

## TREE SWALLOWS TRADE OFF IMMUNE FUNCTION AND REPRODUCTIVE EFFORT DIFFERENTLY ACROSS THEIR RANGE

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**Abstract.** Latitudinal differences in life histories are believed to be underlain by differences in trade-offs between current and future reproduction. I report differences in trade-offs between parent and offspring across the range of a widespread avian species, the Tree Swallow (*Tachycineta bicolor*). I manipulated parental effort and found that in Alaska, where yearly adult return rates are low, breeding females increase their reproductive investment to maintain offspring quality, whereas in Tennessee, where yearly adult return rates are high, breeding females are either unable or unwilling to increase reproductive investment and, consequently, raise offspring of lower quality. I further investigated a critical mechanism of self-maintenance that may underlie differences in survival among sites: immunocompetence. Females breeding in Alaska mounted weaker immune responses when raising enlarged broods, whereas females in Tennessee did not, further suggesting a strategy in Alaskan females to incur costs (i.e., reduce future reproduction) in order to maintain offspring quality. Insect availability increased as the breeding season progressed in both sites, but more food was available in Alaska than in Tennessee. This is among the first studies to report geographic differences in immune function consistent with life history theory, which predicts that individuals with higher survival probabilities should invest more in self-maintenance.

**Key words:** breeding range; geographic variation; immune function; latitudinal gradients; life history trade-offs; offspring quality; parental investment; reproductive effort; self-maintenance; *Tachycineta bicolor*; Tree Swallow.

### INTRODUCTION

Life history theory posits that individuals make allocation decisions between themselves and their offspring based on the value of current and future reproduction (Stearns 1992, Roff 2002). Individuals with high yearly survival rates are hypothesized to invest less in their offspring *per breeding attempt* than are individuals with lower yearly survival rates (Martin et al. 2000, Ghalambor and Martin 2001, Martin et al. 2004). Typically, trade-offs are examined at single sites for a single species (Stearns 1992, Ricklefs and Wikelski 2002), or among species along environmental gradients, such as between tropical and temperate bird species (Skutch 1949, Lack 1966, Martin et al. 2000, Wikelski et al. 2003). For example, temperate birds appear to invest more in current reproduction (e.g., through larger clutches and greater nest defense) because they are shorter lived, thus limiting the value of future reproduction (Martin et al. 2000, Ghalambor and Martin 2001).

Few studies have demonstrated that large-scale gradients in life history trade-offs can occur *within spe-*

*cies*, which would provide clear and strong proof that environmental variation, and not just differences in evolutionary history such as occur between species, has led to the evolution of differing life histories (Stearns 1992, Linden and Møller 1993, Foster and Endler 1996). Latitudinal variation in life history trade-offs has been reported in mosquitos (Armbruster et al. 2001), fish (Kokita 2003), and lizards (Sears and Anguilleta 2003). In birds, most studies have examined geographic variation in life history *traits* (e.g., egg size [Encabo et al. 2002]; molt [Hemborg et al. 2001]; energy expenditure [Sanz et al. 2000]; metabolic rate [Wikelski et al. 2003]; immune function [Martin et al. 2004]) without looking for the trade-offs between suites of traits predicted by life history theory (but see Young 1996, Dhondt 2001). Recent work by Martin et al. (2004) found differences in immune function between tropical and temperate House Sparrows (*Passer domesticus*). The work described here is a natural extension of this study, as it examines how individuals trade off immune function across the species' range. Examining traits without trade-offs is incomplete, because trade-offs can reveal underlying strategies, functional mechanisms, constraints, and selection pressures (Dhondt 2001, Ricklefs and Wikelski 2002).

There is growing evidence that parental trade-offs associated with reproduction are related to immune defense: the ability to fight infection and parasites is important to survival, but is also costly (Gustafsson et al.

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1994, Saino et al. 1999, Lochmiller and Deerenberg 2000). Parental effort can lead to reduced immune function, which in turn affects parental survival, thus enforcing a trade-off between the prospects of offspring and parent, and a trade-off between current and future reproduction (Apanius 1998, Norris and Evans 2000, Ardia et al. 2003), as well as reflecting trade-offs among competing life history demands such as molt and incubation (Hanssen et al. 2003, Sanz et al. 2004). Immune function can reflect long-term strategy, because differences in survival and allocation should be reflected in immunocompetence. Individuals with higher extrinsic survival probabilities should be selected to maintain stronger immune function to ward off long-term health threats than would individuals with lower extrinsic probabilities of survival. However, no published study to date has examined geographic variation in trade-offs between adult immune function and offspring production. Such work would require experimental manipulation of parental reproductive effort across an environmental gradient (Lack 1966, Gustafsson and Sutherland 1988).

