

Trade-offs between molt and immune activity in two populations of house sparrows (*Passer domesticus*)

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Abstract: Molt and immune defense are critical activities in which all birds must invest. Because each is costly, wild passerines may have to decrease their investment in one activity if they are to increase investments to others. Here, I studied such molt-immune trade-offs in one neotropical and one north-temperate population of house sparrows (*Passer domesticus* (L., 1758)). I included two populations in my study to investigate if molt-immune trade-offs in this species are phenotypically plastic or fixed. I expected that if they were fixed, then immune activity, molt, and immune-molt trade-offs would be distinct between populations after they were kept in captivity for 1 year under similar conditions. I found evidence for molt-immune trade-offs in house sparrows. Feather growth was inversely related to cutaneous immune activity to phytohemagglutinin (PHA). Furthermore, feather growth 3 weeks post immune challenge was lower in immune-challenged birds relative to saline-injected controls. However, there was no effect of population of origin on these patterns, or the rate of molt or PHA response at this time of year in each population. Thus, while house sparrows probably do face trade-offs between molt and immune activity in the wild, any variation in these trade-offs between populations are likely plastic responses to different environments.

Résumé : La mue et la défense immunologique sont des activités essentielles dans lesquelles tous les oiseaux doivent investir. Comme ces deux activités sont coûteuses, les passereaux sauvages peuvent être amenés à décroître leur investissement dans l'une d'elle s'ils veulent augmenter leur investissement dans l'autre. Cette étude évalue les compromis entre la mue et la défense immunologique chez deux populations du moineau domestique (*Passer domesticus* (L., 1758)), l'une néotropicale et l'autre tempérée nord. Deux populations sont incluses dans l'étude afin de déterminer si les compromis mue – défense immunitaire sont fixés ou variables du point de vue phénotypique. Si les compromis sont fixés, on peut s'attendre à ce que l'activité immunologique et les compromis mue – défense immunitaires diffèrent dans les deux populations après qu'elles aient été gardées en captivité pendant 1 an dans des conditions semblables. Il y a des indications de l'existence d'un compromis mue – défense immunitaire chez les moineaux domestiques. Il existe une relation inverse entre la croissance des plumes et l'activité immunitaire cutanée à la phytohémagglutinine (PHA). De plus, la croissance des plumes 3 semaines après un défi immunologique est plus faible chez les oiseaux qui ont reçu le défi immunologique que chez les oiseaux témoins injectés avec une solution saline. Cependant, il n'y a pas d'effet de l'origine des populations sur ces patrons, sur les taux de mue ou sur la réaction à la PHA à ce temps de l'année dans les deux populations. Ainsi, bien que les moineaux domestiques en nature doivent probablement faire face à des compromis entre la mue et l'activité immunologique, toute variation dans ces compromis entre les populations consiste sans doute en des réponses variables aux divers environnements.

[Traduit par la Rédaction]

Introduction

An animal faces many demands in its life including the need to reproduce, the need to maintain and replace tissues, the need to generate body heat, and the need to defend against predators, competitors, and diseases. Because each

of these activities requires resources, organisms may be forced to decrease investments in some physiological processes to enhance others (Ricklefs and Wikelski 2002). Prioritization of investments among costly physiological processes, however, likely varies depending on where an organism lives (Cody 1966). For example, a passerine bird living near the equator probably experiences demanding challenges in terms of parasite threat (Janzen 1970; Connell 1971; Ricklefs 1992), competition for food and nest sites (Ricklefs 2000), and predation pressure (Skutch 1985), but relatively weak constraints on thermoregulation (Kendeigh 1976), the scheduling of reproduction (Hau 2001) and molt (Foster 1974), and the availability of daylight for foraging and other activities. Subsequently, birds living in the tropics may prioritize their physiological investments differently than birds living at higher latitudes.

