Morphological plasticity reduces the effect of poor developmental conditions on fledging age in mourning doves

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Developmental plasticity can be integral in adapting organisms to the environment experienced during growth. Adaptive plastic responses may be especially important in prioritizing development in response to stress during ontogeny. To evaluate this, I examined how developmental conditions for mourning doves related to early growth and how this affected fledging age, an important life-history transition for birds. The life history of mourning doves is consistent with strong selective pressure to minimize fledging age. Therefore, I predicted that in the face of nutritional stress associated with experimental brood-size increases, young would prioritize growth to structures that promote early fledging to reduce the effect of slowed overall growth on fledging age. Increasing brood size slowed overall structural growth of nestlings and affected the relative allocation of growth among different body parts. Total wing area was the best predictor of fledging age and individuals from larger broods had larger wings relative to overall body size. Although nestlings from larger broods fledged at later ages owing to slower overall growth, prioritization of wing growth reduced this effect by an estimated 1.6 days relative to the delay if plasticity among body parts had not occurred. This was an 11 per cent reduction in the predicted developmental time it took to reach this important life-history transition. Results demonstrate that preferential allocation to wing growth can affect the timing of this life-history transition and that morphological plasticity during development can have adaptive near-term effects during avian development.

Keywords: fledging; flight; morphology; phenotypic plasticity; stress

1. INTRODUCTION

Plasticity during development is important in both ecological and evolutionary processes (West-Eberhard 1989; Schew & Ricklefs 1998; West-Eberhard 2003; Badyaev 2005; Gil *et al.* 2008). Developmental plasticity can have adaptive fitness consequences realized at different stages of an individual's life history, including long-term benefits for the adult phenotype (West-Eberhard 2003), immediate benefits during development (Altwegg 2002; Gil *et al.* 2008) and mediating effects on transitions between life-history stages (Newman 1992; Badyaev *et al.* 2006; Gotthard 2008). Environmental signals should be most accurate for predicting near-term conditions (Moran 1992) and therefore plasticity may be especially important in the adaptation of organisms to their growth environment and for transitions during development.

Morphological plasticity in response to poor conditions experienced during development has the potential to mitigate the negative effects of stress (Schew & Ricklefs 1998). Recent evidence suggests that adaptive plasticity in beak morphology in response to sibling competition occurs during development of nestling spotted starlings (*Sturnus unicolor*; Gil *et al.* 2008). Just as increased ability to procure food through prioritization of beak growth may be an adaptive response to poor developmental conditions, speeding up the ability to

leave the nest environment may also be beneficial in response to stressor in the nest environment (Raihani & Ridley 2007). Leaving the nest environment, i.e. fledging, is often associated with the attainment of flight ability and marks an important life-history transition for birds that can be directly affected by morphology. Changes in the trajectory of wing growth relative to other body structures may affect timing of fledging, making this an interesting system to examine morphological plasticity during avian development.

It is useful to divide plasticity in structural growth rates in response to resource limitations during development into two types of response: slowed overall growth and differential allocation among body parts (Gotthard & Nylin 1995; Schew & Ricklefs 1998). Slowed overall growth of young can be expected when constraints in resources available for development are dictated by reduced provisioning from parents. Thus, poor conditions can impose a developmental response of slowed overall growth (Smith-Gill 1983; Gotthard & Nylin 1995) with negative implication to organismal development. Differential allocation among body parts may limit negative effects of developmental stress by prioritizing growth of structures most closely tied to immediate fitness. In the case of flight attainment, if birds allocate relatively more resources to wing growth than other structures when conditions are poor, this may reduce the delay in fledging age that results from slower growth rates. This type of response is likely to be adaptive when there is strong selection to leave the nest early and results in a match between

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reaction norm and the developmental trajectory that maximizes fitness (Gotthard & Nylin 1995).

Results from life-history studies point to a set of traits held by mourning doves (*Zenaidura macroura*) that are associated with strong selective pressure for early fledging. Wide variation occurs in the size as a proportion of adult size in juvenile birds at the time of fledging (Ricklefs 1968), and theoretical and empirical data indicate that selective pressure for early fledging is a key factor determining relative size at fledging. Life-history models predict that fledging age will decrease and growth rate will increase as mortality rates in the nest increase (Roff *et al.* 2005). This is supported by the result that altricial species exposed to higher nest predation rates fledged earlier and at a smaller proportion of their adult size than species with low nest predation rates (Bosque & Bosque 1995; Martin 1995; Remeš & Martin 2002; Remeš 2007). This relationship has also been observed within populations where young exposed to greater predation rates in the nesting environment fledged at earlier ages (Raihani & Ridley 2007).