In this paper, I report the results of experimental brood size manipulations in the Tree Swallow (*Tachycineta bicolor*), a widely distributed species with a breeding range across most of North America. Comparing two sites at the extreme of the breeding range, Alaska and Tennessee, I tested whether individuals differ in trade-offs between immune self-maintenance (as a predictor of future reproduction) and offspring measures (as a predictor of current reproduction). By experimentally manipulating offspring demand to force parents to make decisions about reproductive investment in a given season, relative to future seasons, I examined whether adults showed different behavioral and immune responses. If sites differ in parental ability or willingness to increase reproductive effort when offspring demand is experimentally increased, this could be due to differences in resource availability or other constraints, differences in the value of current reproduction, or both. I predicted that Alaskan females, with lower return rates, would increase their feeding effort and thus bear additional costs when offspring demand was increased; Tennessee females, with higher return rates, were expected to show less or no increase in effort when brood size was increased. Parental ability or willingness to bear the costs of reproduction also should be reflected in their immune responses under experimental conditions. Here, I tested whether individuals raising enlarged broods would show reduced immune function. I predicted that females raising enlarged broods in Alaska would have reduced immune responses, whereas females in Tennessee would not, suggesting either a strategy to reduce self-maintenance costs, or a constraint when faced with increased offspring demand in Alaska.

## METHODS

The Tree Swallow (*Tachycineta bicolor* Vieillot 1808) is a widespread and common cavity-nesting North American migrant member of the family Hirundinidae. It breeds from Alaska to northern Mississippi and Alabama, USA (Robertson et al. 1992). During 2001–2003, I studied Tree Swallows breeding in nest boxes erected for their use in Loudon, Anderson, and Knox Counties, Tennessee, USA (centered on 35°53' N, 84°18' W) and near Fairbanks, Alaska, USA (centered on 64°49' N, 147°52' W).

Nests were checked daily to determine date of clutch initiation and clutch size. First broods with the same hatching date were randomly assigned to one of three treatments (enlarged, reduced, or control) to create broods that were roughly 50% larger or smaller than the original clutch size. In total, 157 chicks were moved among nests in Alaska, and 162 chicks in Tennessee to create the following mean number of nestlings per brood type on day 4: for Alaska, 2.94 in reduced ( $N = 16$ ), 5.18 in control ( $N = 17$ ), and 7.88 in enlarged broods ( $N = 16$ ); for Tennessee, 2.94 in reduced ( $N = 18$ ), 5.00 in control ( $N = 18$ ), and 7.72 in enlarged broods ( $N = 18$ ). Chicks were individually marked and swapped for all treatments on day 3 of the nestling period (hereafter all days are referred to by days from hatch of the first nestling, day 0). Breeding females were captured on the nest on day 4. Offspring were measured on days 4, 6, 10, and 12 of the nestling period. Each individual was uniquely marked, using either nail polish applied to claws or metal U.S. Fish and Wildlife Service bands. During each visit, body mass, flattened left-wing length, head–bill length, and tarsus length were recorded for each nestling.

At each site, insect availability was recorded using two 2-m aerial insect samplers powered by a Robbins and Myers (Dayton, Ohio, USA) 1650 RPM 1/12 HP motor (McCarty and Winkler 1999) to collect daily samples of aerial insect abundance during the breeding season. Insect samplers were placed within 10 m of water at locations where electrical power was available. Packed insect volume was measured by centrifuging samples, after removing seeds and other debris, at 31.4 m/s<sup>2</sup> (5000 rpm) for 75 min. To record nest visitation rates, three 60-min behavioral observations were conducted using video cameras between days 8 and 11 for each breeding pair. Sexes were differentiated in video observations by marking females with a small dot of white-out on the back. For each observation, cameras were set with timers to begin recording 15 min after setup to minimize the effect of human disturbance on provisioning behavior. In the year following the manipulation, all breeding females were captured at each site to determine return rates.