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In this study, I investigated trade-offs between molt versus immune activity in two populations of house sparrows (*Passer domesticus* (L., 1758)): one living near the equator (Colon, Panama) and the other living in the north-temperate zone (New Jersey, USA). So far, evidence for molt-immune trade-offs in wild passerines is indirect and equivocal (Moreno et al. 2001; Nava et al. 2001; Whitaker and Fair 2002; Sanz et al. 2004; Greenman et al. 2005). However, many studies have indicated that both immune activity and molt can be energetically (Dolnik 1965; Lindström et al. 1993; Klaassen 1995; Martin et al. 2003; Ots et al. 2001) and nutritionally demanding (Payne 1972; Lochmiller et al. 1993; Klasing and Leshchinsky 1999; Lochmiller and Deerenberg 2000). Moreover, direct molt-immune trade-offs have been well documented in domestic fowl (Holt 1992; Alodan and Mashaly 1999; Kuenzel 2003). I expected therefore that if molt-immune trade-offs are important for wild birds, then (i) immune activity would be inversely related to feather growth in molting birds at the height of their molt and (ii) immune-challenged birds would show less feather growth post challenge than saline-challenged controls.

In addition to testing for molt-immune trade-offs, I was also interested in determining if trade-offs were plastic or fixed traits. Generally, temperate passerines molt at higher rates than tropical passerines (Foster 1974; Helm and Gwinner 1999). In contrast, passerines living in the tropics tend to invest more in immune defense than their temperate relatives (Ricklefs 1992). These patterns suggest that molt-immune trade-offs, if they exist, are likely to be distinct between temperate and tropical passerines. House sparrows, however, are not a typical tropical or temperate passerine species; they were introduced to the USA only 150 years ago and reached Panama in just the past 25 years (Summers-Smith 1988; Ridgely and Gwynne 1989). Although this recent arrival suggests that any geographic variation in this species is more likely due to environmental acclimation than adaptation, in a previous study, collaborators and I found that differences in immune function in these populations were in fact fixed (Martin et al. 2004; but for plasticity of clutch size see Baker 1995). After 18 months in common garden conditions in captivity, relative differences in one type of immune defense persisted between populations.

I expected that if geographic variability in molt-immune trade-offs was fixed between populations (if they existed at all), such trade-offs would remain influenced by latitude of origin even when birds were kept in captivity under controlled conditions prior to experimentation. To test this hypothesis, I captured and housed four groups of house sparrows in controlled conditions in captivity for 1 year: (1) immune-challenged Panamanian sparrows held under tropical-like environmental conditions, (2) immune-challenged New Jersey sparrows held in tropical-like environmental conditions, (3) immune-challenged New Jersey sparrows held in temperate-like environmental conditions, and (4) sham- (saline-) challenged New Jersey sparrows held in temperate-like environmental conditions (as controls). I included the third group to determine if one environmental factor, ambient temperature, would be important if molt-immune trade-offs were actually plastic traits.

Materials and methods

Study species

The house sparrow is a granivorous passerine that can be found on every continent except Antarctica (Summers-Smith 1988). Tropical populations usually lay smaller clutches (Summers-Smith 1988; L. Martin, unpublished data) and have longer breeding seasons (Mathew and Naik 1986; Summers-Smith 1988; L. Martin, unpublished data) than their temperate counterparts. Likewise, tropical populations tend to have lower rates of energy turnover (Kendeigh 1976), lower circulating stress hormone (corticosterone) titers (Martin et al. 2005), and increased investments in immune function (Martin et al. 2004) compared with their high-latitude relatives. Birds in this study originated from two locations: a north-temperate site (Belle Mead, New Jersey, USA; 40°21'N, 74°40'W) and a neotropical site (Zona Libre, Colon, Panama; 9°1'N, 80°1'W). Unlike the few other species that occur at both neotropical and north-temperate latitudes (e.g., yellow warbler, *Dendroica petechia* (L., 1766); house wren, *Troglodytes aedon* Vieillot, 1809), house sparrows can be captured in abundance and are amenable to captivity.

Typically, house sparrows undergo a single molt each year; during this molt, all contour and flight feathers are replaced (Summer-Smith 1988). Occasionally, molt-breeding overlap occurs, most often in males (Summers-Smith 1988). It is not clear if the degree of this overlap varies with latitude, although some subtropical populations do arrest molt to reproduce (India: Mathew and Naik 1986; Texas: Ginn and Melville 1983). Consequently, while north-temperate populations usually complete molt in 2 months (Ginn and Melville 1983), southerly populations can take more than 4 months if they make nesting attempts during this time of year (Mathew and Naik 1986). Currently, the progression of molt (date of onset, duration, daily molt rate) and degree of molt-breeding overlap are unknown for wild birds in either population in this study.

