3% of these juveniles (cutting point $y = -0.16$; Wilks' $\lambda = 0.262$), was used to classify individuals of unknown sex.

Parentage Analysis

Parentage analysis was performed using DNA extracted from blood collected from nestlings and adults during the breeding seasons of 1990–1996. Methods used to determine genetic parentage are presented in detail elsewhere (Raouf et al. 1997; Ketterson et al. 1998). Briefly, established multi-locus minisatellite DNA fingerprinting methods (Rabenold et al. 1990; Piper and Parker Rabenold 1992) were used to either include or exclude putative parents (i.e., adults whose behavior at or near the nest appeared parental). When this method indicated that one putative parent (in all cases except one, the male) was not the genetic parent of the nestling under consideration, additional gels were run to determine the identity of the extrapair parent (repeated use of minisatellites for data from 1990–1993, microsatellites for data from 1994–1996).

Estimation of Genetic Parameters and Variance Components

Pedigree.—We assembled a pedigree of 643 birds, including juveniles that had been banded as nestlings during 1990–1996 and their genetic parents. There were 611 birds with records for at least one of the three traits (wing length, tail length, and tail white), and 490 had records for all three. Before analysis, 10 individuals without phenotypic records and a single familial link were removed, resulting in a pedigree consisting of 633 birds: 397 progeny, 109 sires, and 155 dams (28 birds were both progeny and later parents). In cases of unknown parentage, the female observed at the nest was assumed to be the dam, and the sire was left unknown, resulting in a pedigree that contained more dams than sires.

Genetic models.—We used a restricted maximum-likelihood (REML) method (DXMUX procedure of DFREML v. 3.1; Meyer 1998, 2000) to estimate \mathbf{G} , genetic parameters (heritabilities, h^2 , and genetic correlations, r_g), and their standard errors. The DFREML program uses a derivative-free REML method to estimate additive genetic parameters given a pedigree and individual phenotypic values, while correcting for the influences of fixed or random effects (Meyer 1991, 1998). Unlike conventional ANOVA-based methods, multivariate REML does not require balanced datasets and can account for missing trait values and a complex pedigree (Meyer 1991, 1998). Our model incorporated two fixed effects: sex (to correct for sexual dimorphism) and hormonal treatment of the male associated with the nest that produced the offspring (to correct for potential effects of differential parental investment by T- and C-males, Ketterson et al. 1992). Models that incorporated parental effects, effects of shared nest environment, or birth-year effects did not generate significantly different genetic parameters and are not presented here (J. W. McGlothlin, P. G. Parker, V. Nolan, Jr., and E. D. Ketterson, unpubl. data). Significance of genetic parameters was tested using two-tailed, one-sample t -tests ($H_0: \mu = 0$), with degrees of freedom equal to the number of individuals in the model minus one.

Between-sex genetic correlations.—To determine whether male and female traits should evolve independently or in concert, we also estimated between-sex genetic correlations for the three traits. We used a REML model similar to the previous model, except traits were assigned as sex specific, resulting in a model that included six traits: male wing length, male tail length, male tail white, female wing length, female tail length, and female tail white. The REML values of the genetic correlations calculated between male and female traits provide estimates of the between-sex genetic correlations. This method of estimating genetic correlations does not generate estimates greater than unity or negative standard errors, as is possible using the typical, regression-based method (Price and Burley 1993; Lynch and Walsh 1998; Merilä et al. 1998). We tested for a significant difference from both zero and unity using one-tailed, one-sample t -tests, with degrees of freedom equal to the number of individuals in the model minus one.

Assortative mating.—Because estimates of heritability and genetic correlations may be biased by assortative mating, we tested for nonrandom mating by examining correlations be-

tween phenotypic values of dams with the average phenotypic values of their mates, weighted by the number of offspring sired.

Selection Analysis

Dataset.—We measured selection using birds of known age (i.e., they were first captured as juveniles; 1431 males, 1329 females) hatched between 1989 and 1996. The analysis included only individuals that had measurements available for all three traits. Because none of the individuals in the analysis was still alive at the time the analysis was performed, our sample consisted purely of individuals tracked over their entire lifespan.

Fitness components.—To partition selection into different episodes, we measured selection using each of four fitness components (juvenile survival, adult survival, average mating success, and average fecundity per mate) chosen such that they would multiply to give an estimate of lifetime fitness (Arnold and Wade 1984a,b). Each fitness component was transformed to relative fitness (w) in each regression by dividing by mean fitness. We estimated selection separately for males and females.

Survival.—Juvenile and adult survival were considered separately because natal dispersal (Nolan et al. 2002) is more likely to inflate estimates of mortality at the juvenile stage. Juvenile survival was counted as 1 if an individual was captured or sighted as an adult in the year after hatching or in any subsequent year. Individuals that were not captured were assigned a value of 0. Adult survival refers to the number of summers a bird was recaptured or resighted as an adult after having been banded as a juvenile. Adult survival ranged from 1 to 7. Males that had received testosterone implants that had not been removed at the end of a breeding season were excluded from the analysis of adult survival, because a prolonged exposure to testosterone may inhibit molt, decreasing overwinter survival (Nolan et al. 1992).

Reproductive success.—Measurements of reproductive success (mating success and fecundity per mate) were taken only from those years for which DNA analysis was conducted (1990–1996) and were based on the number of nestlings that survived to day 6, the age at which we collected blood samples for genetic analysis. The three focal traits are not expressed until after the feathers are grown (after fledging), so they should not experience direct selection before day 6. Therefore, measuring reproductive success as counts of day 6 nestlings should not bias our measurements of selection by assigning offspring fitness to the parent (Wolf and Wade 2001).