Breeding females were captured, weighed, measured, and aged by plumage on days 4, 6, and 12 of the nestling period. On day 4, blood was drawn from

the brachial vein to determine pre-exposure levels of antibodies to sheep red blood cells (from 20  $\mu\text{L}$  of plasma), and each bird was injected intraperitoneally with  $5 \times 10^7$  sheep red blood cells (ICN Biomedicals, Aurora, Ohio, USA) suspended in 100  $\mu\text{L}$  of phosphate-buffered saline, PBS (Deerenberg et al. 1997). All individuals were captured 8 days later to draw blood to determine post-exposure primary antibody titers in plasma. Antibody titers were measured in all blood samples using a base-2 serial dilution hemagglutination test conducted with 20  $\mu\text{L}$  of plasma on 96-well microtiter plates (Roitt et al. 1998). Samples were serially diluted starting with 20  $\mu\text{L}$  of PBS; to each well, 20  $\mu\text{L}$  of a 2% suspension of SRBC in PBS was added. Plates were incubated at 37°C for 1 h. Titers are given as the  $\log_2$  of the reciprocal of the highest dilution of plasma showing positive hemagglutination. For each plate, positive and negative control sera were included.

On day 4, 0.15 mg of phytohemagglutinin (PHA-P) in 30  $\mu\text{L}$  of PBS were injected into the patagial wing web of breeding females (Smits and Williams 1999). On day 10, each nestling was injected with 0.1 mg in 20  $\mu\text{L}$  of PBS in the same location. Prior to each injection, the thickness of the wing web was measured three times using a digital micrometer, and was reported as the average thickness. Individuals were remeasured  $\sim 48$  h after injection and wing web thickness was remeasured three times to obtain the average measurement (repeatability: pre-exposure  $F_{645, 646} = 9.06$   $P < 0.001$ ,  $R = 0.91$ ; post-exposure  $F_{645, 646} = 7.53$   $P < 0.001$ ,  $R = 0.86$ ; Lessells and Boag 1987). Cell-mediated immune response was considered to be the ratio of post-injection thickness to pre-injection thickness (Hörak et al. 1999).

Parental immune responses were examined using a Generalized Linear Model (PROC GLM, SAS version 8.02; SAS Institute 2002) with the following variables: standardized clutch initiation date, brood manipulation treatment (reduced, control, enlarged), female age (first-year breeders vs. older breeders), natal clutch size, and breeding site. Because of differences in timing of breeding among sites, clutch initiation date was standardized to a mean of 0 and standard deviation of 1. Because nestlings were switched among nests, nestling measures were analyzed using a mixed-model analysis, with natal nest and nest of rearing as random factors and the following fixed effects: standardized clutch initiation date, brood manipulation treatment (reduced, control, enlarged), clutch size of the natal nest, female age (first-year breeders vs. older breeders), number of brood mates on day 12, and breeding site. All two-way interactions with  $P$  values  $> 0.40$  were removed. Because Tree Swallows show breeding philopatry (Robertson et al. 1992, Winkler et al. 2004), the percentages of birds that returned to breed at each site were compared using a chi-square test.

Nestling condition was characterized using three variables: (1) cell-mediated immune response to PHA, (2)

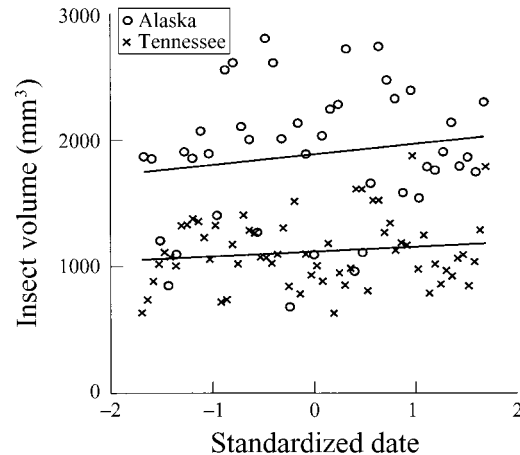


FIG. 1. Insect availability captured in samplers as a function of standardized date from two breeding sites of Tree Swallows: Fairbanks, Alaska, and Loudon County, Tennessee, USA. The standardized date was calculated by centering the middle date of the breeding season as 0. Availability is expressed as packed volume of insects.

