

Diet quality affects an attractive white plumage pattern in dark-eyed juncos (*Junco hyemalis*)

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Abstract Sexually selected traits that act as signals of quality often display some degree of condition dependence. In birds, condition dependence of ornamental plumage is often mediated by production costs related to acquisition or allocation of dietary resources. White plumage ornaments, however, have often been assumed to be inexpensive because their production requires neither pigment nor specialized feather structure. In male dark-eyed juncos (*Junco hyemalis*), the size of a white patch on the tail contributes to attractiveness and mating success. Using captive males, we examined the effects of diet quality on the size and brightness of the tail-white patch. After removing four tail feathers to induce replacement, we maintained subjects on a subsistence (low-protein) or enriched (high-protein) diet while induced feathers grew. Birds that received an enriched diet grew their feathers more quickly and grew larger, brighter white patches. Feather growth rate was positively correlated with the

increase in the size of the tail-white patch, a relationship that was stronger in the subsistence diet group. However, within diet treatments, faster-grown feathers were slightly duller. Taken together, these results suggest that variation in diet quality may lead to condition-dependent expression of tail white and that condition dependence may be stronger in more stressful environments. We suggest a mechanism by which increased feather growth rate may lead to an increase in the size of the tail-white patch and discuss potential trade-offs between signal size and brightness.

Keywords Honest signals · Condition dependence · Sexual selection · Plumage development · *Junco hyemalis*

Introduction

Sexual selection theory predicts that traits that reliably indicate male quality will be used by females to choose mates and by males to assess rivals (Andersson 1994). Reliable signals may evolve when males that differ in quality benefit from having corresponding values of a sexually selected trait (Getty 1998, 2006; Grafen 1990a; Nur and Hasson 1984). In many cases, sexual selection may favor condition-dependent expression, which may maintain signal honesty by linking the development of the trait to the condition of the organism (Grafen 1990b; Pomiankowski 1987; Rowe and Houle 1996). Many studies have presented evidence showing that sexually selected traits are correlated with condition (Andersson 1994; Cotton et al. 2004; Johnstone 1995). Additionally, a number of studies have experimentally manipulated sources of variation in condition such as diet, demonstrating direct effects of condition on the development of sexually selected traits (reviewed in Cotton et al. 2004).

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Ornamental plumage in birds, one of the best-studied classes of sexually selected traits, often shows condition-dependent variation that may be caused by differences in acquisition or allocation of a scarce dietary resource (Hill 2002; Ligon 1999). For example, the attractive red coloration of male house finches (*Carpodacus mexicanus*) is derived from carotenoids that cannot be synthesized but must be obtained from the diet (Hill 1990–1992, 2000, 2002; Hill and Montgomerie 1994; Hill et al. 2002). There is also growing evidence that nutrition may be related to melanin-based ornaments (Jawor and Breitwisch 2003; Veiga and Puerta 1996) as well as to structural coloration, which is produced by specialized nanostructure in feather keratin (Doucet 2002; Keyser and Hill 1999, 2000; McGraw et al. 2002; Prum et al. 1998, 1999; Shawkey et al. 2003; Siefferman and Hill 2003).

Patches of white plumage, which may consist of multiple white body feathers or contrasting patterns of dark and white within feathers (e.g., “flash marks” on flight feathers), are also used as ornaments in a number of species (Gustafsson et al. 1995; Hill et al. 1999; Höglund et al. 1990; Kose et al. 1999; McGlothlin et al. 2005; Mennill et al. 2003; Sheldon and Ellegren 1999; Török et al. 2003; Woodcock et al. 2005). White plumage results from the scattering of light in all directions by unpigmented feather keratin (Prum et al. 1999). Perhaps because the production of white plumage requires neither pigment nor specialized feather structure, proposed mechanisms for maintaining the honesty of unpigmented signals have usually focused on various costs of maintaining the trait, such as greater risk of feather abrasion and breakage, reduced attractiveness when white feathers fail to camouflage ectoparasites, and greater likelihood of inducing male–male aggression (Bonser 1995; Burt 1986; Fitzpatrick 1998; Kose and Møller 1999; Kose et al. 1999; McGlothlin et al. 2005; Qvarnström 1997; Török et al. 2003). One experiment, however, suggests that the production of white plumage ornaments may impose significant costs. In the collared flycatcher, increased brood size led to decreases in adult and nestling condition, as well as decreased expression of the white forehead patch in both (Gustafsson et al. 1995). However, we know little about the mechanisms that may lead to the condition-dependent expression of white plumage.