Mating success was calculated by counting the number of mates with which an individual produced a day 6 offspring. During a given breeding season, mating success ranged from 0 to 3. We were not able to detect individuals, if any, that were unable to pair, so our estimates of sexual selection are conservative (Ketterson et al. 1998). Nevertheless, some individuals did receive a value of zero for a given year; these were males that sired none of the offspring of their social mate and achieved no detectable extrapair fertilizations. Fecundity per mate ranged from 0 to 7 and was calculated by dividing the total number of day 6 offspring produced in a

given year by the number of mates in that year. Individuals that had no young surviving to day 6 were assigned a value of zero. If birds had records of mating success or fecundity from two or more years, we averaged them to generate a single score.

Selection gradients.—We used multiple linear regression to calculate selection gradients, which are estimates of the direct force of selection on a given trait when considered independently of the effects of selection on correlated traits included in the analysis (Lande and Arnold 1983). Linear (directional) selection gradients (β) indicate selection that changes the population mean, and nonlinear selection gradients (γ) indicate selection that acts on either the phenotypic variance of a trait i (γ_{ii} , quadratic selection) or the phenotypic covariance between two traits i and j (γ_{ij} , correlational selection).

Linear gradients were estimated from a regression model that excluded cross products and squared terms, while nonlinear gradients were estimated from a full model (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987; Brodie et al. 1995). Regression residuals were not normally distributed, so we could not use parametric tests of significance for selection gradients (Mitchell-Olds and Shaw 1987). We calculated standard errors of regression coefficients using a simple delete-one-individual jackknife technique and tested for significance using one-sample t -tests of the jackknifed estimates following the method described in Sokal and Rohlf (1995, pp. 820–823). Because of the small sample size in many of the selection analyses, we note trends ($P < 0.1$) as well as statistical significance ($P < 0.05$). We used a Bernoulli process to calculate the probability that the number of significant gradients measured was due to chance (Moran 2003). This method is more appropriate for the interpretation of tables with many small P -values than a sequential Bonferroni (Rice 1989), which is overly restrictive (Moran 2003).

All traits were standardized to zero mean and unit variance to facilitate comparisons among selection gradients (Arnold and Wade 1984a). Because the sample varied across analyses, this standardization was performed separately for each regression.

Male hormonal treatment.—Interpretation of the selection gradients measured in the study may be complicated by hormonal treatment of males, because testosterone treatment is likely to affect some fitness components (e.g., T-males obtain more extrapair fertilizations than C-males; Raouf et al. 1997; W. L. Reed, M. E. Clark, P. G. Parker, S. A. Raouf, N. Arguedas, D. S. Monk, E. Snajdr, V. Nolan, Jr., and E. D. Ketterson, unpubl. ms.). However, measurements of selection should not be affected unless there is a correlation between hormonal treatment and one of the traits under consideration, for example, if larger males were more likely to have T implants (Lande and Arnold 1983). All of the traits in this study were measured on juveniles, and birds were not implanted until the beginning of their first breeding season, so testosterone treatment cannot have affected the development of the traits. Hormone treatment was applied randomly to males; T-males, C-males, and untreated males did not differ with respect to any of the traits in this study (MANOVA, Wilks' $\lambda = 0.98$, $F_{6, 488} = 0.868$, $P = 0.52$). Nevertheless, we tested for an effect of hormone treatment on measures of selection

on adult males (via adult survival, mating success, and fecundity) by running separate regressions that included hormone treatment as an independent variable. Because males did not always receive the same treatment during each breeding season, the covariate included in the analysis was the number of years a male received testosterone implants divided by the total number of years it was alive. The selection gradients from these analyses were not significantly different from those calculated in the original regressions, and hormone treatment did not significantly increase the fit of the models (partial F -test, $F_{1,9} > 3.65$, $P > 0.05$) so we report only the analyses that do not consider treatment.

Lifetime selection.—Measurements of selection over the entire lifetime are necessary to make evolutionary predictions. Because our fitness components multiplied to lifetime fitness, we could add selection gradients measured at different episodes as an estimate of lifetime selection (Arnold and Wade 1984a,b). Selection gradients were summed separately for each sex. To estimate lifetime selection on both sexes combined, we averaged the sex-specific lifetime selection gradients. We calculated standard errors on these lifetime selection gradients by taking the square root of the sum of the squared standard errors estimated for each fitness component using jackknifing. This method assumes that the selection gradients from each analysis are independent (i.e., covariance between all pairs of selection gradients is zero). To test for significance, we performed one-sample t -tests using sums of jackknifed selection gradient estimates.

Fitness surfaces.—Plotting fitness surfaces allows visualization of the form of selection simultaneously acting on two traits (Phillips and Arnold 1989; Brodie et al. 1995). We plotted a nonparametric representation of the fitness surface generated using a thin-plate spline fit, the three-dimensional analog of the cubic spline (Green and Silverman 1994; Blows et al. 2003). The smoothing parameter λ for each spline was chosen by minimizing the generalized cross-validation score (Green and Silverman 1994). We used R software (available at <http://www.r-project.org>; routine TPS, package FIELDS) to fit splines for fitness surfaces for each of the individual selection episodes. Where appropriate, we also used selection gradients (from both individual selection episodes and lifetime selection) to generate parametric fitness surfaces (Lande and Arnold 1983; Phillips and Arnold 1989; Brodie et al. 1995). Because parametric fitness surfaces are constrained to a limited number of shapes and their interpretation may at times be misleading (e.g., because of extrapolation into areas based on few observations), the nonparametric splines were used as a guide to interpreting these fitness surfaces (Schluter 1988; Schluter and Nychka 1994; Brodie et al. 1995). Due to the composite nature of our measurements of lifetime selection as the product of individual episodes of selection, we were only able to generate parametric surfaces for lifetime fitness.