growth rate, and (3) residual body mass. Growth rate was calculated as the growth rate constant  $K$  of a logistic growth function connecting 10–90% of the asymptotic values for three nestling measures: primary wing feather, tarsus, and head–bill measurements (Starck and Ricklefs 1998). Because the three nestling measures were highly correlated,  $K$  values were combined in a principal components analysis and the first principal component (which explained 79% of the variation) was used in statistical analyses. Nestling residual body mass was considered to be the residual of a regression of body mass against head–bill size, a structural measure of body size ( $N = 691$ ,  $\beta = 0.825$ ,  $F_{1, 690} = 61.84$ ,  $P < 0.001$ ,  $R^2 = 0.85$ ). Head–bill size was chosen due to a higher  $R^2$  in the model with body mass (0.85 vs. 0.76).

## RESULTS

Insect availability showed considerable daily variation at both sites, but overall prey availability showed a linear trend as the breeding season progressed, with no differences in the rate of increase among sites (Fig. 1). For Julian date vs. packed bug volume (measured as cubic millimeters),  $\beta = 4.60$ ,  $F_{1, 103} = 4.01$ ,  $P = 0.04$ ,  $R^2 = 0.11$ ; for site-level difference in slope,  $F_{1, 102} = 1.43$ ,  $P = 0.15$ . There were more insects available in Alaska than in Tennessee (for site-level difference in abundance,  $F_{1, 102} = 16.16$ ,  $P < 0.0001$ ).

Females breeding in Tennessee (TN) were more likely to return to breed in the year following the experiment than were females breeding in Alaska (AK): TN 34/54 females, 59%; AK 15/34 females, 44% ( $\chi^2 = 3.99$ ,  $P = 0.04$ ).

Sites differed in the effect of the brood manipulation on breeding female behavior. Alaska females raising enlarged broods increased their feeding visits relative

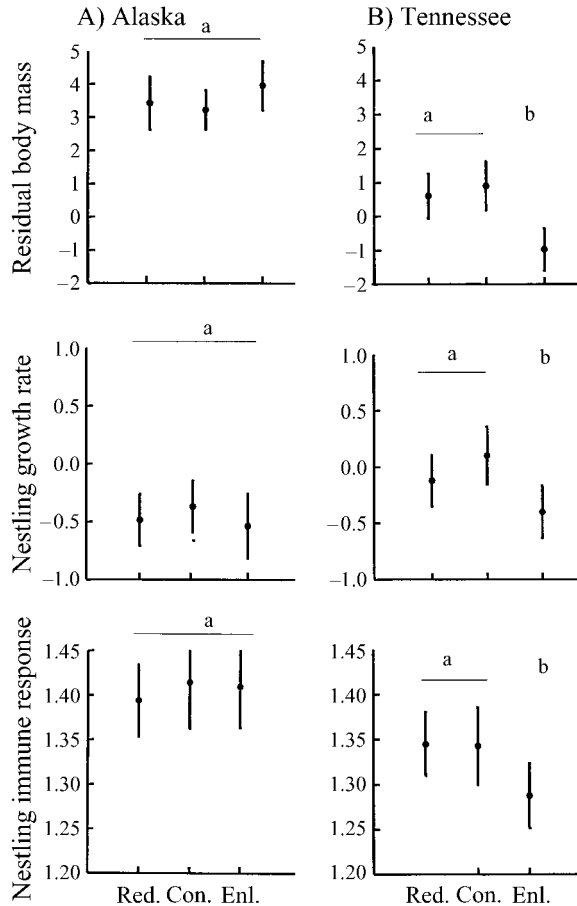


FIG. 2. Effect of brood manipulation treatment on offspring condition measures at the edges of the range of the Tree Swallow: (A) Alaska, (B) Tennessee. Key to abbreviations: Red., reduced treatment; Con., control treatment; Enl., enlarged treatment. Values presented are least-square mean estimates  $\pm$  SE. Different letters (a, b) refer to least-square mean differences ( $P < 0.05$ ) between treatment groups within each site for each offspring quality measure. Note the same y-axis scale between sites for each measure.

to control and reduced-brood females, whereas Tennessee females showed no difference in feeding behavior, regardless of offspring demand (for effect of site,  $F_{1,84} = 0.10$ ,  $P = 0.75$ ; for brood-size treatment,  $F_{2,84} = 5.57$ ,  $P = 0.005$ ; for site  $\times$  treatment,  $F_{2,84} = 4.65$ ,  $P = 0.03$ ). The number of feeding visits/min (least-square mean  $\pm$  SE) in AK was  $0.132 \pm 0.015$  visits/min for control broods,  $0.124 \pm 0.013$  for reduced, and  $0.174 \pm 0.016$  for enlarged; in TN there were  $0.151 \pm 0.013$  visits/min for control broods,  $0.145 \pm 0.014$  for reduced, and  $0.152 \pm 0.015$  for enlarged broods.