In the dark-eyed junco (*Junco hyemalis*, Emberizidae), both males and females have a white patch on the outer tail feathers (rectrices) referred to as tail white (Hill et al. 1999; Nolan et al. 2002). The area of the tail-white patch relative to the total feather area varies substantially; males have more tail white than females, and older birds have more tail white than younger birds (Wolf et al. 2004; Yeh 2004). Much of the variation among individuals is heritable (McGlothlin et al. 2005). Male juncos display their tail-white patch during both inter- and intrasexual interactions

(Balph et al. 1979; Nolan et al. 2002). Artificially enhancing male tail-white size increases male attractiveness to females (Hill et al. 1999) but not female attractiveness to males (Wolf et al. 2004), and male juncos with more tail white (due to natural variation or experimental enhancement) tend to win in competitive interactions (Balph et al. 1979; Holberton et al. 1989). In a natural population, male tail white interacts with body size to determine mating success; larger males with more tail white have higher mating success (McGlothlin et al. 2005). This pattern of correlational sexual selection creates different optima for males of different body size, which should favor increases in signal honesty and potentially, condition-dependent expression (Getty 2006; McGlothlin et al. 2005).

In this study, we examined the effects of diet quality on the development of tail-white size and brightness. In addition, we measured feather growth rate, which has been shown to be affected by diet quality (Grubb 1989, 1995; Jenkins et al. 2001) and is hypothesized to affect the development of feather patterns (Prum and Williamson 2002). We asked whether variation in growth rate might act as a link between dietary intake and tail-white size. Rapidly grown feathers might contain less keratin, which is responsible for the scattering of light in white feathers, so we also examined the relationship between feather growth rate and plumage brightness.

Materials and methods

Capture and housing

All subjects used in this study were captured between April 1998 and September 2001 using baited mist nets near Mountain Lake Biological Station in Giles County, VA (37° 22' 31"N, 80° 31' 24"W), and transported to Kent Farm Bird Observatory (KFBO) in Bloomington, IN (39° 09' 02"N, 86° 23' 46"W). Sex was determined using wing length and plumage coloration. Our identification of sex was confirmed by the development of cloacal protuberances after the completion of the experiment. Age (first-year or older adults) was determined by the contrasting coloration of the primary wing coverts and secondarily, by differences in eye color (Nolan et al. 2002).

On 1 February 2002, 39 male juncos (19 first-year adults, 20 older adults) were randomly assigned to one of two diet treatments: a seed-only subsistence diet or a diet enriched with supplemental items (described below). Birds were housed in flocks in four identical indoor rooms (each 2.6×2.1×2.4 m) and kept on a constant (10L:14D) photoperiod. We elected to house the birds in groups to simulate group feeding, which is characteristic of the junco social system at the time of the annual molt (compare

Jenkins et al. 2001). Two of these rooms received the enriched diet, and two received the subsistence diet. One room of each treatment housed first-year adults, and the other housed older adults. Birds were housed separately by age to avoid potential effects of social dominance by older birds (Ketterson 1979).

In the wild, juncos feed on a mixture of animal matter (mostly insects) and vegetable matter (mostly seeds), with the proportion of vegetable matter increasing in the non-breeding season (Nolan et al. 2002). In this experiment, diet treatments were designed to fall within the natural range of diet quality. The subsistence diet treatment consisted entirely of seed, and thus simulated the harsh conditions faced when insects are scarce and protein content of the diet is low. In this treatment, birds had ad libitum access to a mixture of two parts red millet, two parts white millet, and one part crushed sunflower hearts in a single large feeding dish. In the enriched-diet treatment, birds were given an identical seed dish as well as a second, smaller dish containing ~100 g of ground mixture of approximately seven parts Purina Dog Chow (21% protein, 10% fat), one part hard boiled eggs, one part carrots, and one part high-protein turkey starter, as well as ~20 mealworms (~2 g), and one orange slice (5–10 g). This treatment was designed to mimic a diet with increased protein content experienced when insects are plentiful. Similar diet manipulations have been used in other studies of feather development (e.g., Jenkins et al. 2001).