Bird capture and care

I captured Panamanian birds using mist nets in early July 2001. At capture, I marked each bird with numbered metal and colored plastic leg bands, and noted sex and age (juvenile versus adult) based on plumage (Summers-Smith 1988). From August–September 2001, birds were held at the Tupper Building of the Smithsonian Tropical Research Institute, Ancon, Panama. In October 2001, I exported them to our USDA–APHIS (US Department of Agriculture – Animal and Plant Inspection Service) certified quarantine facility at Princeton University, where they were subsequently held for 30 days and tested for Newcastle's disease virus and avian influenza. All birds were negative for these viruses, and no birds died or showed obvious signs of sickness during or after the quarantine period.

In late July 2001, I captured additional birds from Belle Mead, New Jersey, and held them in outdoor aviaries at Princeton University until the birds from Panama arrived. Just before they were released to common gardens, I dusted all birds from both populations with Sergeant's flea and tick powder (0.1% pyrethrin; Sergeant's, Omaha, Nebraska,

USA) and treated them with an antibacterial medication (sulfanox; Belle Mead Farmer's Co-op, Belle Mead) to control existing parasite infections. For 12 months prior to the experiment, I kept all birds in one of two large, indoor, climate-controlled aviaries to maximize their body condition and allow juveniles to mature. From October 2001 – September 2002, I provided birds with an ad libitum diet of seed (Kaytee Supreme™; Kaytee, Chilton, Wisconsin, USA), boiled chicken eggs, mealworms (*Tenebrio molitor* L., 1758; Fluker Farms, Port Allen, Louisiana, USA), Bag O' Bugs and a vitamin supplement (Daily Supplement 3; both from Golden West Bird Products, Mission Hills, California, USA), fresh oranges and spinach, gravel, and crushed oyster shells. Photoperiod in the aviaries varied seasonally to match ambient light levels in Princeton (to encourage breeding in all groups for a separate experiment).

While birds were in captivity, I modified ambient temperature in aviaries to mimic levels at each locale. I kept one aviary (tropical) at a mean temperature of 29.1 °C (SD = 1.7 °C), which did not vary over the course of the year prior to the experiment. All house sparrows from Panama ($n = 11$; 6 males, 5 females) and some house sparrows from New Jersey ($n = 13$; 6 males, 7 females) were housed in this aviary; populations were physically separated from each other at all times. The other aviary (temperate) had seasonally variable temperature more characteristic of New Jersey. Mean temperature was 22.5 °C (SD = 4.1 °C; minimum temperature 17.2 °C, maximum temperature 30.0 °C), and fluctuated to mirror outdoor conditions over the year. All remaining New Jersey house sparrows ($n = 22$; 10 males, 12 females) were kept in this aviary. I also attempted to regulate ambient humidity between aviaries; however, because of high air exchange rates, moisture levels remained relatively low but did not differ between aviaries (tropical: mean = 26.1%, SD = 7.6%; temperate: mean = 32.4%, SD = 11.0%). In total, my experimental design gave me four groups for comparison: three groups for immune challenge (i.e., two from New Jersey held in both "temperate" and "tropical" climates and one from Panama held in a "tropical" climate) and one group from New Jersey to serve as a control (i.e., held in "temperate" climate). Because of import regulations, I was not able to include additional Panamanian house sparrows in this study.

During the experimental period (October 2002), I moved all birds to wire cages where they were kept in male–female pairs to reduce the stress that they may have experienced if I had repeatedly caught them from aviaries. Birds were given 4 days to adjust to their new housing conditions prior to experimentation. While they were in cages, I fed the birds only finch seeds (Kaytee Supreme™) and water ad libitum to simulate the diet that they would take in the wild during the molting season (Summers-Smith 1988). Also, for this part of the study, I changed photoperiod to 10 h light : 14 h dark, temperature to 24 °C, and relative humidity to 26%, as these conditions were more representative of environmental conditions in the wild (New Jersey) at this time of year. Although this photoperiod is unlike what tropical birds would experience in the wild, longer light periods may have prohibited molt in temperate birds. Similar numbers of male and female birds were allocated between experimental and control groups.