Alaskan females maintained offspring condition in enlarged broods, whereas Tennessee females did not. Offspring raised in enlarged broods in Alaska were similar in condition to offspring in control or reduced broods (Fig. 2A;  $N = 543$  nestlings, effect of treatment: for nestling growth rate,  $F_{2,38.4} = 1.34$ ,  $P = 0.28$ ; for nestling residual body mass,  $F_{2,33.3} = 0.47$ ,  $P = 0.63$ ; for nestling immunocompetence,  $F_{2,43.5} = 1.06$ ,  $P = 0.35$ ). In contrast, Tennessee offspring in enlarged broods grew at slower rates, were in lower condition, and showed weaker cell-mediated immunity than did offspring in control or reduced broods (Fig. 2B; effect of treatment: for nestling growth rate,  $F_{2,41.5} = 3.97$ ,  $P = 0.02$ ; for nestling residual body mass,  $F_{2,33.6} = 3.84$ ,  $P = 0.03$ ; for nestling immunocompetence,  $F_{2,196} = 4.78$ ,  $P = 0.01$ ).

Breeding females responded differently when faced with an experimental manipulation of offspring demand. Alaska females raising enlarged broods mounted weaker immune responses to immunochallenge with PHA and SRBC than did controls, whereas Tennessee females raising enlarged broods showed no difference from controls ( $N = 103$ ; Table 1, Fig. 3).

#### DISCUSSION

Tree Swallows breeding in Alaska and Tennessee responded differently to brood manipulations, consistent with differences in life history pressures across

TABLE 1. Output of mixed-model analysis of factors affecting immune performance of female Tree Swallows breeding in Alaska and Tennessee.

Effect	Num. df	F	P
Immune response to PHA			
<b>Breeding site</b>	<b>1</b>	<b>23.33</b>	<b>&lt;0.0001</b>
<b>Brood manipulation treatment</b>	<b>2</b>	<b>3.34</b>	<b>0.04</b>
Female age	1	1.22	0.27
<b>Clutch initiation date</b>	<b>1</b>	<b>15.77</b>	<b>0.0001</b>
Clutch size	1	0.07	0.79
<b>Breeding site <math>\times</math> Brood manipulation treatment</b>	<b>2</b>	<b>4.82</b>	<b>0.01</b>
Immune response to SRBC			
Breeding site	1	1.60	0.21
<b>Brood manipulation treatment</b>	<b>2</b>	<b>14.29</b>	<b>&lt;0.0001</b>
Female age	1	0.37	0.54
<b>Clutch initiation date</b>	<b>1</b>	<b>17.86</b>	<b>0.0001</b>
Clutch size	1	1.03	0.34
<b>Breeding site <math>\times</math> Brood manipulation treatment</b>	<b>2</b>	<b>3.67</b>	<b>0.04</b>

Note: Significant factors are shown in boldface; denominator df = 86.