Each treatment group had access to the same amount of water, which was mixed with a multivitamin supplement. All birds were fed three times per week. At each feeding, seed dishes were filled, water was changed, and fresh supplemental food was provided to the enriched-diet treatment group (any leftover supplemental food was discarded). There was always leftover seed in both treatments, so both diets seemed to meet the birds' caloric needs. The supplemental food seemed to be preferred to the seed, as it was sometimes completely consumed by the enriched-diet treatment group.

At the time birds were placed into their diet treatments, we removed two rectrices from each side of the tail (hereafter *original* feathers) to induce the growth of new feathers (hereafter *induced* feathers; cf. Jenkins et al. 2001). Rectrices are numbered 1–6 from the center of the tail in the order of molt. In our study population, male juncos commonly have white patches on rectrices 4–6 and occasionally on rectrix 3 (see also McGlothlin et al. 2005, Fig. 1; Wolf et al. 2004). We chose to remove rectrices 4 and 5, because these feathers represent most of the variation in tail white (Wolf et al. 2004). When feather replacement was complete (15 March), we removed induced rectrices 4 and 5 from each side of the tail for measurement. This experimental protocol allowed us to isolate the effects of our treatment on a few specific feathers without a molt of

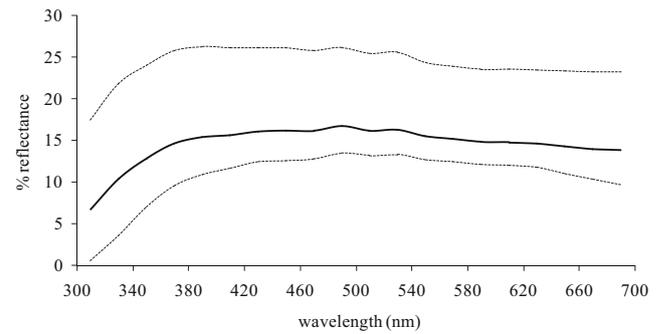


Fig. 1 Reflectance spectra of the tail-white patch of dark-eyed juncos ($n=145$ feathers, 38 individuals). Values shown are percent reflectance with respect to a white standard. The *solid line* represents the average of all spectra, and the *dotted lines* the upper and lower limits of the range. Means, maxima, and minima were calculated separately for each 20-nm wavelength bin (see text)

the entire plumage. Juncos also will regrow tail feathers if they are lost in the wild (JWM, personal observation).

Twenty-one of the birds used in the experiment were captured in September 2001, which meant that the feathers removed before the diet treatment had been grown in the wild while consuming a natural diet. The other 18 subjects had grown these feathers in captivity at KFBO. During molt, they received a diet that was identical to the enriched diet used in this experiment. Birds were assigned to diet treatment randomly with respect to when they had first been captured.

Measurement

Feather growth rate was measured following Grubb (1989) and Jenkins et al. (2001). Twenty-four-hour intervals of feather growth are represented by growth bars, which are bands of alternating high and low keratin density (Michener and Michener 1938; Riddle 1908). The right fourth rectrix was attached to an index card and a section consisting of ten alternations of light and dark bars (or, if ten were not detectable, the maximum number detectable) in the middle third of the feather was marked using size 0 insect mounting pins. The width of this section was measured using digital calipers to the nearest 0.1 mm, and this measurement was divided by the number of growth bars present to calculate the average daily growth rate. We repeated this measurement three times for each feather. Repeatability of this measurement was low, ($r=0.13$, $p=0.08$), indicating that measurement error was likely a problem. Therefore, we used the median as our summary statistic for analysis to reduce the influence of measurement error.

To measure tail-white size, we obtained an image of each feather using a digital camera at a standardized distance and under standardized lighting. These images were analyzed using a Macintosh computer and NIH Image (<http://rsb.info.nih.gov/nih-image>). Each feather's tail-white value was defined as the ratio of white area to total feather area. Tail-

white measurements from the left and right sides were averaged when both were available for the fourth and fifth rectrices separately. When a measurement from one side was unavailable, because of feather loss or breakage, we used only the measurement from the intact feather. One individual did not have a usable original fourth rectrix on either side and thus, was removed from the dataset. For analysis, we summed measurements from the fourth and fifth rectrices.