Response to Selection

Change in trait means.—We used lifetime selection gradients to predict evolutionary response to selection. The predicted response in trait means was calculated using the multivariate breeders' equation,

TABLE 2. Genetic parameters and variance components estimated using restricted maximum-likelihood and an animal model. (a) Heritabilities, $h^2 \pm \text{SE}$, are shown on the diagonal, genetic correlations, r_g , are below the diagonal, and phenotypic correlations are above the diagonal. (b) Additive genetic (co)variance components ($\mathbf{G} \pm \text{SE}$) are shown below the diagonal, and phenotypic (co)variance components are shown above the diagonal. Significance was tested with two-tailed, one-sample t -tests ($H_0: \mu = 0$).

	Trait	Wing length	Tail length	Tail white
a. h^2 and r_g	Wing length	$0.33 \pm 0.100^{**}$	(0.46)	(0.09)
	Tail length	$0.76 \pm 0.118^{***}$	$0.53 \pm 0.095^{***}$	(0.09)
	Tail white	$0.41 \pm 0.174^*$	0.04 ± 0.147	$0.50 \pm 0.082^{***}$
b. \mathbf{G}	Wing length	(2.06)	(1.37)	(0.03)
		$0.67 \pm 0.223^{**}$		
	Tail length		(4.32)	(0.05)
		$0.94 \pm 0.264^{***}$	$2.29 \pm 0.492^{***}$	
	Tail white			(0.06)
		$0.060 \pm 0.027^*$	0.010 ± 0.040	$0.032 \pm 0.006^{***}$

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

$$\Delta \bar{z} = \mathbf{G}\beta \quad (2)$$

(Lande and Arnold 1983). Although maternal effects may affect a predicted response to selection (Lande and Kirkpatrick 1990), to simplify the calculation we ignore them here.

Change in variance.—To estimate how the genetic variance-covariance matrix should change in response to selection, we used the equation

$$\Delta \mathbf{G} = \mathbf{G}(\gamma - \beta\beta^T)\mathbf{G} \quad (3)$$

(Phillips and Arnold 1989). This equation describes change in the \mathbf{G} matrix that occurs within a generation; between-generation changes should be smaller due to the effects of recombination (Tallis and Leppard 1988; Tallis 1989; Wolf and Brodie 1998). We used a standardized \mathbf{G} matrix (h^2 -values on the diagonal, $r_{ij}h_i h_j$ off the diagonal) in both equations so that responses would be in standardized units.

RESULTS

Quantitative Inheritance of Size and Plumage Traits

Additive genetic effects.—Wing length, tail length, and tail white were all significantly heritable (i.e., showed significant additive genetic variance, Table 2). Wing length was genetically correlated with both tail length and tail white, but tail length and tail white were not genetically correlated (Table 2).

Between-sex genetic correlations.—Genetic correlations between the sexes were high for all traits ($r_g \pm \text{SE}$: wing length 0.81 ± 0.406 , tail length 0.89 ± 0.231 , tail white 0.97 ± 0.270). All between-sex genetic correlations were significantly different from zero (one-tailed, one-sample t -tests, $df = 632$, $P < 0.05$), but not from unity ($P > 0.05$).

Assortative mating.—Heritability measurements were not biased by assortative mating, as individuals did not mate assortatively based on any of the three traits ($0.006 \leq r \leq 0.076$, $P > 0.47$). Genetic correlations were probably also not affected by assortative mating. One trait pair (dam's tail white and sire's wing length) showed a trend toward assortative mating, but in the opposite direction of the observed genetic correlation ($r = -0.200$, $P = 0.079$). Other trait pairs were not correlated ($-0.120 \leq r \leq 0.122$, $P > 0.352$).

Selection

Juvenile survival.—There was no directional selection via juvenile survival in either sex (Table 3). There was a trend toward pure quadratic selection acting to increase variance in male wing length (Table 3, Fig. 2a), and the nonparametric fitness surface suggests the existence of two fitness peaks, one for very small males, and one for males that are only slightly larger than average (Fig. 3a). There were no other significant nonlinear selection gradients in either sex.

Adult survival.—There was no significant evidence of selection based on adult survival on any of the three traits in males (Table 3). There was no directional selection acting on females, but we detected significant correlational selection acting on wing length and tail white (positive, Table 3, Fig. 2c) and tail length and tail white (negative, Table 3). Nonparametric fitness surfaces suggest that larger females with more tail white may have a survival advantage (Fig. 3f), and that two fitness peaks—larger with more tail white and smaller with less tail white—may exist for males (Fig. 3b).

Mating success.—Sexual selection was most evident in males; males with longer wings (significant) and shorter tails (nonsignificant) had higher mating success (Table 3). Although there was no directional sexual selection on tail white, there was a trend toward correlational sexual selection between tail white and wing length (Table 3). The combination of this correlational selection gradient and the significant linear selection gradient on wing length results in males with the longest wings and the whitest tails having the highest mating success (Fig. 2b). The nonparametric fitness surface suggests the existence of a fitness ridge with one peak at relatively large values for each trait (Fig. 3c).

Sexual selection was weak in females, but as in males, there was a significant negative correlational gradient between wing length and tail white (Table 3). In other words, females with matching tail white and wing length (less white with shorter wings or more white with longer wings) had fewer mates (Fig. 2d). Both fitness surfaces are nearly flat, but suggest that small females with more tail white have slightly higher mating success (Figs. 2d, 3g).

Fecundity.—Fecundity selection was negligible in males, but relatively strong in females. Directional selection favored females with shorter wings and longer tails (Table 3, Figs.