Mourning dove life histories are characterized by high nest predation rates, rapid early growth, early fledging age and fledging at a small proportion of their adult size (Westmoreland *et al.* 1986). Martin (1995) found that nest success (proportion of nests to fledge at least one young) for 123 species of North American passeriformes and piciformes averaged from 40 to 85 per cent depending on the type of nesting habitat used. The most comprehensive estimate of nest success for mourning doves based on 6950 nests from sites throughout their range estimated that 33 per cent of nests fledged young with a daily mortality rate of 4.2 per cent (Geissler *et al.* 1987). Daily mortality rates immediately after fledging calculated based on data from Grand *et al.* (1984) were much smaller, averaging less than 1 per cent (Westmoreland & Best 1987). Westmoreland *et al.* (1986) found that total nesting cycle length was 22 per cent shorter than average lengths corrected for weight for columbids compared with other open nesting altricial species and that mourning doves were in the lower half of the range for columbids. Finally, Ricklefs (1968) found the ratio of fledging weight to adult weight ranged from 0.60 to 1.84 for 94 species of birds. The ratio is 0.63 for mourning doves (Westmoreland *et al.* 1986). Overall, these traits are consistent with a life history evolved under strong selective pressure to minimize fledging age (Bosque & Bosque 1995; Martin 1995; Remeš & Martin 2002; Roff *et al.* 2005; Remeš 2007).

I manipulated brood sizes to examine the effect of nutritional stress on morphological growth and fledging age of juvenile mourning doves. I predicted that if differential allocation among body parts in response to increased brood size was adaptive, it should reduce the delay in fledging age associated with slowed growth. First, I determined whether plasticity in overall growth rates and differential allocation in growth among body parts occurred in response to differences in brood size. Then, I examined how morphological variation directly related to fledging age. Finally, to test the prediction directly, I examined the relationship between observed patterns of morphological growth and predicted effects on fledging ability to determine the effect of plasticity with respect to brood size on fledging age.

2. MATERIAL AND METHODS

(a) Data collection

I studied growth in mourning dove nestlings from nests found in central Iowa, USA, during the summer of 2007. All nestlings used in this study came from nests found during the incubation period and for which hatching dates were observed. Eggs were candled to determine their age ± 1 day once a nest was found (Hanson & Kossack 1957) and I returned to the nest at the time of hatch to determine hatch dates of nestlings.

Mourning doves have a determinate clutch size, laying two eggs per nest (Blockstein 1989). To systematically affect resource allocation to nestlings, I manipulated brood sizes of nests to create one- and three-nestling broods in addition to naturally occurring two-nestling broods. Previous studies of mourning doves show that increasing or decreasing brood size has significant effects on nestling growth but that these effects are within the range of capabilities for adults to successfully rear (Holcomb & Jaeger 1978; Westmoreland & Best 1987; Blockstein 1989). Adjustments were done opportunistically less than or equal to 1 day after all eggs hatched. Nestlings were moved between nests hatching at the same time, with a single nestling removed from one nest and placed in another to create a one-nestling and three-nestling brood. I moved nestlings so that transplants to three-nestling nests were of intermediate size between the two original nestlings to minimize size asynchrony within a nest. All birds were returned to a nest within 30 min of removal.

To monitor flight ability and growth after fledging, nestlings were removed from nests at 10–11 days of age and were brought into an aviary. Because mourning dove young are fed by parents until they are at least 21 days old (Hitchcock & Mirarchi 1984), birds were hand-fed twice daily in the aviary. Birds were fed a diet consisting of a standard dove seed mixture (Parkview Dove Mix, Des Moines Feed Company; 13% protein and 3.5% fat) and a soft food mixture (Exact Hand Feeding Formula, Kaytee Products, Inc.; 22% protein and 9% fat) at rates that generate typical variation in growth trajectories of mourning doves found in the wild. Beginning at 13 days, feeding rates for birds were assigned with equal probability to one of three levels based on a full-factorial study design crossed with brood size. The ratio of seeds to soft mixture was approximately 5:3 for all levels and feeding rates were 8.5, 11 and 14 g d⁻¹. Feeding rates mimicked variation in conditions likely to occur in the wild and the proportion of individuals in each of the three feeding-rate levels were balanced as far as possible with respect to all brood-size treatment levels. Feeding-rate treatments began late in the study period around the average age of fledging and effects were not a primary interest for this study. Therefore, I incorporated feeding-rate treatments as a fixed-effect blocking factor in all analyses and tested for an interaction between feeding rate and brood size.