Feather brightness was measured using a PS1000 spectrometer (Ocean Optics, Dunedin, USA) with a tungsten light source. Feathers were placed on a black velvet background for measurement. Three measurements were taken from the white portion of each feather by placing a fiber-optic probe (connected to the light source and the spectrometer) directly on the feather at randomly chosen locations. The probe was covered with a metal sheath that ended in a 45° angle. Spectra from each location were collected using OOI Base 32 v. 1.0.0.8 software and were measured as percent reflectance compared to a white reflectance standard (COL120-1). A typical spectrum is shown in Fig. 1. To summarize data, we first took averages for 20-nm wavelength bins within the avian visual spectrum (300–700 nm). Preliminary principal component analysis revealed that the first principal component, which can be interpreted as average brightness (Cuthill et al. 1999), explained 91% of the variance in spectra. We therefore simply used mean reflectance to summarize spectra. For each bird, reflectance was averaged first within and then across feathers within the original and induced groups.

Measurements of feather growth rate and tail-white size from the original feathers did not significantly differ with respect to whether birds had grown these feathers in the wild or captivity ($t_{36}=0.80$, $p=0.43$; $t_{36}=1.529$, $p=0.14$). However, birds that molted in captivity had brighter original feathers on average ($t_{36}=3.18$, $p=0.003$).

All feather measurements were conducted by an observer (JLH) who was blind to treatment.

Analysis

To test for differences in feather growth rate of original and induced feathers, we used a general linear model (GLM) that included diet treatment (subsistence or enriched), age (first-year or older adult), and an interaction term. To control for a possible effect of initial condition, we added initial mass (g) as a covariate to this model. To test for the effect of diet on tail-white size and brightness, we used GLMs that included induced tail-white size or brightness as the dependent variable, age and diet as fixed factors, and induced feather growth rate, initial mass, and initial value of tail-white size or brightness as covariates. Original models included both a two-way interaction between fixed effects and all possible fixed-effect \times covariate interactions.

The latter type of interaction would indicate that diet or age affected the slope of the relationship between the covariate (e.g., growth rate) and the dependent variable (e.g., tail-white size). Covariate interaction terms with $p>0.10$ were removed from the final models (Engqvist 2005).

Because birds were housed in flocks, we asked whether individuals could be treated as statistically independent by employing restricted maximum likelihood to compute intraclass correlation coefficients. Positive intraclass correlation coefficients indicate greater than expected similarity among group members, which may lead to unwarranted rejections of null hypotheses, whereas negative values arise from larger than expected within-group variance and make conventional tests conservative (i.e., null hypotheses are more difficult to reject; Haggard 1958). For induced feather growth rate and tail-white brightness, the intraclass correlations were not significantly different from zero, suggesting statistical independence of flock members ($r\leq 0.14$, Wald $Z\leq 0.83$, $p\geq 0.41$); for induced tail-white size, the intraclass correlation was significantly negative, suggesting that our statistical tests are conservative ($r=-0.11$, $Z=-305.27$, $p<0.0001$).

All analyses were performed using SPSS v. 14.0 for Windows.

Results

Feather growth rate

As would be expected, growth rate of the original (prediet treatment) feathers did not differ according to diet treatment, age, or an interaction between age and treatment ($F_{1,33}\leq 1.43$, $p\geq 0.24$; Fig. 2). The relationship with initial mass was slightly negative but nonsignificant ($b=-0.02$, $F_{1,33}=2.81$, $p=0.10$). Diet treatment had a significant effect on the growth rate of the induced feathers (Fig. 2). Birds grew induced feathers more slowly on the subsistence diet than they did on the enriched diet ($F_{1,33}=6.60$, $p=0.02$). There was no effect of age and no interaction between age and diet ($F_{1,33}\leq 0.008$, $p\geq 0.93$). The effect of mass was positive and nonsignificant ($b=0.02$, $F_{1,33}=2.78$, $p=0.11$).

Tail-white size and brightness

Tail-white size and brightness were correlated between the original and induced feathers (only the size correlation was significant, Table 1), indicating the presence of individual variation that was independent of our treatment. When correcting for this correlation, diet treatment had a significant effect on both tail-white size and brightness. Birds that were fed an enriched diet showed a larger increase in tail-white size (mean change \pm SE = 0.06 ± 0.019) than birds in the subsistence diet treatment (0.03 ± 0.030 ,