Immune challenge

I used the phytohemagglutinin (PHA) wing-web technique to assess cutaneous immune activity of house sparrows (Smits et al. 1999). PHA is a mitogen derived from the kidney bean (*Phaseolus vulgaris* L.) that stimulates many cell types, particularly T cells, to divide and secrete cytokines. This cytokine secretion and mitogenesis causes local edema and swelling, and is accompanied by tissue infiltration by multiple immune cell types including basophils, macrophages, and lymphocytes (McCorkle et al. 1980). Larger swellings are thought to represent stronger immune responses (McCorkle et al. 1980). Although this index of immune function is one of the most popular in the ecological immunology literature, a single assay alone cannot fairly characterize the diversity of the avian immune system. Still, the PHA response is an expensive immunological process that at least represents an individual bird's investment in immune defense at a given point in time (McCorkle et al. 1980; Martin et al. 2003). For this reason, a decrease in the swelling response likely represents a weak immune response.

I quantified the PHA responses of individual house sparrows by subtracting the pre-injection thickness of the left wing-web patagium from the thickness measured 24 h post injection (Smits et al. 1999). In a previous study, collaborators and I found that peak tissue swelling occurred at 24 h in house sparrows challenged with PHA (Martin et al. 2003). I chose to use the single wing-web technique of Smits et al. (1999), as it reduces handling time and thus potential effects of stress on the immune response (Martin et al. 2005). For all challenges, I injected 100 µL of a 1 mg·mL⁻¹ solution of PHA-P (L9017; Sigma–Aldrich, St. Louis, Missouri, USA) in cell-culture-grade saline solution (P3813; Sigma–Aldrich) into the wing-webs of house sparrows and measured the thickness of wing-webs three times per bird using a Teclock pocket thickness gauge (Model No. SI-510; Penn Tool, Manglewood, New Jersey, USA). After all web measurements and prior to PHA challenge, I weighed each bird to the nearest 0.1 g using a Pesola® spring scale. In all cases, injections were conducted rapidly to minimize the effects of handling (stress) on swelling responses (Martin et al. 2005).

Molt scoring

I scored molt in all birds twice during the experiment: once immediately prior to the immune challenge and again 3 weeks post immune challenge. Each scoring procedure took 5–10 min and entailed removing birds from cages and systematically investigating every remige, retrix, and contour feather tract. I attempted to minimize handling stress to ensure that it did not confound my results; there was no systematic bias in handling times among experimental groups. To score molt, I used a modification of the technique outlined in Ginn and Meville (1983). This system ranks each wing and tail feather on a scale of 0–5, with old feathers scored as 0, new feathers scored as 5, and missing or intact pin feathers scored as 1. Growing feathers are scored as 2, 3, or 4, depending on their completeness. Unbroken pin feathers were included in category 2 in my study to separate actively growing feathers from missing feathers; Ginn and Melville (1983) included these feathers in category 1. I used this technique to score every primary, secondary, and tail

feather of all birds in the study (per wing: primaries = 9, secondaries = 8, maximum score = 140; tail = 12, maximum score = 60). Scores of all individual feathers were summed on both wings to obtain a composite wing molt score, and all scores from tail feathers for a composite tail molt score.

To examine trade-offs between molt and immune activity, I tallied the number of wing and tail (flight) feathers growing on each bird prior to the immune challenge and related it to the PHA response of the same bird. Because molt score itself represents the progression of molt in a bird (Ginn and Melville 1983) and not how much effort a bird is putting into feather growth at any point in time, I used the number of growing flight feathers (total wing and tail feathers in categories 2–4) as an indicator of molt effort in birds rather than molt score. In addition, I calculated the number of flight feathers that began growing in the 3 weeks post immune challenge (feathers in categories 2–4) to determine if induced immune activity directly affected feather growth. Specifically, I compared the number of flight feathers that increased in score from 0 or 1 to 2–4 or remained in the 2–4 category 3 weeks post immune challenge between the two groups; the birds with the highest values experienced the most feather growth during this 3 weeks post injection period. In addition, I counted the number of body tracts ($n_{\max} = 13$) molting on each bird and calculated the percentage of body tracts in molt and compared this value among groups. This value also represents molt effort more so than it represents molt progression, but I have not included it in my regression analyses because body molt on all birds in the study was very high. All experiments were approved by the Princeton University Animal Care Committee and comply with the principles of animal care (Pub. 86-23, National Institutes of Health) and current US laws.

