VOL. 193, NO. 5 THE AMERICAN NATURALIST MAY 2019

Higher Nest Predation Favors Rapid Fledging at the Cost of Plumage Quality in Nestling Birds

Lea M. Callan,[1] Frank A. La Sorte,[2] Thomas E. Martin,[3] and Vanya G. Rohwer[1,*]

1. Cornell University Museum of Vertebrates, Ithaca, New York 14850; 2. Cornell Lab of Ornithology, Ithaca, New York 14850; 3. US Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana 59812

Submitted September 29, 2018; Accepted December 21, 2018; Electronically published March 27, 2019

Online enhancements: appendix. *Dryad data:* https://dx.doi.org/10.5061/dryad.p6m33p3.

ABSTRACT: High predation risk can favor rapid offspring development at the expense of offspring quality. Impacts of rapid development on phenotypic quality should be most readily expressed in traits that minimize fitness costs. We hypothesize that ephemeral traits that are replaced or repaired after a short period of life might express trade-offs in quality as a result of rapid development more strongly than traits used throughout life. We explored this idea for plumage quality in nestling body feathers, an ephemeral trait. We found a strong trade-off whereby nestlings that spend less time in the nest produced lower-quality plumage with less dense barbs relative to adults across 123 temperate and tropical species. For a subset of these species ($n = 67$), we found that variation in the risk of nest predation explained additional variation in plumage quality beyond development time. Ultimately, the fitness costs of a poor-quality ephemeral trait, such as nestling body feathers, may be outweighed by the fitness benefits of shorter development times that reduce predation risk. At the same time, reduced resource allocation to traits with small fitness costs, such as ephemeral traits, may ameliorate resource constraints from rapid development on traits with larger fitness impacts.

Keywords: development time, nestling, plumage quality, predation, time in the nest, trade-off.

Introduction

Life-history theory predicts that rapid growth and development creates resource allocation trade-offs that reduce phenotypic quality and impact adult survival across taxa (McCay 1933; Arendt 1997; Olsson and Shine 2002; Roff 2002; Metcalfe and Monaghan 2003). Surprisingly, predicted trade-offs between development rate and annual survival probability of adult birds were not found when examined across 90 songbird species with extensive variation in development rates (Martin et al. 2015). In other words, species that evolved faster development rates did not experience lower adult survival rates on average in contrast to observations within species (see Metcalfe and Monaghan 2003). These results raise the question of why evolved differences in development rates across species may not yield the adult survival costs predicted by life-history theory and observed within species.

Adult survival costs of rapid development may be ameliorated in part through differential resource allocation among traits as a function of their relative fitness impacts. We hypothesize that resource constraints during development may be imposed most strongly on traits that can be repaired or replaced over a short time interval and thus have small impacts on fitness compared with resource constraints on traits with large fitness consequences. For example, increased predation risk is associated with faster growth and shorter development times among taxa (e.g., Benard 2004; Relyea 2007). Similarly, nest predation is strongly related to growth rates and the time that nestlings spend in the nest (Bosque and Bosque 1995; Martin 1995, 2014; Remeš and Martin 2002). We suggest that the traits that are compromised to allow this faster growth and shorter development time should be those with relatively small fitness costs.

We explore this idea using body feathers that young birds grow in the nest. In many species, these feathers are replaced shortly after leaving the nest (Rohwer et al. 2005; Butler et al. 2008), and variation across species in the texture of body feathers is remarkable (fig. 1). Juveniles of some species have body feathers that are downier and softer, making them easily distinguishable from adults, while juveniles of other species have feathers so similar in texture to adults that distinguishing between age classes is difficult (Dwight 1900; Rohwer and Manning 1990; Jenni and Winkler 1994). For species that quickly replace loosely textured nest-grown plumage, their new feathers are much more adultlike (Dwight 1900; Jenni and Winkler 1994; Pyle 1997), demonstrating that these feather morphologies are relatively independent across life stages. Yet the selection pressures driving variation in nestling feather structure among species remain poorly understood (Butler et al. 2008; Moreno and Soler 2011; Minias et al. 2015).

---

* Corresponding author; email: vgr7@cornell.edu.

ORCIDs: Callan, https://orcid.org/0000-0001-5241-0712; Martin, https://orcid.org/0000-0002-4028-4867; Rohwer, https://orcid.org/0000-0002-2505-3761.