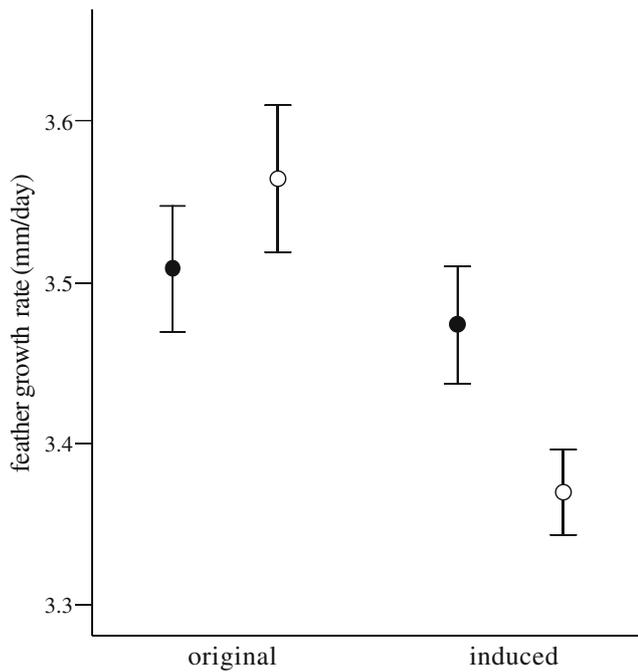


Fig. 2 Effect of diet treatment (*black circles* indicate enriched diet, *white circles* indicate subsistence diet) on feather growth rate. Values are mean \pm SE

Table 1). Both diet treatments displayed a decrease in brightness with respect to the original feather, but birds in the enriched-diet treatment decreased less (mean change enriched = -0.45 ± 0.55 , subsistence = -1.10 ± 0.41 , Table 1).

Averaged across treatments, birds that grew their feathers faster exhibited a greater increase in tail-white size (Table 1, Fig. 3). However, there was a significant interaction between diet treatment and growth rate, indicating that the nature of the relationship differed between treatments (Table 1). In the subsistence-diet treatment, the relationship was positive ($b=0.64$), whereas in the enriched-diet treatment there was no significant relationship ($b=-0.04$, Fig. 3). Within both treatments, there was a similar decrease in tail-white brightness with increasing feather growth rate ($b=-3.38$, Table 1, Fig. 4).

There was no main effect of initial mass on either variable, but there was a significant diet \times mass interaction

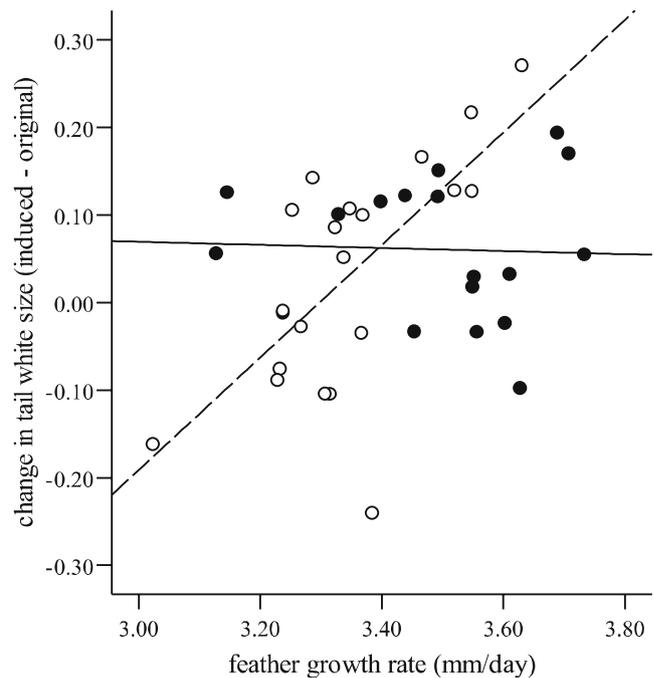


Fig. 3 Effect of diet treatment on the relationship between feather growth rate and tail-white size in induced feathers. Change in tail-white size is plotted to correct for the correlation between original and induced measures. Individuals in the enriched-diet treatment are represented by *black circles* and a *solid regression line*; individuals in the subsistence-diet treatment are represented by *white circles* and a *dashed regression line*

affecting brightness (Table 1). Specifically, the regression slope was steeper in the enriched diet ($b=0.33$) than in the subsistence diet ($b=-0.09$). There were no effects of age class or interactions between age and diet on either variable (Table 1).

Discussion

In this experiment, we found that birds that were fed an enriched, high-protein diet grew replacement feathers more quickly and developed larger, brighter tail-white patches than birds that were fed a low-protein, subsistence diet.