Data analysis

Prior to analyses, I tested all data for normality using one-sample Kolmogorov–Smirnov tests, and I compared variable variances using Levene's tests. In most cases, data did not violate the assumptions of parametric statistics; when they did, I attempted to transform them. That failing, I used nonparametric tests. To compare molt, immune activity, and body mass among experimental groups, I used general linear models. To identify trade-offs between immune activity and molt, I used backward multiple regression analysis, setting F to remove variables at 0.10, with latitude of origin, housing conditions, body mass, sex, and the number of growing flight feathers at the time of PHA challenge as independent variables and the PHA response of each bird as the dependent variable. To determine what factors influenced feather growth in the 3 weeks post immune challenge, I used backward multiple regression analysis (F to remove = 0.10) with the same predictors as above plus the type of injection administered (saline or PHA) as independent variables. In this analysis, however, the dependent variable was the number of flight feathers that began growing in the 3 weeks post injection period. Also, I included information from the fourth group of house sparrow (saline-injected New Jersey birds in the temperate aviary) here. All analyses were completed with SPSS® version 10 (SPSS Inc. 2000) with $\alpha = 0.05$.

Results

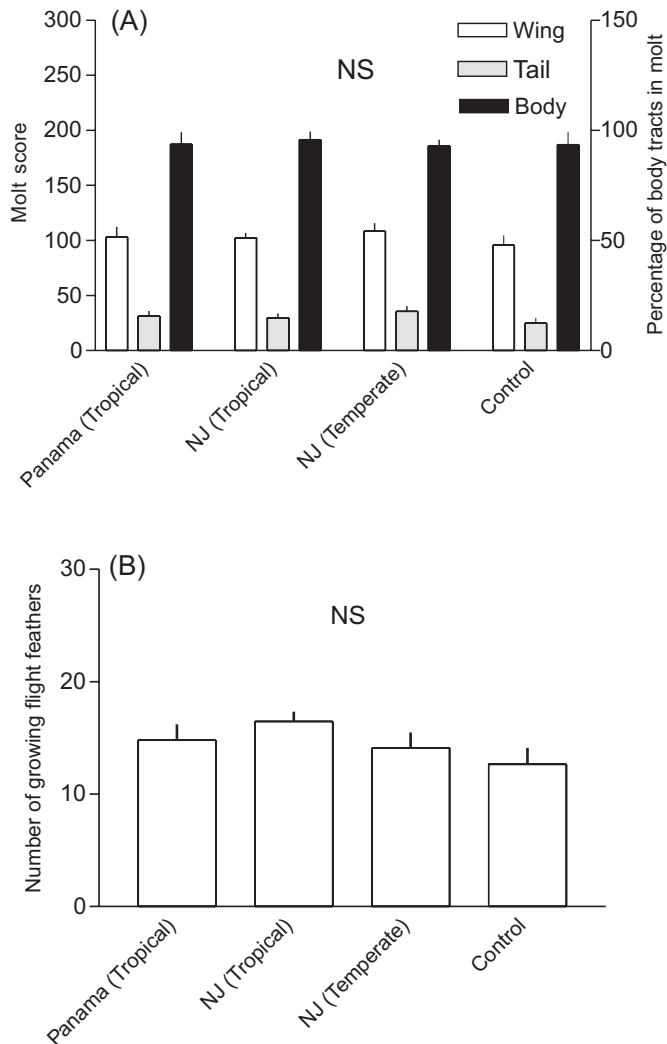
The percentage of body tracts in molt was the only non-normally distributed variable, probably because all birds in all groups were at an advanced stage of molt. These data could not be successfully transformed, so body molt was compared among groups using a multiple-sample Kolmogorov–Smirnov test. All other variables were compared using general linear ANOVA models with latitude, holding conditions, and treatment (PHA vs. saline, when necessary) as fixed factors. I found no significant differences among house sparrow groups prior to PHA challenge in mass ($F_{[3,45]} = 1.4$, $p = 0.25$), wing molt score ($F_{[3,45]} = 0.44$, $p = 0.73$; Fig. 1A), tail molt score ($F_{[3,45]} = 0.92$, $p = 0.44$; Fig. 1A), or the number of growing flight feathers ($F_{[3,45]} = 1.66$, $p = 0.19$; Fig. 1B). Percentage of molting body feather tracts was also not different ($\chi^2 = 6.00$, $p = 0.11$; Fig. 1A). However, all birds were at an advanced stage of molt; on average, birds were growing 13–15 flight feathers and 90% of body feather tracts (Fig. 1A). I also found no difference in molt rate (calculated as the change in molt score 3 weeks post PHA challenge minus molt score the day of the PHA challenge; ANOVA, $F_{[2,33]} = 0.24$, $p = 0.79$) or the strength of the PHA response during molt ($F_{[2,33]} = 2.05$, $p = 0.15$) among the three PHA-challenged groups of birds.