Am. Nat. 2019. Vol. 193, pp. 717–724. © 2019 by The University of Chicago. 0003-0147/2019/19305-58769$15.00. All rights reserved.
DOI: 10.1086/702856

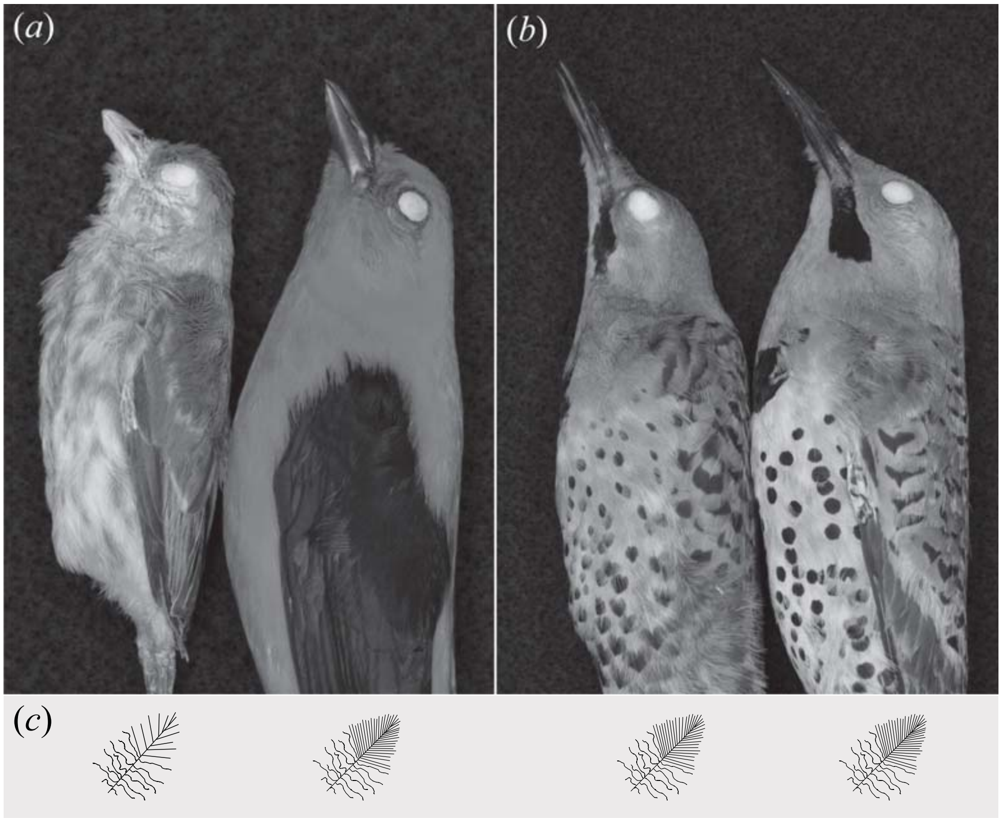

Figure 1: Photos of scarlet tanagers (*Piranga olivacea*; *a*) and northern flickers (*Colaptes auratus*; *b*). Recently fledged young of each species are on the left, and adults are on the right. Below each individual is a drawing of a body feather illustrating the variation in feather structure that we measured (*c*). Scarlet tanagers are cup-nesting species with nestlings that develop rapidly and grow loosely textured body feathers compared to adults. By contrast, northern flickers are cavity-nesting woodpeckers with safe, low-predation nest sites; nestling flickers develop slowly and produce body feathers similar in texture to those of adults. A color version of this figure is available online.

We hypothesize that birds that grow and develop rapidly as a result of selection from high nest predation risk reduce allocation of resources to their body feathers (Fogden 1972; Dawson et al. 2000; Butler et al. 2008; Kiat and Izahaki 2016). While poor-quality nest-grown feathers may reduce effectiveness of thermoregulation, the fitness costs of this short-term effect are likely small. Ultimately, the fitness costs of a poor-quality ephemeral trait, such as body feathers, are outweighed by the fitness benefits of facilitating shorter development times that reduce nest predation risk. At the same time, reduced resource allocation to traits with small fitness costs may ameliorate resource constraints from rapid development on traits with larger fitness impacts. Here we examine whether resource allocation costs of rapid development driven by high rates of nest predation might be strongly expressed in ephemeral, nest-grown body feathers.

Additional factors may influence the quality of nestling plumage. Enclosed-nest morphologies can provide thermal benefits compared with open nests and thereby increase net energy resources for feather development (Dunn 1975; Martin et al. 2017). Larger body size is associated with longer time developing in the nest (Lack 1968), which might allow for development of higher-quality juvenal body feathers. Higher-quality feathers might be necessary if young birds do not replace their nest-grown plumage before migrating (Rohwer et al. 2005; Kiat and Izhaki 2016). Finally, tropical species often have high adult survival and slower peak rates of growth that are thought to be associated with higher phenotypic quality than temperate species (Ricklefs and Wikelski 2002; Martin 2015; Martin et al. 2015, 2017). Consequently, we might expect tropical species to have higher-quality feathers associated with higher adult survival and slower peak growth rates.

Here we explore variation in feather structure of nestling plumage in relation to factors that might favor different feather qualities across 123 altricial bird species. We first examine five variables that could influence nestling plumage structure (temperature, latitude, time in the nest, body size, and timing of feather replacement relative to migration). Second, we examine whether nest predation rates explain variation in plumage quality in a subset of 67 species for which we were able to obtain nest predation data.