I monitored growth of nestlings at regular intervals throughout their ontogeny. Full sets of structural measurements were taken at 9, 11, 13 and 19 days (± 1 day) after hatch. I took 15 structural length measurements using dial callipers and a wing rule. I measured body (base of skull to base of tail feathers), flat wing chord, sixth primary and sixth secondary to ± 0.5 mm, and bill length, bill width and bill depth at base, head (base of the bill to back of the skull), tail (central rectrices), tail covert (body feathers just above the tail feathers), tarsus, tibiotarsus, middle toe and ulna to ± 0.1 mm. Birds were weighed daily on a digital

scale (± 0.1 g). A reduced set of structural measurements were also recorded daily in the aviary: wing chord, sixth primary and sixth secondary. I calculated wing area based on a prediction equation generated for wing area on a subset of 43 birds that were photographed with wing extended on a known-size grid from which wing area was measured. Estimating wing area indirectly rather than by taking daily photographs avoided extra handling. Predictions were a function of linear wing measurements used as explanatory variables. Among potential models using wing measures and their interactions, the equation that best predicted wing area based was wing area (cm^2) = $-31.401 - 0.211 \times \text{wing chord} + 1.825 \times \text{sixth secondary} + 0.181 \times \text{ulna} + 0.024 \times \text{wing chord} \times \text{ulna}$ ($r^2 = 0.96$). I used linear interpolation to generate values for ulna length on days when the full set of measurements were not taken to calculate daily estimates of wing area.

I examined birds brought into captivity to determine the role of morphology in determining fledging ability. I recorded whether a bird was able to make a sustained horizontal flight of at least 3 m each morning. The bird was given three to five chances to make the flight when released in a flight chamber. If a bird was able to fly horizontally or gain altitude, I considered birds capable of leaving a nest, and I used this as an index of fledging ability. I chose to index fledging ability in the captive environment because birds could be checked daily, no ambiguity existed as to whether a bird had fledged from a nest or been depredated, and growth could be monitored after flight ability was attained. Because mourning doves leave the nest quickly after gaining the ability to fly (Hitchcock & Mirarchi 1984), this measure served as a proxy for fledging age.

(b) *Determining factors affecting fledging age*

Statistical models to predict daily fledging ability were estimated using a maximum-likelihood hazard function that allowed for the incorporation of covariates and for model selection (Dinsmore *et al.* 2002). The procedure is commonly used for known-fate survival analyses and correctly treats all days for an individual as the sample unit rather than day as an independent observation. The probability of fledging for each age was estimated using a generalized linear model with a logit-link function for the daily values of the factors included in the model. The statistic correctly accounted for the lack of independence within individuals among repeated measures across days.

I considered five time specific covariates as predictors of fledging age: age, mass, overall structural size (see §2c for calculation of this parameter), wing area and wing loading (weight/wing area). Because of the observational nature of the fledging ability analysis and the need to compare non-nested models, I selected among models using AIC_c (Akaike's information criterion corrected for sample size; Burnham & Anderson 1998). For each covariate, I considered models which included (i) only the single covariate, (ii) the covariate and either brood size or feeding-rate treatment, and (iii) the covariate, brood size or feeding rate, and the interaction of the covariate with the treatment effect. The treatment effects and interaction terms allowed me to determine if different thresholds in fledging ability occurred for each treatment level and thus whether the covariate alone was an adequate predictor of fledging or alternatively whether treatments had an effect independent of its effect on the covariate.

(c) *Analysis of growth patterns*

I examined two components of growth, plasticity in (i) overall size and (ii) size-independent shape to determine, respectively, whether plasticity in overall growth and differential allocation among body parts occurred. The first principal component (PC1) of a set of log-transformed structural measurements is commonly used as a measure of overall size (Rising & Somers 1989). Because rapid feather growth occurred during ages I monitored individuals for this study, PC1 of all of the log-transformed measures loaded heavily for feather measurements, which primarily came from the wing. Thus, this measure was not useful in examining wing growth relative to the rest of the body because it was essentially a measure of wing size. Instead, I used PC1 for the variance-covariance matrix for a reduced set of log-transformed measurements: body, head, tarsus, tibio-tarsus and ulna length. This set of measurements includes skeletal components of structure spaced throughout the body. Loadings for PC1 were similar for all five measures (0.35–0.53). Measures of structural size used for estimating fledging ability were estimated by linear interpolation for days in between when the complete set of measurements was taken. Size-independent shape variables were generated by regressing each of the individual measurements on structural size and using the residual as the shape measure.