The strength of the PHA-induced immune response was predictable using the above independent variables (full model: $F_{[2,33]} = 5.987$, $p = 0.01$); immune activity in birds growing many feathers was generally weaker (Fig. 2A). However, only the total growing flight feathers at the time of the immune challenge was a significant coefficient in the model ($t = -2.35$, $p = 0.026$, $\beta = -0.37$), although housing conditions did marginally affect the relationship ($t = 2.010$, $p = 0.053$, $\beta = 0.31$). I also found that new feather growth post immune challenge was predictable using a similar set of variables ($F_{[1,37]} = 7.65$, $p = 0.01$; see Methods above). The only significant factor remaining in this model, however, (after backwards removal) was the type of injection administered (saline vs. PHA: $t = 2.77$, $p = 0.01$, $\beta = 0.42$). Figure 2B depicts the effect of type of injection on feather growth in the 3 weeks post immune challenge.

Discussion

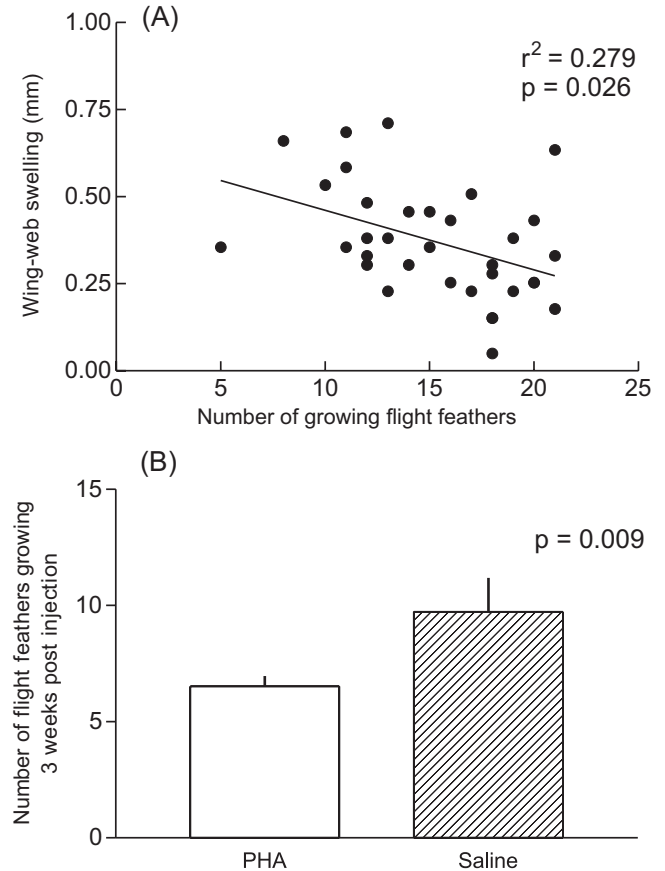
Previous studies have demonstrated that trade-offs between molt and immune activity occur in domestic fowl (Kuenzel 2003). Alodan and Mashaly (1999) found that circulating leukocyte densities were decreased in molting red junglefowls (*Gallus gallus* L., 1758), although primary antibody responses to sheep red blood cells (SRBC) were not affected. Similarly, Holt (1992) showed that blood lymphocyte densities and cell-mediated immune responses (delayed-type hypersensitivity to dinitrofluorobenzene) were depressed in the same species, although antibody responses to SRBC and *Brucella abortus* were not. Such studies in wild birds are rare and equivocal. In support of trade-offs, nestling mountain chickadees (*Poecile gambeli* (Ridgway, 1886)) challenged with Newcastle's disease virus or SRBC had increased wing feather asymmetry compared with controls (Whitaker and Fair 2002; see also Nava et al. 2001). Additionally, Sanz et al. (2004) found that breeding male pied