Material and Methods

Measuring Feather Structure

We measured feather structure as the number of barbs per centimeter of rachis, following methods developed by Butler et al. (2008). We examined museum specimens under a ×10 dissecting microscope, isolated a feather from the upper flank region of the chest, and counted the number of pennaceous barbs along the rachis of the isolated feather; care was taken to ensure that focal feathers originated from the same region of the body across species. For most species in our analyses, we measured feather structure in two recently fledged nestlings (i.e., those that just left the nest) and two adults, with equal sampling of males and females, but sample sizes and sexes varied for some species depending on the availability of specimens in museum collections (for sample sizes for each species, see the appendix, available online). Importantly, variation in the age of fledglings does not influence characteristics of feather quality because the pennaceous sections of feathers that we measured were already fully grown. Our sample sizes were limited most strongly by the availability of recently fledged nestlings in collections, as fledglings of many species are absent in collections. We measured feather structure in fledglings that had all wing or tail feathers still growing. This criteria helped ensure that we were measuring the first plumage of body feathers that were grown while the bird was in the nest and not feathers replaced by the juvenal molt, because feathers replaced after leaving the nest should be independent of the trade-offs associated with growth rate in the nest. The number of barbs per centimeter of rachis varies considerably across adults of different species. To control for differences in adult plumage structure among species, we divided nestling feather structure by adult feather structure, allowing for across-species comparisons. Thus, our measure of nestling feather structure for each species is the proportion of adult barbs found on nestlings, where one represents nestling barb counts that are identical to adults and 0.5 represents nestling barb counts that are half of that observed in adults.

Data Assembly

We assembled data from the literature or existing databases on five variables that could influence the quality of nestling plumage: nestling duration (the number of days from hatching to leaving the nests), mean ambient temperature during the nestling period, mean breeding latitude, body mass, and whether young migrate before replacing their nest-grown plumage. Sources for data included the Birds of North America database (Rodewald 2015), the *Handbook of Birds of the World* (del Hoyo et al. 1992–2013), Dunning (2007), New et al. (2002), Pyle (1997), BirdLife International and NatureServe (2015), and taxon-specific references summarized in the Dryad Digital Repository (https://dx.doi.org/10.5061/dryad.p6m33p3; Callan et al. 2019). For species where we found multiple measures of the nestling duration, we used the mean of these measures unless locations of specimens matched locations of published data; in these cases, we used data that matched specimen localities.

We acquired data for average temperature during the breeding season from the CRU CL data set, version 2.0 (New et al. 2002). Data for breeding range maps came from BirdLife International and NatureServe (2015). Temperature across the breeding range was gridded at a 10-arc-minute spatial resolution, and values were averaged across days by month for the combined period of 1961–1990. We averaged mean monthly temperatures across a species' breeding range during the months of peak breeding activity. For North American birds, we assessed peak breeding season using Birds of North America (Rodewald 2015), and for most other species we used the *Handbook of Birds of the World* (del Hoyo et al. 1992–2013) or taxon-specific references.

We acquired data for breeding latitude using range maps from BirdLife International and NatureServe (2015). Breeding latitude is the centroid value of the breeding range for each species. Data for breeding latitude were bimodal, with peaks near 0° and 42°. We could not normalize these data, so we grouped them into two categories: tropical and temperate. We used absolute values of latitude and grouped species with centroid values between 0 and 23.4 as tropical and species with centroid values >23.4 as temperate.

We examined how the timing of molt relative to migration might influence the quality of nest-grown body feathers by grouping species into three categories: (i) those that replace their nest-grown body feathers prior to migration, (ii) those that do not, and (iii) residents that do not migrate. We used Pyle (1997) to categorize molt scheduling of migratory species and excluded species that lacked this data from analyses.

Data for risk of predation during the nestling period were amassed from long-term studies of breeding biology by T. E. Martin and colleagues (Martin 1995, 2015; Martin et al. 2015, 2017). We used daily predation rates for the nestling period because this provides less biased measures of nestling predation compared to predation rates calculated over the entire nesting period. We calculated nestling predation rates using the logistic exposure method (Shaffer 2004), which requires no assumptions about when nest loss occurs during a breeding attempt.

Statistical Analyses

We conducted two tests. First, we examined which variables were associated with nestling plumage structure. Plumage structure (the proportion of nestling to adult barbs) was the dependent variable, with duration of the nestling period, body mass, and average temperature during the breeding season included as continuous covariates, and latitude and molt schedule were included as factors with two and three levels, respectively. We included one interaction term between time in the nest and latitude to examine whether temperate and tropical species differed in any relationships between plumage quality and development time. Second, we directly examined whether nest predation was associated with nestling plumage quality. For this test, plumage structure was our dependent variable and daily rates of nestling predation and time in the nest were our covariates, with latitude as a factor.