TABLE 3. Matrices of standardized directional (β) and quadratic (γ) selection gradients for wing length, tail length, and tail white. Diagonal elements in the quadratic selection matrix represent quadratic (γ_{ii}) selection and off-diagonal elements represent correlational selection (γ_{ij}). Selection gradients are partial regression slopes \pm one standard error. Gradients are estimated separately for each sex, using four components of fitness. Sample size for each regression is reported below each set of matrices. Gradients with $P < 0.10$ are shown in boldface. The probability of obtaining nine gradients with $P < 0.10$ by chance is 0.12, and the probability of obtaining six gradients with $P < 0.05$ is 0.08 (Moran 2003). Standard errors are jackknife estimates; significance is estimated by t -tests.

Fitness component	Trait	Males				Females			
		β	γ			β	γ		
			Wing length	Tail length	Tail white		Wing length	Tail length	Tail white
Juvenile survival	wing length	-0.063 ± 0.0593	0.191 † ± 0.1062			-0.050 ± 0.0626	0.092 ± 0.1088		
	tail length	0.010 ± 0.0546	-0.114 ± 0.0868			0.071 ± 0.0621	-0.046 ± 0.0813	0.078 ± 0.0878	
	tail white	0.029 ± 0.0511 ($N = 1431$)	0.013 ± 0.0620	0.071 ± 0.0590	0.068 ± 0.0734	0.069 ± 0.0552 ($N = 1329$)	0.003 ± 0.0629	-0.006 ± 0.0718	-0.006 ± 0.0724
Adult survival	wing length	0.009 ± 0.0512	-0.047 ± 0.0918			0.062 ± 0.0496	0.136 ± 0.0786		
	tail length	-0.012 ± 0.0515	-0.021 ± 0.0745	0.034 ± 0.0976		-0.044 ± 0.0551	-0.074 ± 0.0619	0.082 ± 0.0582	
	tail white	-0.027 ± 0.0433 ($N = 249$)	0.082 ± 0.0602	-0.038 ± 0.0580	0.072 ± 0.0698	-0.020 ± 0.0399 ($N = 264$)	0.099 * ± 0.0547	-0.076 * ± 0.0504	-0.001 ± 0.0492
Mating success	wing length	0.173 ** ± 0.0669	-0.011 ± 0.1726			-0.027 ± 0.0344	-0.003 ± 0.0416		
	tail length	-0.117 † ± 0.0693	0.125 ± 0.1856	-0.048 ± 0.2234		0.046 ± 0.0689	0.013 ± 0.0504	0.060 ± 0.1402	
	tail white	0.014 ± 0.0456 ($N = 88$)	0.137 † ± 0.0740	-0.143 ± 0.0868	0.011 ± 0.0900	0.009 ± 0.0334 ($N = 77$)	-0.064 * ± 0.0361	0.035 ± 0.0706	0.022 ± 0.0706
Fecundity per mate	wing length	-0.010 ± 0.0995	-0.191 ± 0.2248			-0.143 * ± 0.0685	0.080 ± 0.1248		
	tail length	0.073 ± 0.1014	0.100 ± 0.1893	0.055 ± 0.2496		0.196 * ± 0.0774	0.027 ± 0.1331	-0.037 ± 0.1268	
	tail white	0.072 ± 0.0721 ($N = 106$)	0.115 ± 0.1110	-0.040 ± 0.1122	-0.122 ± 0.1306	0.013 ± 0.0702 ($N = 95$)	0.076 ± 0.0945	-0.156 ± 0.1101	0.084 ± 0.1150

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$.