Fig. 1. Comparisons of molt stage and body condition of house sparrow (*Passer domesticus*) groups prior to PHA injection: (A) molt scores are based on wing feather scores (open bars) and tail feather scores (shaded bars), and percentage of body tracts ($n_{\max} = 13$) in molt (right y axis); (B) active feather growth. Panama (tropical): Panama origin, tropical climate ($n = 11$); NJ (tropical): New Jersey origin, tropical climate ($n = 13$); NJ (temperate): New Jersey origin, temperate climate ($n = 10$); and control: New Jersey origin, temperate climate, saline-injected ($n = 12$). NS indicates no significant difference among groups based on univariate ANOVA and values are means \pm SE.



flycatchers (*Ficedula hypoleuca* (Pallas, 1764)) challenged with SRBC delayed the onset of their molt relative to saline-challenged controls. In contrast to these studies though, Moreno et al. (2001) found that the relationship between molt and immune function may not be obligatorily negative. They found a marginally positive relationship between molt score and daily energy expenditure (DEE) in molting male (but not female) pied flycatchers. Furthermore, they found a marginally positive relationship between the PHA response and the DEE in molting males, but negative relationships between PHA responses and DEE in both molting and non-molting females. Based on these results, it remains unclear

Fig. 2. Two-way trade-offs between immune activity and feather growth in house sparrows: (A) number of growing feathers at the time of injection is negatively related to the PHA skin-swelling response (r^2 and p value from backward multiple regression); (B) new feather growth over 3 weeks post injection is lower in PHA-challenged birds (open bar, $n = 27$) relative to saline-injected controls (hatched bar, $n = 11$; p value from backward multiple regression). Values in B are means \pm SE.



whether molt-immune trade-offs occur in wild adult passerine birds.

Here, I provide new direct evidence for molt-immune trade-offs in two populations of wild-caught house sparrows. First, I found that immune function was inversely related to feather growth, where birds growing more feathers mounted weaker immune responses to PHA. Second, I found that induction of immune activity hindered molt, where immunologically challenged birds grew fewer feathers during the 3 weeks post immune challenge compared with those in the saline-injected controls. These trade-offs may occur for a variety of reasons. First as noted above, both molt and immune activity impart high resource demands. Co-authors and I found a 29% per day increase in the resting metabolic rate of house sparrows during an immune response to PHA (Martin et al. 2003; see also Ots et al. 2001); we found an even greater metabolic response to the same challenge in house sparrows from Panama (L. Martin, D. Hasselquist, and M. Wikelski, unpublished data). Comparable increases in energy expenditure also occur during molt. Dolnik (1965) noted a 24.9% increase in standard metabolic rate throughout the 80 day molt period in house sparrows (as cited in

Payne 1972). Lindström et al. (1993) estimated that molt increased resting metabolic rate of common redpolls (*Carduelis flammea* (L., 1758)) and bluethroats (*Luscinia svecica* (L., 1758)) by 13% and 30%, respectively. Molt-immune trade-offs therefore may be mediated by energy availability.