For all analyses, we used phylogenetically controlled linear models from the package phylolm (Ho and Ane 2014) in R (R Core Team 2016). We controlled for phylogenetic uncertainties by extracting 2,000 trees from BirdTree.org (Jetz et al. 2012) and running each analysis 2,000 times, each with a different tree (1,000 with the Hackett backbone, 1,000 with the Erikson backbone), following Rubolini et al. (2015). Models were weighted using corrected Akaike information criterion values that account for model fit for a particular phylogeny, giving less emphasis to models that fit data poorly. We used the MuMIn package (Bartoń 2014) in R to extract model average parameter estimates weighted by model fit and present the number of models that contained each predictor variable. For all analyses, we used Ornstein-Uhlenbock (OU) models of trait evolution (Butler and King 2004). OU models differ from Brownian motion (BM) models by two terms, α (the strength of selection) and θ (the optimum trait value), and allow traits to have multiple optimum values, a prediction consistent with different lineages that are exposed to different selective pressures favoring different trait values. When α in OU models approaches zero (i.e., selection is absent), these models become functionally equivalent to BM models.

Prior to running models, we $\log_{10}$ transformed body mass to better approximate a normal distribution. We checked the assumptions of our models by plotting model residuals against predictor variables and checking that the distribution of model residuals did not deviate from normality using Shapiro-Wilk tests, following Zuur et al. (2009). We checked for similarity among residual variances for categorical predictor variables "latitude" and "molt schedule" using Bartlett's test.

Results

Factors Influencing Feather Structure

Two variables were associated with the structure of body feathers of young sampled within a couple days of fledging (leaving the nest): time spent in the nest and latitude (fig. 2; table 1). Species that spend more time in the nest grew more adultlike feathers compared to species that spend less time in the nest ($P < .001$). Recently fledged young of tropical species grew on average less adultlike feathers compared to temperate species controlling for time in the nest ($P = .015$; fig. 2). Body size, ambient temperature, and the scheduling of molt relative to migration did not explain variation in the quality of nestling plumage (table 1). Slopes of plumage quality versus time in the nests did not differ between temperate and tropical species.

Linking Plumage Structure to Nest Predation

Because species with a high risk of nestling predation have shorter nestling periods compared to species with a low risk of nestling predation (Remeš and Martin 2002; Martin et al. 2011; Martin 2015) and because species with shorter nestling periods produce less adultlike plumage (fig. 2), we examined possible links between nest predation and plumage quality. Species with high rates of nestling predation produced less adultlike juvenal plumage compared with species with low rates of nestling predation (fig. 3*a*), even after controlling for the significant effects of time in the nest (fig. 3*b*; table 1). Latitude was no longer a significant predic-

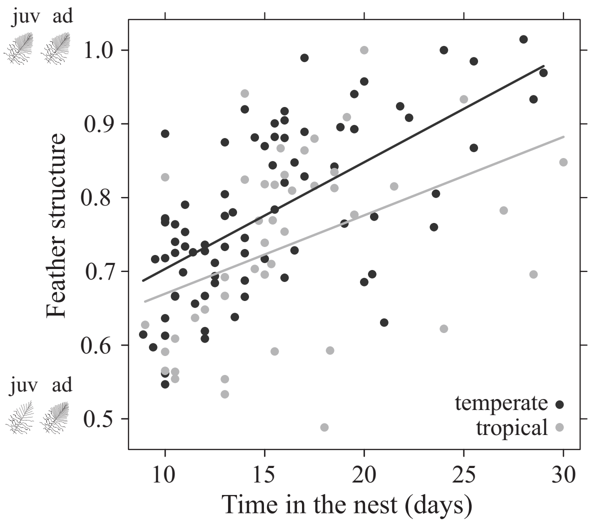

Figure 2: Plumage quality (measured as a ratio of nestling barbs cm^{-1} to adult barbs cm^{-1}) of recently fledged young increases with the amount of time that nestlings spend in the nest for both temperate ($n = 79$) and tropical ($n = 44$) species. Tropical species also grow on average lower-quality plumage relative to temperate species for the same amount of time spent in the nest; there is no significant difference in the slopes of lines between these groups. A color version of this figure is available online.