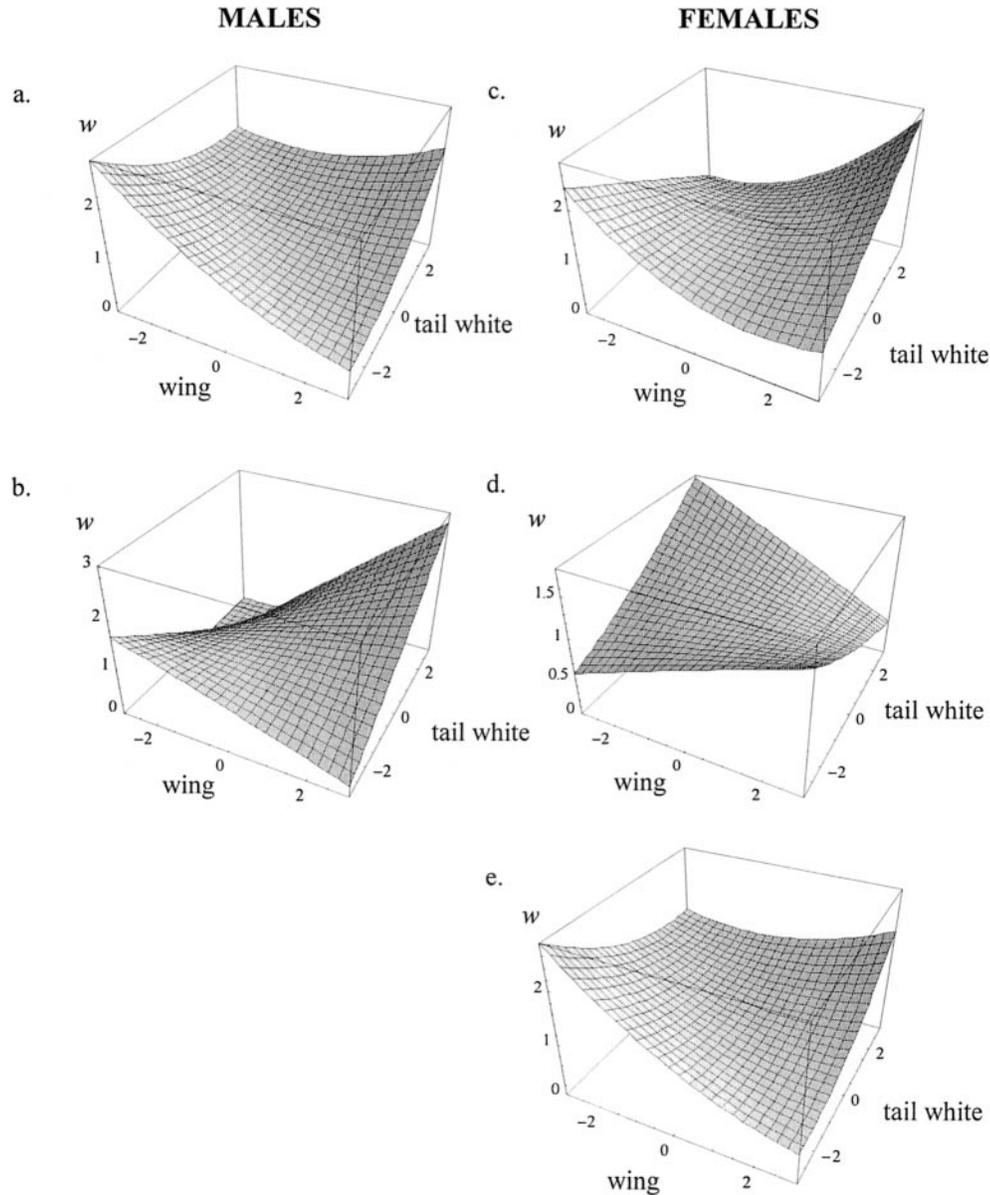


FIG. 2. Parametric fitness surfaces for wing length and tail white, drawn using all gradients from Table 3. Trait values (x- and y-axes) are standardized to zero mean and unit variance, and w (z-axis) represents relative fitness. Scales differ for each graph according to the range of trait and fitness values used in the analysis. (a) Male juvenile survival; (b) male mating success; (c) female adult survival; (d) female mating success; (e) female fecundity per mate.

2e, 3h). There was no significant evidence of nonlinear fecundity selection.

Lifetime selection.—When we considered selection combined over all episodes, we found that selection significantly favored long tails in females and a correlation between wing length and tail white in males (Table 4). This correlational selection gradient was also significant when selection was averaged across the sexes, and it was the main determinant of the shape of the wing–tail white fitness surfaces in both sexes (Table 4, Fig. 4). There was also significant negative correlational selection between tail length and tail white when the sexes were combined, favoring a decreased relationship between the two traits (Table 4). None of the other lifetime selection gradients was significant.

Response to Selection

Combining genetic data with measurements of lifetime selection led to predictions of very small increases in all three trait means over time (Table 5). Small increases in the genetic variance were also predicted (Table 5) due to the absence of strong directional selection and the weak positive quadratic selection acting on all traits (Table 4). Predicted changes in genetic covariance were in the same direction as the observed genetic correlations (Table 2, Table 5).

DISCUSSION

We found that the three traits examined in this study, wing length, tail length, and tail white, were heritable, and wing