Table 1 General linear models of tail white size and brightness of induced feathers

Effect	Tail white size		Tail white brightness	
	$F_{1, 30}$	p	$F_{1, 30}$	P
Diet treatment	10.05	0.003	4.71	0.04
Age class	0.002	0.96	2.40	0.13
Age class \times diet treatment	1.28	0.27	1.98	0.17
Initial mass (g)	0.04	0.85	1.77	0.19
Feather growth rate (mm/day)	7.63	0.01	6.58	0.02
Original measure (size or brightness)	109.20	<0.0001	3.78	0.06
Diet treatment \times feather growth rate	10.15	0.003		
Diet treatment \times initial mass			5.89	0.02
R^2	0.80		0.43	

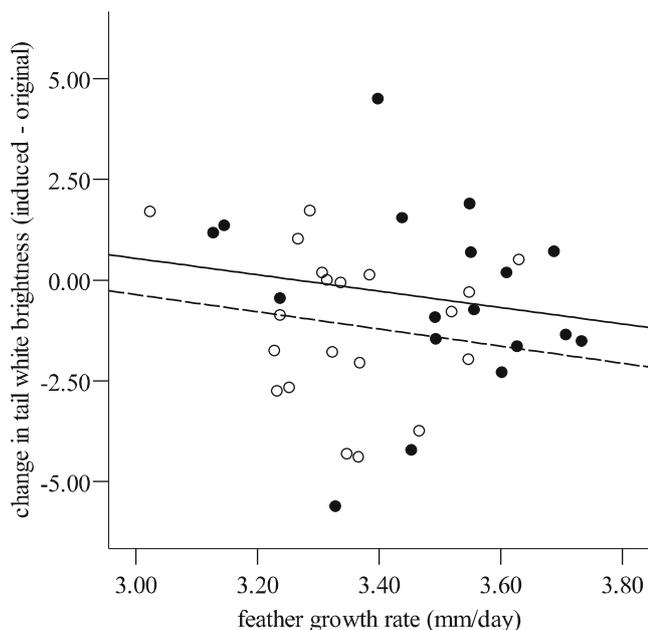


Fig. 4 Effect of diet treatment on the relationship between feather growth rate and tail-white brightness in induced feathers. Change in tail-white brightness is plotted to correct for the correlation between original and induced measures. Diet treatments are represented as in Fig. 3

Further, faster-grown feathers had larger areas of white. However, the strength of this relationship differed between diet treatments. There was no significant correlation between rate of feather growth and ornament size within the enriched diet treatment, where feather growth was faster overall and most birds either increased or showed no change in the size of the tail-white patch. In the subsistence-diet group, however, more birds grew their feathers at a slower rate, giving rise to more variation in the change in tail-white size and strong covariation between this change and feather growth rate. Although the enriched-diet treatment led to the production of brighter feathers than the subsistence diet, within each treatment, faster-grown feathers were duller. Together, these results indicate that the quality of the diet consumed during feather growth may affect the development of the tail-white patch, suggesting that tail white can convey information about a male's environment or his ability to cope with it.

The effect of diet treatment on the relationship between feather growth rate and tail-white size suggests that condition dependence of the trait may be stronger in more stressful environments. If so, the type or amount of information conveyed by variation in tail-white size may differ across environments (Badyaev and Qvarnström 2002). In poor environments, the differences among individuals of varying quality may become magnified. In stalk-eyed flies (*Cyrtodiopsis dalmanni*), males display genetic variation in the extent to which their eye span responds to nutritional stress, which enhances differences among males of different genotypes, increasing the amount

of information conveyed by the signal (David et al. 2000). Similarly, in collared flycatchers (*Ficedula albicollis*), the heritability of the forehead patch was lower when the trait was developed in unfavorable conditions, indicating that the environment played a greater role in determining variation in poor environments (Qvarnström 1999).

The association between feather growth rate and the size of the tail-white patch may be a simple consequence of the developmental mechanisms of feather patterns (Prum and Williamson 2002). Feathers grow as a tube from a basal follicle, with the distal end developing first. Pigment is incorporated into the keratin of the growing feather by melanocytes that extend their pseudopodia into the growing tube and release melanosomes (reviewed in Prum and Williamson 2002; Yu et al. 2004). In a developmental model, Prum and Williamson (2002) proposed that patterns such as tail white are produced by a temporal series of ring-shaped developmental fields that control pigment deposition. Patterns such as tail white, where pigment is concentrated at the proximal end of the feather (Fig. 5, see also McGlothlin et al. 2005; Fig. 1), would be produced via a transition from fields that deposit less pigment during early feather growth to fields that deposit more pigment during later growth.