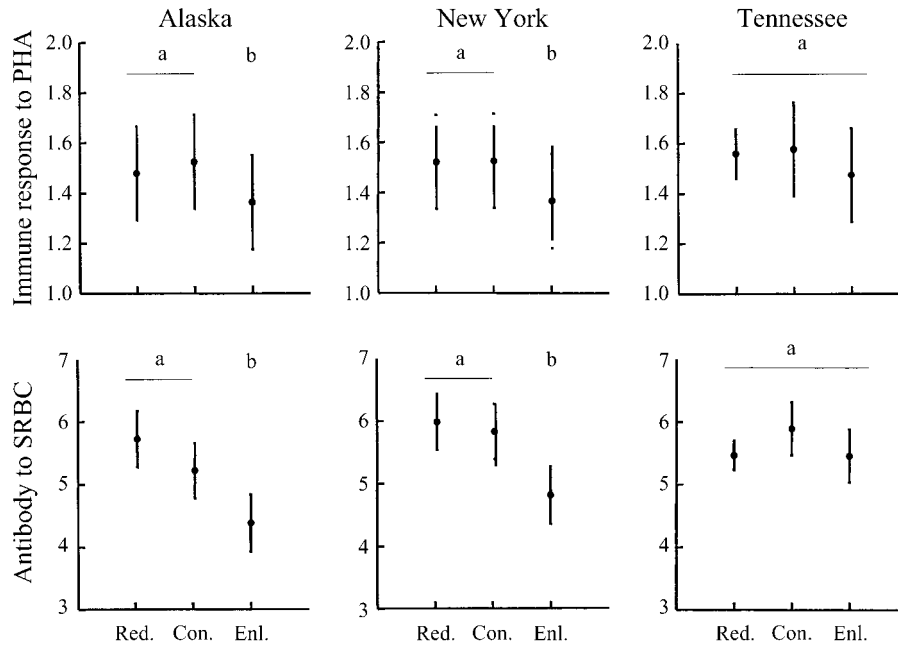


FIG. 3. Immune response of breeding female Tree Swallows to PHA (cell-mediated response) and sheep red blood cells (SRBC, humoral response) while raising manipulated broods. Values presented are least-square mean estimates  $\pm$  SE. Different letters refer to least-square mean differences *within each site* at  $P < 0.05$ . Data from New York are adapted from Ardia (2005).

their range. In Alaska, females appeared able and willing to increase reproductive effort and to reduce their own immune system self-maintenance. Alaska females increased their effort to a level necessary to maintain offspring condition, because offspring in enlarged broods were of similar condition to offspring in control broods. These results, coupled with low return rates, are consistent with a view that Alaska individuals exhibit strategies reflecting an emphasis on current payoffs, such as offspring condition, rather than future payoffs. In contrast, Tennessee females did not change behavior when faced with increased offspring demand, and showed no depression in their own immune function. Consequently, Tennessee females raised offspring in enlarged broods in lower condition relative to controls. Thus, Alaska females may be more constrained than are Tennessee females, or may strategically invest in offspring vs. self-maintenance differently than females in Tennessee. These results are consistent with a view that increased female survival is linked with decreased fecundity (Martin et al. 2000).

Why aren't Tennessee females increasing their effort? Lack of response by Tennessee females could be interpreted as an inability to increase effort (Lack 1966). However, an equally parsimonious explanation is that parents are strategically maintaining reproductive effort at its optimal level and thus are *unwilling* to increase effort, in order to minimize costs to future reproduction. If benign environmental conditions contribute to higher yearly return rates, this might allow Tennessee females to increase short-term effort with

minimal costs. Insect availability was lower in Tennessee; hence, females might show reduced reproductive investment solely due to increased costs of foraging. However, Tennessee females with control broods raise nestlings in similar condition to those in Alaska and still return at higher rates, suggesting a more complicated explanation for why Tennessee females do not increase effort with brood supplementation. It is more likely that individuals are making adjustments to multiple environmental stressors, and the combination of these phenotypic responses creates the pattern reported here.

Another contributing factor is that Tennessee females may have greater exposure to pathogens and parasites, thus increasing the need to invest in immune function at the cost of resources available for offspring (Martin et al. 2004). Individuals with high exposure to disease also may be unwilling to down-regulate immune performance, because short-term immune reduction may have long-term survival costs (Ardia et al. 2003). If Tennessee females indeed do survive at higher rates, the strategy of minimizing investment in a single breeding effort is effective because the value of a single year of reproduction is lower. Thus, high survival does not directly select for low reproductive effort, but it does create the conditions whereby behavioral and physiological responses to environmental pressures that stress self-maintenance over offspring will lead to higher fitness returns.

Although the use of return rates does not provide the same rigor as a survival analysis, extensive work on

Tree Swallows in Ithaca has revealed that few birds disperse between breeding seasons (Winkler et al. 2004), and the results reported here are consistent with true differences in mortality between sites. However, long-term assessments of survival, rather than return rates, are needed to conclusively determine whether the geographic variation reported here is due directly to differences in survival. At the edge of the range, different strategies of philopatry may prevail, causing lower apparent return rates in Alaska. Thus, the pattern of differences in trade-offs reported here may not be due to a trade-off between current and future reproduction, but rather to other selection pressures affecting reproductive trade-offs, such as parasite exposure, as previously mentioned. Other strong possibilities are differences in thermoregulation between sites, and the probability of renesting if a single nest attempt fails (which should be much higher in Tennessee).