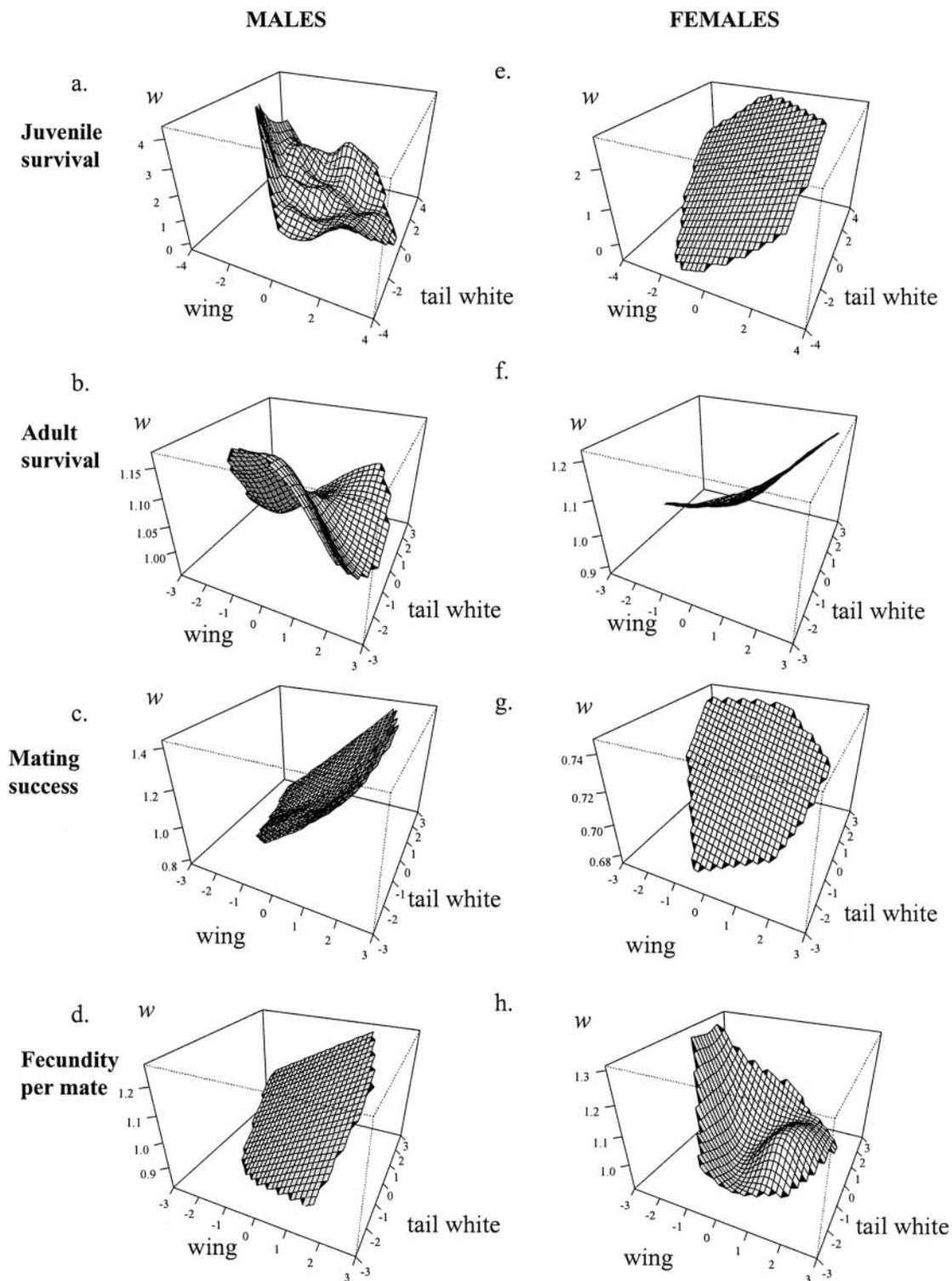


FIG. 3. Nonparametric fitness surfaces for wing length and tail white, fitted using a thin-plate spline. Trait values (x- and y-axes) are standardized to zero mean and unit variance, and w (z-axis) represents relative fitness. Scales differ for each graph according to the range of trait and fitness values used in the analysis. (a) Male juvenile survival; (b) male adult survival; (c) male mating success; (d) male fecundity per mate; (e) female juvenile survival; (f) female adult survival; (g) female mating success; (h) female fecundity per mate.

TABLE 4. Lifetime selection acting on males, females, and both sexes combined, calculated using selection gradients from Table 3 (see text for details). Diagonal elements in the quadratic selection matrix represent quadratic (γ_{ii}) selection and off-diagonal elements represent correlational selection (γ_{ij}). Selection gradients are partial regression slopes \pm one standard error. Gradients with $P < 0.10$ are shown in boldface.

Trait	Males				Females				Sexes combined			
	β		γ		β		γ		β		γ	
	Wing length	Tail length	Tail length	Tail white	Wing length	Tail length	Tail length	Tail white	Wing length	Tail length	Tail length	Tail white
Wing length	0.109 ± 0.143	-0.069 ± 0.316	-0.157 ± 0.111	0.304 ± 0.188	-0.024 ± 0.091	0.118 $\pm 0.065^\dagger$	0.053 ± 0.119	0.054 ± 0.074	0.111 ± 0.069	0.053 ± 0.119	0.054 ± 0.074	0.064 ± 0.044
Tail length	-0.046 ± 0.144	0.186 ± 0.287	0.269 $\pm 0.133^*$	-0.079 ± 0.175	0.183 ± 0.216	0.183 ± 0.216	0.183 ± 0.216	0.183 ± 0.216	0.111 ± 0.069	0.053 ± 0.119	0.054 ± 0.074	0.064 ± 0.044
Tail white	0.087 ± 0.108	0.346 $\pm 0.159^*$	0.071 ± 0.103	0.114 ± 0.131	-0.203 ± 0.157	-0.203 ± 0.157	-0.203 ± 0.157	0.100 ± 0.161	0.079 ± 0.053	0.230 $\pm 0.073^{**}$	-0.175 $\pm 0.080^*$	0.064 ± 0.044

(Average $N = 1380$)(Average $N = 1329$)(Average $N = 1431$)

$^\dagger P < 0.10$; * $P < 0.05$; ** $P < 0.01$.

length, which is representative of overall body size, was positively genetically correlated with both tail length and tail white. While a positive genetic correlation between wing length and tail length is probably inevitable due to common developmental pathways, the genetic correlation between wing length and tail white may have evolved via correlational selection. We detected positive lifetime correlational selection acting on the two traits, which was largely the result of sexual selection on males, which favored large males with whiter tails. While directional sexual selection on males was largely opposed by other selection episodes and selection on females, correlational sexual selection was reinforced. We discuss the implications of each of these results below.

Correlational Sexual Selection

In males, the sexual selection surface for wing length and tail white is a rising ridge, a pattern that can lead to the evolution of honest signals via the handicap principle (Getty 1998). If wing length, which is a good indicator of body size, is also indicative of overall phenotypic quality, then positive correlational selection on wing length and tail white may function to maintain tail white as an honest signal. Getty's (1998) original formulation required an interaction between sexual selection and viability to create a fitness ridge, but other kinds of interaction can produce the same result. A rising fitness ridge could arise from pure sexual selection when mating success depends on an interaction between intrasexual and intersexual interactions (Berglund et al. 1996; Ligon 1999). Larger males with large ornaments should have the highest mating success, while mismatched males should fare more poorly due either to decreased attractiveness to females or decreased ability to compete with other males.

In juncos, larger males may be more successful in intrasexual competition for access to mates during the breeding season, as they are in contests over food during the winter (Balph et al. 1979; Ketterson 1979; Holberton et al. 1989). If so, they may be better able to defend against intrusions from rival males seeking extrapair copulations or better able to invade neighboring territories where they might be more likely to inseminate fertile females. Females may choose among the males they encounter based on tail white (Hill et al. 1999), causing the larger males with more tail white to have the highest mating success. Because a female that has settled on a male's territory may choose only among him and a limited number of neighbors, and the males that she encounters may be restricted by male-male competition, her choices may be limited. This may explain why tail white, despite its attractiveness to females (Hill et al. 1999), is correlationally, but not directionally, selected.