Other evidence indicated that trade-offs between molt and immune activity may also be driven by availability of protein. Lochmiller et al. (1993) found that an 8% protein diet (relative to 15% and 33%), reduced PHA-induced immune activity (but not SRBC responses) in the northern bobwhite (*Colinus virginianus* (L., 1758)). Similarly, Murphy and King (1991) showed that a low protein diet prolonged molt by 60 days and decreased feather growth rate and feather quality in the Gambel's white-crowned sparrow (*Zonotrichia leucophrys gambelii*). Still other factors probably also affect molt-immune trade-offs. For example, agonistic relationships between molt and immune activity may be driven by differences in circulating hormone levels at various times of the year or across latitudes. Particular hormones (e.g., prolactin) vary seasonally and affect the onset and progression of molt in both domestic and wild species (Dawson 1998; Kuenzel 2003). Some studies have indicated that temperate and tropical birds tended to differ in circulating steroid hormone titers (Wikelski et al. 2003; Hau et al. 2004; Martin et al. 2005), although molt-related hormone levels are unknown to date.

One other unexplored aspect of molt-immune interactions in this study is that both the quality and the quantity of trade-offs may be variable. That is, negative relationships between molt and immune activity may manifest in other ways besides just their intensity. For instance during molt, birds may be forced to deactivate their most costly immune responses (e.g., inflammatory responses; Klasing and Leshchinsky 1999) to regenerate feathers. Alternatively, birds forced to engage in immune activity during feather regeneration may have to produce lower quality feathers (sensu Whitaker and Fair 2002) and (or) prolong the duration of the molting process. In the future, other indexes of immune activity and other molt characters warrant study.

In terms of population variability, I found no evidence for geographic variation in molt-immune trade-offs in sparrows in this study. As noted above, previous work on these populations has indicated that some aspects of immune function are distinct between these house sparrow populations (Martin et al. 2004, 2005). In other species, temperate populations replace feathers at much faster rates and over shorter time periods than their tropical relatives (Foster 1974). For instance, Helm and Gwinner (1999) found that Kenyan stonechats (*Saxicola torquata axillaris*) began molt earlier and molted faster than Austrian stonechats (*Saxicola torquata rubicola*; see also Hemborg et al. 1998, 2001). Like the immune function in our house sparrows, Helm and Gwinner (1999) provided strong evidence that the differences in their stonechat populations were genetic, as F_1 hybrids molted at intermediate rates and began at intermediate dates compared with the parent populations. This suggests that in resident passerine, molt-immune trade-offs, if they exist, may in fact be fixed characters.

In this study, the lack of population distinctiveness in molt-immune trade-offs may have occurred for several rea-

sons. The first involves methodological limitations. I was unable to establish the date of onset of molt, repeatedly score molt, or characterize the quality of new feathers in my house sparrows (Dawson et al. 2000) to avoid stressing animals, which itself can affect immune function in this species (Martin et al. 2005). In addition, I did not include additional groups of Panamanian birds because of import restrictions. Other experimental groups, particularly saline- and PHA-injected Panama origin, temperate climate birds, may have been informative. A second possibility for the lack of population variability includes a genuine lack of distinctness in molt phenology or immune activity at this time of year in this species. Immune function is indeed latitudinally variable between these populations (Martin et al. 2004), but during molt it may be weak in all populations. Although populations of this species show latitudinal variability in many traits (Kendeigh 1976; Summers-Smith 1988; Martin et al. 2004), other traits including molt may not have had sufficient time to conform to local conditions (Baker 1995). In part, this lack of variation in some traits may be related to the non-migratory nature of the species. Like other year-round residents, house sparrows may not face demanding molt-immunity trade-offs because they have ample time to complete molt prior to the onset of winter, whereas migratory species may face demanding trade-offs because they must condense molt to a relatively shorter window of time (Sanz et al. 2004).

In conclusion, in this study, I demonstrate that trade-offs between molt and immune activity can occur in wild house sparrows. Moreover, it is clear that trade-offs between molt and immune activity can operate in both directions; i.e., increased investment in molting was associated with decreased investment in immune responsiveness, whereas increased immune investment led to decreased molt activity. Future studies should seek to conduct additional controlled, captive studies on other species and examine whether trade-offs can be qualitative as well as quantitative. Also, additional temperate and tropical populations of house sparrows should be studied (in both wild and captive conditions) to determine if the patterns indicated in the comparison of these two populations is robust across latitudes.

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