Analyses for effects of experimental manipulations were based on a standard hypothesis testing framework. All univariate responses were tested using mixed models analysis of covariance (ANCOVA) with a random effect included for individuals and an effect for brood to account for correlation in conditions within a nest. Multivariate responses were measured using multivariate analysis of covariance (MANCOVA), and Pillai's D was used as the test statistic to determine statistical significance. Measures of sampling variance were generated based on 1000 bootstrap simulations with individuals as the sampling unit (Efron & Tibshirani 1994). I present 95% confidence intervals (CI) determined as the 2.5 and 97.5 per cent quantiles of the ordered estimates from the bootstrap results.

3. RESULTS

(a) *Fledging age*

A total of 68 mourning doves were included in the study. This included 19, 33 and 16 individuals from one-, two- and three-nestling broods, respectively. High nest predation rates meant that many of the nests involved in the brood manipulations did not survive long enough to be brought into captivity and two birds died of unknown causes shortly after being brought into the aviary. The best predictor for fledging probability was the model including a linear effect of wing area. The model that included only wing area had a lower AIC_c value than models where I also included brood size or feeding-rate treatment effects and their interaction with wing area ($\Delta AIC_c \geq 1.06$). Overall size was the next best explanatory variable for fledging probability. However, the best model including overall size was a much poorer fit for the data ($\Delta AIC_c = 13.78$). Wing loading was a relatively poor predictor of fledging age ($\Delta AIC_c = 43.95$) probably because wing loading values remained relatively constant across ages with weight gain occurring at a similar rate to growth in wing area. Wing area was also a much better predictor than models that only included brood size

($\Delta AIC_c = 56.40$) or feeding rate ($\Delta AIC_c = 58.94$). I used a 50 per cent probability of fledging as the threshold wing area for fledging, which was predicted to be 146.9 cm² (95% CI = 142.0–155.4; figure 1).

(b) *Plasticity*

I took 212 sets of measurements from the birds between 8 and 20 days of age. Results were consistent with a plastic response to brood size for overall growth and differential allocation (size and shape; table 1). Size increased significantly with age and inversely to brood size, while the interaction was not significant. Similarly, shape was significantly related to age and brood size, while the interaction term was non-significant. Brood-size manipulations had an effect on overall growth, with larger brood size leading to smaller individuals (figure 2). This is consistent with brood-size manipulations having the expected effect on developmental conditions with larger broods leading to lower *per capita* allocation of resources to nestlings. Brood size also affected shape, demonstrating differential allocation among body parts. I did not find significant interactions between age and brood size affecting size or shape. Thus, effects of treatments were realized prior to 8 days, the age at which growth measurements began in this study, and after this age birds grew along the parallel growth trajectories (figure 2).

(c) *Plasticity and fledging age*

Given that differential allocation among morphological components occurred and that fledging age is correlated with the structural measurement wing area, I examined the relationship between observed plasticity and predicted fledging age. Wing area was related to overall size and to the brood-size treatments (table 1). On average, individuals from larger broods had greater wing area relative to body size than did individuals from smaller broods (figure 3). Thus, while overall slowing of growth in large broods has a negative effect on wing area owing to its correlation with size, differential allocation reduces this effect by increasing wing area relative to the rest of the body for larger broods. I estimated the expected difference in fledging age assuming size alone determined fledging probability based on the estimated coefficients from the ANCOVA for age as a function of brood size and overall size. This difference was the expected difference in fledging age assuming that no prioritization of wing growth occurred with increased brood size. Based on this scenario, young from three-nestling broods would have been expected to fledge 3.8 days later than from one-nestling broods (95% CI = 2.9–4.7 days). To determine the predicted effect of differential allocation, I calculated the expected differences in overall size when wing area reached the predicted threshold size for fledging, and then divided the size difference by the estimated change in size per day to estimate the predicted number of days that differential allocation reduced fledging age. I estimated that the effect of differential allocation on fledging age was to reduce the fledging age by 1.6 days for three-nestling broods versus one-nestling broods (0.9–2.4 days), relative to the scenario where fledging was determined by overall size alone. Observed fledging ages for birds in this study were 14.6 days

Figure 1. Predicted probability of fledging with respect to wing area for mourning dove nestlings. Wing area was the best predictor of fledging probability with a 50% probability of fledging occurring when wing area reached 146.9 cm².