Table 1: Parameter estimates of predictor variables for plumage structure without inclusion of nest predation (pt. A) and with inclusion of nest predation for the subset of species with nest predation data (pt. B)

Variable	Estimate	SE	t	P	α	Count
A. Factors influencing plumage structure:						
Intercept	.623	.039	16.197	<.001	.229	2,000
Time in the nest	.011	.002	4.859	<.001	.229	2,000
Latitude (tropical)	−.053	.019	−2.766	.007	.240	1,974
Breeding temperature	−.004	.002	−1.974	.063	.101	22
B. Linking plumage structure to nest predation:						
Intercept	.652	.063	10.393	<.001	.593	2,000
Nestling predation rate	−2.095	.758	−2.763	.007	.593	2,000
Time in the nest	.011	.003	3.433	.001	.593	2,000

Note: We show variables that were included in at least 20 (1%) of 2,000 phylogenetically controlled regressions for both analyses. The complete model with all variables tested for part A is plumage structure ~ time in nest + latitude + temperature + body mass + migration in juvenal plumage + latitude × time in nest, and the complete model for part B is plumage structure ~ predation + latitude + time in nest + predation × latitude, but parameter estimates are presented only for variables that were included in a minimum of 1% of models. Parameter estimates are weighted by the number of models in which they were included ("Count") and by each model's corrected Akaike information criterion (AICc). The α value is the averaged phylogenetic correlation parameter weighted across models by AICc. All variables absent from these tables were not included in at least 1% of models.

tor of plumage structure once nest predation was taken into account (table 1).

Discussion

Faster development is widely thought to require resource allocation trade-offs that impact phenotypic quality with long-term consequences for adult survival (McCay 1933; Stearns 1992; Roff 2002; Metcalfe and Monaghan 2003), but the vast majority of evidence has been based on proximate variation within species. Over evolutionary time, selection should instead favor allocational trade-offs with the lowest fitness costs. Adult survival has a major impact on fitness (Clutton-Brock 1988), such that we might expect resources to be preferentially allocated to traits affecting long-term survival over ephemeral traits with potentially smaller fitness costs. The fact that evolution of faster growth rates was not associated with reduced adult survival across a large array of songbird species

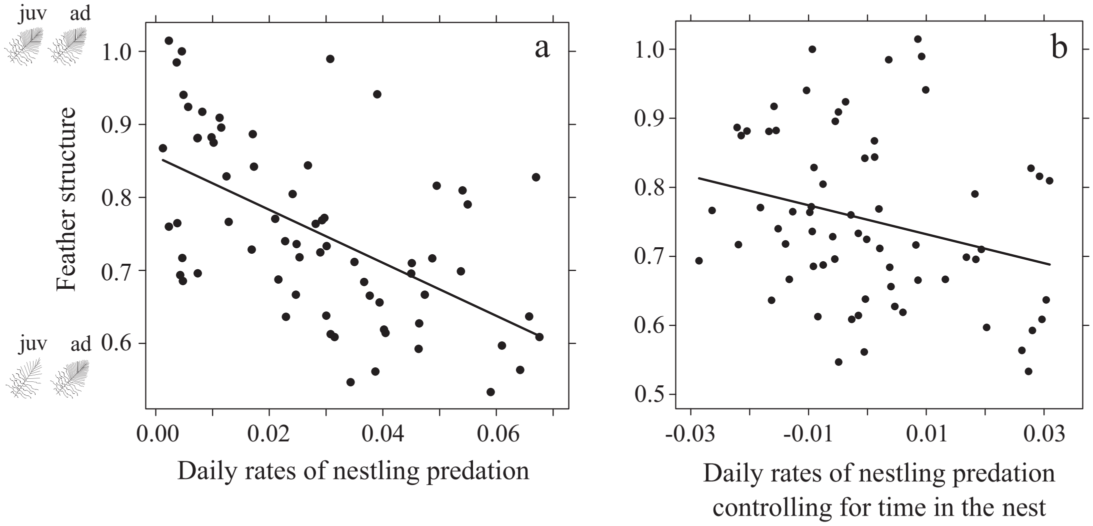

Figure 3: Indirect and direct effects of nest predation risk on plumage quality using a subset of species ($n = 67$), for which we had data on nestling predation risk. *a*, Plot shows indirect effects of nest predation on nestling feather structure because predation risk is strongly correlated with time spent in the nest. *b*, Direct effects of nest predation on plumage structure are evident even after controlling for the effects of time spent in the nest. Species with a high risk of nest predation spend less time in the nest and grow more loosely textured, less adultlike feathers. Feather structure along the *Y*-axis is the ratio of nestling barb counts per centimeter of rachis to adult barb counts per centimeter of rachis; thus, values closer to one indicate nestling feather morphologies that resemble those of adults.

(Martin et al. 2015) supports the first part of this idea. Our results here showing that resource allocation costs to plumage quality of offspring were associated with development rates across species (fig. 2) support the second part of this idea. Nestling body feathers are transitory and, in many species, replaced soon after fledging (Rohwer et al. 2005), such that fitness costs may be relatively small. Indeed, replacement of nest-grown body feathers of golden-winged warblers (*Vermivora chrysoptera*) began only 11 days after leaving the nest and finished on average 15 days later (~26 days after leaving the nest; D. J. McNeil, C. J. Fiss, V. G. Rohwer, A. A. Dhondt, A. D. Rodewald, K. V. Rosenberg, R. E. Bennett, and J. L. Larkin, unpublished data). Reduced feather quality may require greater energy expenditure for thermoregulation, but impacts on juvenile survival over such short time intervals are likely to be small. Thus, resource allocation trade-offs associated with rapid development may be expressed through reduced resource allocation to ephemeral traits with small fitness costs compared to traits that have larger fitness costs, such as those that impact adult survival.