In conducting a similar study in New York, a location in the center of the Tree Swallow range, I found that Ithaca females show patterns intermediate between these two extreme sites (Fig. 3; Ardia 2005). New York females increased their reproductive effort when raising enlarged broods, but not to the level necessary to maintain all measures of offspring condition. However, New York females showed decreased immune responses when raising enlarged broods, similar to Alaska females, and had similar return rates (48% in Ithaca vs. 44% in Alaska). At the same time, females show levels of immune function more similar to those in Alaska, reflecting a less long-term strategy of self-maintenance resource allocation. These similarities between New York and Alaska relative to Tennessee suggest that different conditions in the southern edge of the range drive the differences.

Although the intraspecific, geographic variation in life history reported here is not as marked as that often reported between species, this study provides additional evidence that the patterns of evolutionary trade-offs used to explain life history differences between tropical and temperate birds also could also occur within a species. Tropical-temperate differences are hypothesized to be underlain by differences in environmental conditions, and similar patterns appear to occur in Tree Swallows. In Alaska, individuals make large investments in offspring production, apparently by reducing self-allocation, as reflected in immune responses. In Tennessee, individuals invest significantly in themselves, with the consequence of less investment in offspring. These patterns appear to be built by individual-level responses to important environmental stresses, such as food availability, disease exposure, and nest predation. Differences in return rates among sites are consistent with these differences, but are unlikely to be the ultimate cause of differences. Overall, we should view parental responses as a mix of both constraint and strategy that will increase our understanding of how differences in relative costs and ben-

efits affect both short-term behavior and physiology, as well as life history variation. This work also demonstrates that the interaction between behavioral and physiological responses and environmental variation can vary within a species due to differing trade-offs among competing life history demands.

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#### LITERATURE CITED

- Apanius, V. 1998. Stress and immune defense. Pages 133–153 in A. P. Moller, M. Milinski, and P. J. B. Slater, editors. *Advances in the study of behavior*. Volume 27. Elsevier, Amsterdam, The Netherlands.
- Ardia, D. R. 2005. Individual quality mediates tradeoffs between reproductive effort and immune function. *Journal of Animal Ecology* **74**:517–524.
- Ardia, D. R., K. A. Schat, and D. W. Winkler. 2003. Reproductive effort reduces long-term immune function in breeding tree swallows (*Tachycineta bicolor*). *Proceedings of the Royal Society of London B* **270**:1679–1683.
- Armbruster, P., W. E. Bradshaw, K. Ruegg, and C. M. Holzapfel. 2001. Geographic variation and the evolution of reproductive allocation in the pitcher-plant mosquito, *Wyeomyia smithii*. *Evolution* **55**:439–444.
- Deerenberg, C., V. Apanius, S. Daan, and N. Bos. 1997. Reproductive effort decreases antibody responsiveness. *Proceedings of the Royal Society of London B* **264**:1021–1029.
- Dhondt, A. A. 2001. Tradeoffs between survival and reproduction in Tits. *Ardea* **89**:155–166.
- Encabo, S. I., E. Barba, J. A. Gil-Delgado, and J. S. Monros. 2002. Geographical variation in egg size of the Great Tit *Parus major*: a new perspective. *Ibis* **144**:623–631.
- Foster, S. A., and J. A. Endler. 1999. *Geographic variation in behavior*. Oxford University Press, New York, New York, USA.
- Ghalambor, C. K., and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science* **292**:494–497.
- Gustafsson, L., D. Nordling, M. S. Andersson, B. C. Sheldon, and A. Qvarnström. 1994. Infectious diseases, reproductive effort and the cost of reproduction in birds. *Philosophical Transactions of the Royal Society of London B* **346**:323–331.
- Gustafsson, L., and W. L. Sutherland. 1988. The cost of reproduction in the Collared Flycatcher *Ficedula albicollis*. *Nature* **335**:813–815.
- Hanssen, S. A., I. Folstad, and K. E. Erikstad. 2003. Reduced immunocompetence and cost of reproduction in common eiders. *Oecologia* **136**:457–464.
- Hemborg, C., J. J. Sanz, and A. Lundberg. 2001. Effects of latitude on the trade-off between reproduction and moult:

- a long-term study with pied flycatcher. *Oecologia* **129**:206–212.
- Hörak, P., L. Tegelmann, I. Ots, and A. P. Møller. 1999. Immune function and survival of great tit nestlings in relation to growth condition. *Oecologia* **121**:316–322.
- Kokita, T. 2003. Potential latitudinal variation in egg size and number of a geographically widespread reef fish, revealed by common-environment experiments. *Marine Biology* **143**:593–601.
- Lack, D. 1966. *Population studies of birds*. Oxford Press, Oxford, UK.
- Linden, M., and A. P. Møller. 1993. Cost of reproduction and covariation of life history traits in birds. *Trends in Ecology and Evolution* **4**:367–371.
- Lochmiller, R. L., and C. Deerenberg. 2000. Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos* **88**:87–98.
- Martin, L., M. Pless, J. Svoboda, and M. Wikelski. 2004. Immune activity in temperate and tropical House Sparrows: a common garden experiment. *Ecology* **85**:2323–2331.
- Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000. Parental care and clutch sizes in North and South American birds. *Science* **287**:1482–1485.
- McCarty, J. P., and D. W. Winkler. 1999. Relative importance of environmental variables in determining the growth of nestling tree swallows *Tachycineta bicolor*. *Ibis* **141**:286–296.
- Norris, K., and M. R. Evans. 2000. Ecological immunology: life history trade-offs and immune defense in birds. *Behavioral Ecology* **11**:19–26.
- Ricklefs, R. E., and M. Wikelski. 2002. The physiology-life history nexus. *Trends in Ecology and Evolution* **17**:462–468.
- Robertson, R. J., B. J. Stutchbury, and R. R. Cohen. 1992. Tree Swallow. In A. Poole, P. Stettenheim, and F. B. Gill, editors. *Birds of North America*, Number 11. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and American Ornithologists Union, Washington, D.C., USA.
- Roff, D. A. 2002. *Life history evolution*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Roitt, I., J. Brostoff, and D. Male. 1998. *Immunology*. Mosby, London, UK.
- Saino, N., S. Calza, P. Ninni, and A. P. Møller. 1999. Barn swallows trade survival against offspring condition and immunocompetence. *Journal of Animal Ecology* **68**:999–1009.
- Sanz, J. J., J. Moreno, S. Merino, and G. Tomas. 2004. A tradeoff between two resources-demanding functions: post-nuptial molt and immunity during reproduction in male pied flycatchers. *Journal of Animal Ecology* **73**:441–447.
- Sanz, J. J., J. M. Tinbergen, J. Moreno, M. Orell, and S. Verhulst. 2000. Latitudinal variation in parental energy expenditure during brood rearing in the great tit. *Oecologia* **122**:149–154.
- SAS Institute. 2002. *SAS PROC GLM*. Version 8.02. SAS Institute, Cary, North Carolina, USA.
- Sears, M. W., and M. J. Angilletta, Jr. 2003. Life-history variation in the sagebrush lizard: phenotypic plasticity or local adaptation? *Ecology* **84**:1624–1634.
- Skutch, A. E. 1949. Do tropical birds rear as many young as they can flourish? *Ibis* **91**:430–455.
- Smits, J. E., and T. D. Williams. 1999. Validation of ecotoxicology techniques in passerine chicks exposed to oil sands tailings water. *Ecotoxicology and Environmental Safety* **44**:105–112.
- Starck, J. M., and R. E. Ricklefs. 1998. Variation, constraint, and phylogeny. Comparative analysis of growth. Pages 247–265 in J. M. Starck and R. E. Ricklefs, editors. *Avian growth and development. Evolution within the altricial-precocial spectrum*. Oxford Ornithology Series, Oxford University Press, Oxford, UK.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, UK.
- Wikelski, M., L. Spinney, W. Schelsky, A. Scheurlein, and E. Gwinner. 2003. Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. *Proceedings of the Royal Society of London B* **270**:2383–2388.
- Winkler, D. W., P. H. Wrege, P. E. Allen, T. L. Kast, P. Senesac, M. F. Wasson, P. E. Llambias, V. Ferretti, and P. J. Sullivan. 2004. Breeding dispersal and philopatry in the Tree Swallow. *Condor* **106**:768–776.
- Young, B. E. 1996. An experimental analysis of small clutch size in tropical House Wrens. *Ecology* **77**:472–488.