Although feather growth rate was included as a fixed parameter in their model, Prum and Williamson (2002) did not examine how varying growth rate would affect feather pattern development. If the developmental fields change at a rate that depends on the amount of feathers grown (i.e., change faster when feathers grow faster), then the development of the pattern would be independent of growth rate. However, if the progression through developmental fields depends on time, patterns should develop differently under different rates of feather growth. Specifically, faster feather growth would cause the developing feather to “pass through” the fields that are early in the temporal sequence more quickly. Thus, the spatial representation of these fields on the resulting feather should be larger. In the case of tail



Fig. 5 Original (top) and induced (bottom) fourth rectrices of one individual in the enriched-diet treatment. Original tail-white value = 0.21, original growth rate = 3.38 mm/day, induced tail-white value = 0.40, induced growth rate = 3.57 mm/day

white, faster feather growth would lead to a larger white area, as was observed in this study.

There are a number of possible mechanisms, which are not mutually exclusive, that may explain how diet affected feather growth rate and tail-white size. First, this effect may have been a direct consequence of the higher protein content of the enriched diet. Higher protein intake may have led to faster keratin production (and thus feather growth) in birds on the enriched diet. Second, our subsistence diet treatment may have induced hormonal differences that suppressed feather growth and led to a reduction in tail-white expression. Acute and chronic stressors often lead to an increase in glucocorticoids (primarily corticosterone in birds), which may have a variety of physiological effects, among them a decrease in protein synthesis and an increase in protein catabolism (Sapolsky et al. 2000). Romero et al. (2005) found that artificially elevated corticosterone decreased feather growth rate in European starlings (*Sturnus vulgaris*). Although we did not measure hormones in this study, it is possible that corticosterone increased in response to the subsistence diet, leading to slower feather growth. Third, the effect may have been mediated by differences in social interactions between the two diet treatments. Our birds were held in flocks, which is how they live naturally during the nonbreeding season. If competitive interactions in the flocks differed between diet treatments, for example, because birds were competing for food sources of different value, hormonal changes (such as androgen increases) could have been induced that indirectly affected the expression of tail white. A similar phenomenon was demonstrated in house sparrows (*Passer domesticus*), in which groups that were more aggressive during molt grew larger chest badges, a melanin-based trait that is used as status signal (McGraw et al. 2003). Further physiological and behavioral studies are necessary to test these hypotheses.

We also found that the birds fed with the enriched diet grew brighter feathers. This effect was stronger in heavier birds, suggesting that males in a better condition may be able to take greater advantage of the higher quality resources. In addition, feathers that grew relatively faster within each treatment were duller. These effects likely arise from differences in keratin deposition. Plumage whiteness derives from incoherent scattering of light by feather keratin (Prum et al. 1999), so duller feathers may be those with lower keratin density.

Because the importance of variation in tail-white brightness has not been examined in a behavioral or ecological context, it is difficult to explain what these effects might mean in nature. However, brighter white plumage has been linked to dominance, attractiveness, and mating success in black-capped chickadees (*Poecile atricapillus*) (Doucet et al. 2005; Mennill et al. 2003; Woodcock

et al. 2005), so it is reasonable to expect that tail-white brightness may also be important in juncos. If conspecifics assess tail-white brightness as well as area, the beneficial effect of increased feather growth on tail-white size may be balanced by the negative effect on signal brightness.

In sum, our results indicate that a portion of the variation in tail-white size is dependent on the diet and that differences in feather growth rate may mediate this effect. Although differences in tail-white size among individuals are largely heritable (McGlothlin et al. 2005), the effect of diet demonstrated here adds an additional source of variation that may fine-tune the development of the trait to condition. A relationship between feather growth rate and tail-white expression may help maintain or enhance an association between tail-white size and overall quality, providing information to females choosing a mate or males assessing an opponent (Balph et al. 1979; Hill et al. 1999; Holberton et al. 1989). Further, trade-offs that arise because feather growth affects area and brightness in opposite directions may ensure that only high-quality males benefit from increasing feather growth rate. Because within-feather patterns such as tail white are common in birds (Fitzpatrick 1998), such effects of diet quality and feather growth rate may be of widespread importance.

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