Nest predation can be an important selective pressure shaping resource allocation during development. Nest predation favors shorter development time (Bosque and Bosque 1995; Remeš and Martin 2002; Martin et al. 2011; Martin 2015), which is associated with reduced plumage quality (fig. 2). However, higher nest predation risk also yields poorer feather structure independent of time spent in the nest (table 1; fig. 3*b*), suggesting direct selection on resource allocation to this trait. Both comparative (Cheng and Martin 2012; Martin 2015) and experimental (Coslovsky and Rickner 2011; LaManna and Martin 2016) studies show that as nest predation risk increases, nestlings preferentially develop traits such as wing feathers that improve escape from predators and increase juvenile survival (Dial et al. 2006; Martin 2014; Martin et al. 2018). Ultimately, costs of rapid development may be minimized for traits with fitness impacts on juvenile and adult survival and instead be shifted to ephemeral traits with presumably lower fitness costs.

Fledglings of tropical species had on average poorer-quality plumage compared to temperate species for similar developmental periods in the nest (fig. 2), and this difference was not explained by nest predation (table 1, pt. B). At least two explanations may underlie these differences in plumage quality between temperate and tropical species. First, more loosely textured plumage of tropical nestlings may be less costly because they are in warmer environments and thermoregulation is less important. Second, differences between temperate and tropical species may reflect different resource allocation strategies during development. Tropical species have slower peak growth and higher adult survival on average compared with temperate relatives (reviewed in Martin 2015). Life-history theory predicts that tropical species with slower peak growth rates and higher adult survival should produce offspring with higher phenotypic quality (Roff 2002; Stearns 1992). Consequently, we might expect a result opposite to ours where plumage quality is higher rather than lower in tropical birds. However, adult survival has the largest impact on fitness in long-lived species (Sæther and Bakke 2000). Thus, long-lived tropical species may preferentially reduce resource allocation to ephemeral traits with relatively small fitness costs, such as nestling body feathers, to allow prioritization of resources to other traits that facilitate survival and have larger fitness consequences.

Costs of rapid development to adult survival may be particularly minimized when the development and expression of ephemeral traits are relatively independent of the traits that replace them (Moran 1994; Aguirre et al. 2014). The correlation between nestling and adult body feather morphology is weak, suggesting that age class does not firmly constrain feather morphology (see the appendix). Similarly, *Hyla versicolor* tadpoles exposed to higher predation during development produced morphologies better suited for early-life predator avoidance, but these morphological changes had no carryover effects on adult morphology and survival (Relyea and Hoverman 2003). Also, oxidative stress in rodents was highest in tissues that turn over fastest (serum), and these same tissues had the lowest measures of agents that protect tissues from oxidative stress compared to tissues that turn over at slower rates (Xu et al. 2014). Costs of oxidative stress in tissues that are rapidly replaced are likely relatively small compared with longer-term tissues that may accumulate damage from oxidative stress and thereby explain why fewer resources were allocated to protective responses in the more ephemeral tissues. While a growing body of work recognizes stronger links between developmental stages than previously thought (Podolsky and Moran 2006; Marshal and Morgan 2011), few studies have examined which traits contribute most strongly to fitness costs of juvenile and adult survival and which traits express the most pronounced trade-offs in quality in response to rapid development or transitions between life stages. If our predictions hold, then reduced resource allocation should be most strongly expressed in ephemeral traits that have minimal carryover costs to adult survival.

Acknowledgments

We thank the following museums that provided specimens for this work: the Cornell University Museum of Vertebrates, the Louisiana State Museum of Natural Sciences, and the American Museum of Natural History. Special thanks to Steve Cardiff, Paul Sweet, and Lydia Garetano for their help with visits to collections and specimen loans and to Eliot Miller for initial help with analyses. The Lovette Lab, Sievert Rohwer, Yosef Kiat, Alice Winn, Christina Riehl, and one anonymous reviewer provided helpful comments on earlier drafts of the article. L.M.C. received support from the Cornell University Alumni Association, and the contributions of T.E.M. were supported by grants from the National Science Foundation (DEB-1241041, IOS-1349178, DEB-1651283, IOS-1656120). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government. All data for this article have been deposited in the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.p6m33p3 (Callan et al. 2019).

Literature Cited

Aguirre, J. D., M. W. Blows, and D. J. Marshall. 2014. The genetic covariance between life cycle stages separated by metamorphosis. Proceedings of the Royal Society B 281:20141091.

Arendt, J. D. 1997. Adaptive intrinsic growth rates: an integration across taxa. Quarterly Review of Biology 72:149–177.