Consistent correlational selection acting on wing length and tail white should lead to an increase in the genetic correlation between the two traits. The positive genetic correlation we observed suggests that correlational selection may have integrated these two traits in the past. Furthermore, quantitative genetic models of evolutionary change predict that the genetic covariance between the two traits should continue to increase. Consequently, to the extent that body size is associated with quality, tail white is an honest signal that should be reliable across generations. Other studies have

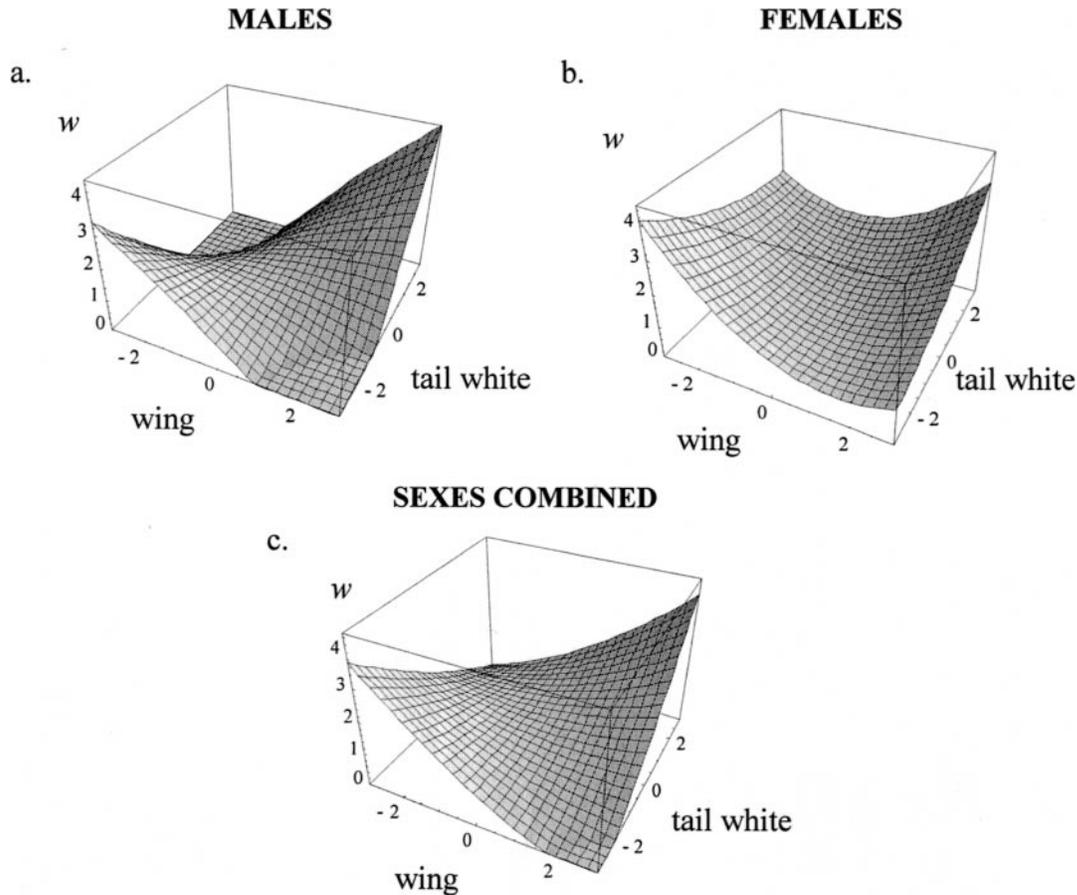


FIG. 4. Fitness surfaces for wing length and tail white, drawn using all gradients from Table 4. Trait values (x- and y-axes) are on a standardized scale, and w (z-axis) represents relative fitness. (a) Male lifetime selection; (b) female lifetime selection; (c) total lifetime selection.

shown concordance between correlational selection and genetic correlations (Brodie 1989, 1992, 1993b; Conner and Via 1993; Morgan and Conner 2001), but to our knowledge, this is the first study to demonstrate such a relationship for a sexually selected trait in animals. LeBas et al. (2003) suggested that correlational sexual selection may lead to a genetic correlation that maintains signal honesty of a female ornament in dance flies, but they did not demonstrate a genetic correlation. In that study, correlational sexual selection favored a positive relationship between a female ornament (size of pinnate scales on the hind femur) and fecundity, and as a result, males that chose to mate with females with larger

scales were able to sire more offspring. Because fecundity may also be related to nuptial gifts received from males, however, the phenotypic correlation observed by LeBas et al. (2003) may be largely environmental.

Strength of Selection and Interaction of Selection Episodes

In addition to correlational selection, we found some evidence of directional selection, although it was quite weak; the strongest directional selection gradients were close to the median ($|\beta| = 0.16$) of those reported in a recent review (Kingsolver et al. 2001). In accordance with the findings of Hoekstra et al. (2001), the strongest directional selection occurred via sexual and fecundity selection; as expected, males were selected most strongly due to variance in mating success, while females were selected most strongly due to variance in fecundity (Shuster and Wade 2003).

Although we found no evidence of directional survival selection in this study, it probably occurs over short periods of time in relation to short-term environmental changes. Indeed, survival selection tends to be stronger when it is measured over a shorter period of time (see Hoekstra et al. 2001). If these episodes of selection balance each other out (e.g., because the environment fluctuates), no net selection would be detectable over a period of years as was the case in our study.