Bartoń, K. 2014. MuMIn: multi-model inference. R package version 1.10.0. http://CRAN.R-project.org/package = MuMIn.

Benard, M. F. 2004. Predator-induced phenotypic plasticity in organisms with complex life histories. Annual Review of Ecology, Evolution, and Systematics 35:651–673.

BirdLife International and NatureServe. 2015. Bird species distribution maps of the world. Version 5.0.

Bosque, C., and M. T. Bosque. 1995. Nest predation as a selective factor in the evolution of developmental rates in altricial birds. American Naturalist 145:234–260.

Butler, L. K., S. Rohwer, and M. G. Speidel. 2008. Quantifying structural variation in contour feathers to address functional variation and life-history trade-offs. Journal of Avian Biology 39:629–639.

Butler, M. A., and A. A. King. 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. American Naturalist 164:683–695.

Callan, L. M., F. A. La Sorte, T. E. Martin, and V. G. Rohwer. 2019. Data from: Higher nest predation favors rapid fledging at the cost of plumage quality in nestling birds. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.p6m33p3.

Cheng, Y.-R., and T. E. Martin. 2012. Nest predation risk and growth strategies of passerine species: grow fast or develop traits to escape risk? American Naturalist 180:285–295.

Clutton-Brock, T. H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago.

Coslovsky, M., and H. Rickner. 2011. Predation risk affects offspring growth via maternal effects. Functional Ecology 25:878–888.

Dawson, A., S. A. Hinsley, P. N. Ferns, R. H. C. Bonser, and L. Eccleston. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proceedings of the Royal Society B 267:2093–2098.

del Hoyo, J., A. Elliott, J. Sargatal, and D. A. Christie, eds. 1992–2013. Handbook of the birds of the world. Lynx, Barcelona.

Dial, K. P., R. J. Randall, and T. R. Dial. 2006. What use is half a wing in the ecology and evolution of birds? BioScience 56:437–445.

Dunn, E. H. 1975. The timing of endothermy in the development of altricial birds. Condor 77:288–293.

Dunning, J. B., Jr. 2007. CRC handbook of avian body masses. CRC, London.

Dwight, J., Jr. 1900. Sequence of plumages and moults of passerines birds in New York. Annals of the New York Academy of Sciences 13:73–360.

Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114:307–343.

Ho, L. S. T., and C. Ane. 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. Systematic Biology 63:397–408.

Jenni, L., and R. Winkler. 1994. Moult and ageing of European passerines. Academic Press, London.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. Nature 491:444–448.

Kiat, Y., and I. Izhaki. 2016. Why renew fresh feathers? advantages and conditions for the evolution of complete post-juvenile moult. Journal of Avian Biology 47:47–56.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

LaManna, J. A., and T. E. Martin. 2016. Costs of fear: behavioural and life-history responses to risk and their demographic consequences vary across species. Ecology Letters 19:403–413.

Marshall, D. J., and S. G. Morgan. 2011. Ecological and evolutionary consequences of linked life-history stages in the sea. Current Biology 21:R718–R725.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101–127.

———. 2014. A conceptual framework for clutch-size evolution in songbirds. American Naturalist 183:313–324.

———. 2015. Age-related mortality explains life history strategies of tropical and temperate songbirds. Science 349:966–970.

Martin, T. E., A. J. Boyce, K. Fierro-Calderón, A. E. Mitchell, C. E. Armstad, J. C. Mouton, and E. E. Bin Soudi. 2017. Do enclosed nests provide greater thermal than nest predation benefits compared with open nests across latitudes? Functional Ecology 31:1231–1240.

Martin, T. E., P. Lloyd, C. Bosque, D. C. Barton, A. L. Biancucci, Y. R. Cheng, and R. Ton. 2011. Growth rate variation among passerine species in tropical and temperate sites: an antagonistic interaction between parental food provisioning and nest predation risk. Evolution 65:1607–1622.

Martin, T. E., J. C. Oteyza, A. E. Mitchell, A. L. Potticary, and P. Lloyd. 2015. Postnatal growth rates covary weakly with embryonic development rates and do not explain adult mortality probability among songbirds on four continents. American Naturalist 185:380–389.

Martin, T. E., B. Tobalske, M. M. Riordan, S. Case, and K. P. Dial. 2018. Age and performance at fledging is a cause and consequence of juvenile mortality. Science Advances 4:eaar1988.

McCay, C. M. 1933. Is longevity compatible with optimum growth? Science 77:410–411.

Metcalfe, N. B., and P. Monaghan. 2003. Growth versus lifespan: perspectives from evolutionary ecology. Experimental Gerontology 38:935–940.

Minias, P., R. Włodarczyk, A. Surmacki, and T. Iciek. 2015. Silver spoon effects on plumage quality in a passerine bird. Royal Society Open Science 2:140459.

Moran, N. A. 1994. Adaptation and constraint in the complex life cycles of animals. Annual Review of Ecology and Systematics 25:573–600.

Moreno, J., and J. J. Soler. 2011. Sources of distinctness of juvenile plumage in western Palearctic passerines. Biological Journal of the Linnean Society 102:440–454.

New, M., D. Lister, M. Hulme, and I. Makin. 2002. A high-resolution data set of surface climate over global land areas. Climate Research 21:1–25.

Olsson, M., and R. Shine. 2002. Growth to death in lizards. Evolution 56:1867–1870.

Podolsky, R. D., and A. L. Moran. Integrating function across marine life cycles. Integrative and Comparative Biology 46:577–586.

Pyle, P. 1997. Identification guide to North American birds. I. Columbidae to Ploceidae. Slate Creek, Bolinas, CA.

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Relyea, R. A. 2007. Getting out alive: how predators affect the decision to metamorphose. Oecologia 152:389–400.

Relyea, R. A., and J. T. Hoverman. 2003. The impact of larval predators and competitors on the morphology and fitness of juvenile treefrogs. Oecologia 134:596–604.

Remeš, V., and T. E. Martin. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. Evolution 56:2505–2518.

Ricklefs, R. E., and M. Wikelski. 2002 .The physiology/life-history nexus. Trends in Ecology and Evolution 17:462–468.

Rodewald, P., ed. 2015. Birds of North America. Cornell Laboratory of Ornithology, Ithaca, NY. https://birdsna.org.

Roff, D. A. 2002. Life-history evolution. Sinauer, Sunderland, MA.

Rohwer, S., L. K. Butler, and D. Froehlich. 2005. Ecology and demography of east-west differences in molt scheduling of Neotropical migrant passerines. Pages 87–105 *in* R. Greenberg and P. R. Marra, eds. Birds of two worlds. John Hopkins University Press, Baltimore.

Rohwer, S., and J. Manning. 1990. Differences in timing and number of molts for Baltimore and Bullock's orioles: implications to hybrid fitness and theories of delayed plumage maturation. Condor 92:125–140.

Rubolini, D., A. Liker, L. Z. Garamszegi, A. P. Møller, and N. Saino. 2015. Using the BirdTree.org website to obtain robust phylogenies for avian comparative studies: a primer. Current Zoology 61:959–965.

Sæther, B. E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Xu, Y.-C., D.-B. Yang, J. R. Speakman, and D.-H. Wang. 2014. Oxidative stress in response to natural and experimentally elevated reproductive effort is tissue dependent. Functional Ecology 28:402–410.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

References Cited Only in the Online Appendixes

Broggi, J., A. Gamero, E. Hohtola, M. Orell, and J.-Å. Nilsson. 2011. Interpopulation variation in contour feather structure is environmentally determined in great tits. PLoS ONE 6:e24942.

Dickerman, R. W. 1981. Geographic variation in the juvenal plumage of the lesser nighthawk (*Chordeiles acutipennis*). Auk 98:619–621.

Eisenmann, E. 1965. The use of the terms "juvenal" and "juvenile." Auk 82:105.

Howell, S. N. G., C. Corben, P. Pyle, and D. I. Rogers. 2003. The first basic problem: a review of molt and plumage homologies. Condor 105:635–653.

Koskenpato, K., K. Ahola, T. Karstinen, and P. Karell. 2016. Is the denser contour feather structure in pale grey than in pheomelanic brown tawny owls *Strix aluco* an adaptation to cold environments? Journal of Avian Biology 47:1–6.

Lei, F.-M., Y.-H. Qu, Y.-L. Gan, A. Gebauer, and M. Kaiser. 2002. The feather microstructure of passerine sparrows in China. Journal für Ornithologie 143:205–213.

Ligon, R. A., and G. E. Hill. 2012. Is the juvenal plumage of altricial songbirds an honest signal of age? evidence from a comparative study of thrushes (Passeriformes: Turdidae). Journal of Zoological Systematics and Evolutionary Research 51:64–71.

Lucas, A. M., and P. R. Stettenheim. 1972. Avian anatomy and integument. II. US Department of Agriculture Handbook no. 362. Washington, DC.

Pennycuick, C. J., H. H. Obrecht, and M. R. Fuller. 1988. Empirical estimates of body drag of large waterfowl and raptors. Journal of Experimental Biology 135:253–264.

Rohwer, V. G., F. Bonier, and P. R. Martin. 2015. Conflict between biotic and climatic selective pressures acting on an extended phenotype in a subarctic, but not temperate, environment. Proceedings of the Royal Society B 282:20151585.

Tucker, V. A. 1990. Body drag, feather drag and interference drag of the mounting strut in a peregrine falcon, *Falco peregrinus*. Journal of Experimental Biology 149:449–468.

Associate Editor: Christina Riehl
Editor: Alice A. Winn