TABLE 5. Predicted response to selection (see text for details of calculations). Predicted between-generation change in the mean in standard deviation units is shown on the left; predicted within-generation change in standardized additive genetic variances (diagonal) and covariances (below the diagonal) are on the right.

Trait	$\Delta\bar{z}$	ΔG		
		Wing length	Tail length	Tail white
Wing length	0.040	0.036		
Tail length	0.053	0.031	0.041	
Tail white	0.037	0.029	0.001	0.052

We did not detect quadratic selection in individual selection episodes, although when all episodes were combined, there was a trend toward quadratic selection for an increase in the variance of wing length. The strongest quadratic gradients were not much larger than the median value ($|\gamma| = 0.10$) found by Kingsolver et al. (2001). Correlational selection, as indicated above, was pervasive but was not particularly strong at any one episode when compared to other published measurements (e.g., Sinervo and Svensson 2002).

Although the strength of selection differed among episodes, there was no strong evidence of opposing selection (i.e., significant selection gradients of opposite sign) within a sex. Directional selection tended to be important at only one episode in each sex (sexual selection in males and fecundity selection in females). The importance of these selection episodes is apparent when examining the lifetime fitness surfaces. The lifetime fitness surface for males, like the sexual selection surface, resembles a rising ridge. In females, the lifetime fitness surface is shallower and valley-shaped; similar in shape to the fecundity selection surface.

In most cases, quadratic and correlational selection measured at different episodes tended to be reinforcing. One notable case of this was correlational selection on male wing length and tail white. Although it was only detectable in one selection episode (sexual selection), this correlational selection was consistently positive across all episodes, leading to a fairly strong lifetime selection gradient.

Selection and Sexual Dimorphism

Opposing selection in males and females may lead to the evolution of sexual dimorphism (Lande 1980a; Slatkin 1984; Andersson 1994; Badyaev and Martin 2000; Shuster and Wade 2003). In this study, selection favored an increase in sexual dimorphism in wing length (larger males, smaller females favored), and a decrease in sexual dimorphism for tail length (females with longer tails favored). All lifetime selection gradients involving only wing length and tail length were of opposite sign in males and females, suggesting that size-related traits are under substantially different selection pressures in males and females. Despite the differences in male and female selection regimes, however, the high between-sex genetic correlations we measured may constrain further evolution of sexual dimorphism (Lande 1980a; Price and Burley 1993; Merilä et al. 1998). When both sexes were considered, selection gradients for size-related traits were nearly zero, leading to very little predicted evolutionary change in the trait means, despite heritability measures that were typical of morphological traits (Mousseau and Roff 1987).

In contrast to selection on size-related traits, selection gradients related to tail white were all of the same sign for males and females. This is especially notable for correlational selection acting on size-related traits and tail white. The correlational selection in males that may maintain the honesty of tail white as a sexual signal is actually reinforced by selection in females, making an evolutionary change in the G matrix more likely.

The interaction of lifetime selection on males (a rising ridge shape) and lifetime selection on females (a flatter, val-

ley-like shape) creates a total fitness surface more similar to a saddle. The defining feature of this surface is the strong correlational selection between wing length and tail white, which derives primarily from sexual selection on males. However, because directional selection on males is balanced by opposing selection on females, the two points of high fitness are roughly equivalent. This concave selection surface should maintain the correlation between wing length and tail white while also maintaining genetic variance in wing length (Brodie 1992; Blows et al. 2003).

Conclusions

This study provides one of the few reported examples of correlational sexual selection in a natural population (Moore 1990; Fairbairn and Preziosi 1996; Rodriguez et al. 2002; LeBas et al. 2003, 2004), and to our knowledge it is the first to show concordance between such selection and genetic correlations between sexually selected traits. This finding, along with those of other studies (Brodie 1989, 1992, 1993b; Conner and Via 1993; Morgan and Conner 2001), suggests an important role for correlational selection in generating and maintaining genetic integration between functionally related traits. Such studies cannot directly implicate selection as the cause of genetic correlations, however, because genetic correlations are observed at only one point in time. Future work should use long-term field data or experimental systems to document how correlational selection affects changes in genetic correlations over time.

Correlational sexual selection may be of general importance in the evolution of sexually selected traits. As we have suggested, correlational sexual selection may lead to the evolution of signal honesty (see also LeBas et al. 2003). Correlational sexual selection may also serve to integrate multiple ornamental traits (Moore 1990; Rodriguez et al. 2002; Candolin 2003) or multiple aspects of a composite ornamental trait (Badyaev et al. 2001). This process of phenotypic integration may be opposed when there are genetic constraints, such as tight linkage (Brooks and Endler 2001). In such cases, correlational sexual selection may create multiple, stable fitness peaks for combinations of attractive traits, which may lead to the preservation of genetic variance in individual attractive traits (Blows et al. 2003). More studies of correlational sexual selection, and correlational selection in general, should be conducted to allow us to evaluate its evolutionary importance (Kingsolver et al. 2001; Sinervo and Svensson 2002).

Although studies such as this one are useful because they allow quantification of the way selection acts on natural populations, experiments are necessary to understand the mechanisms of how selection occurs (Kalisz and Wade 1990). Although some such studies have already been conducted on male juncos (Balph et al. 1979; Ketterson 1979; Holberton et al. 1989; Hill et al. 1999), more studies are necessary to determine how male traits interact to generate the correlational sexual selection observed here. As we have demonstrated here, selection operating on females is important for understanding the evolution of male traits. Consequently, future studies of sexually selected traits in males should also explore selection on correlated traits in females.

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