Table 1. Phenotypic plasticity in overall size and shape occurred in response to brood-size treatments (treatment) in developing mourning doves. A treatment effect on size and wing area was tested using ANOVA with a random effect for individuals and brood; while a treatment effect on shape was tested using MANOVA. Feeding rate after 13 days was used as a blocking factor. Significance values for main effects are without the interaction term included in the model. Results demonstrate a relationship between brood size and size and shape, which does not depend on age (interaction term). A specific consequence of plasticity in shape (differential allocation) is that the relationship between wing area and overall size depends on the number of nestlings in the brood.

	Pillai's D	F (d.f.)	p
<i>size</i>			
treatment		14.07 (2,32.2)	<0.001
age		2048.38 (1,146)	<0.001
treatment × age		2.39 (2,144)	0.095
feeding rate		1.66 (2,57.8)	0.200
<i>shape</i>			
treatment	0.519	5.28 (26,392)	<0.001
age	0.308	6.68 (13,195)	<0.001
treatment × age	0.172	1.40 (26,388)	0.095
feeding rate	0.153	1.23 (26,388)	0.202
<i>wing area</i>			
treatment		6.83 (2,35.7)	0.003
size		4551.77 (1,154)	<0.001
treatment × size		1.90 (2,151)	0.153
feeding rate		0.34 (2,61.3)	0.711

(13.9–15.4 days), 15.1 days (14.5–15.6 days), 15.9 days (15.1–16.8 days) for birds from one-, two- and three-nestling broods. The difference of 1.3 days for fledging age between one-nestling and three-nestling broods is much less than the 3.8 days difference based on size alone. The difference was consistent with the result that prioritization of wing growth for young from three-nestling broods reduced fledging age.

4. DISCUSSION

Differential allocation to growth among body parts for young developing under nutritional stress has been

Figure 2. Relationship between size and age for mourning dove nestlings from one-nestling brood (red), two-nestling brood (green) and three-nestling brood (blue). Lines connect measurements for the same individual. Young from one-nestling broods grew faster than young from three-nestling broods, demonstrating that increased competition in the nest has a negative effect on overall growth rate that is likely to delay fledging.

Figure 3. Relationship between wing area and size for mourning dove nestlings from one-nestling brood (red), two-nestling brood (green) and three-nestling brood (blue). Lines connect measurements for the same individual. Wing area was greater for young from three-nestling broods than young of the same size from smaller broods. Plasticity in the allocation of growth to wings versus other body parts leads to earlier predicted fledging age under stressful conditions by affecting the relationship between overall size and wing area, reducing the effects of overall slower growth on fledging age.

observed in many species of birds (e.g. Øyan & Anker-Nilssen 1996; Schew & Ricklefs 1998; Lepczyk & Karasov 2000; Benowitz-Fredericks *et al.* 2006; Tobón & Osorno 2006). Fewer studies have quantified and compared these patterns to determine whether developmental plasticity may be adaptive in tuning growth patterns to the environmental conditions experienced during ontogeny (Schew & Ricklefs 1998). Two recent studies suggest that morphological development can adaptively shift in response to stressors encountered in the nesting environment (Nilsson & Gårdmark 2001;

Gil *et al.* 2008). Results from this study add to the previous work by demonstrating that examining patterns of differential allocation in relation to testable adaptive hypotheses can help to better understand the function of morphological plasticity during development. Results suggest that morphological plasticity can be an important source of adaptation during avian development.

I predicted the adaptive reaction norm in this study based on the relationship of morphological plasticity to predicted fitness and then testing whether this predicted reaction norm matched the observed reaction norm for the population (Gotthard & Nylin 1995). Variation in wing area had a direct relationship to fledging time and this relationship was independent of brood size. Based on the life history of mourning doves, which is characterized by high nest predation, fast growth and relatively small fledging size compared with adult size, there was evidence that selective pressure acts to minimize fledging age (Bosque & Bosque 1995; Martin 1995; Remeš & Martin 2002; Roff *et al.* 2005; Remeš 2007). Based on these observations, I predicted that the adaptive reaction norm in allocation of growth under nutritional limitation would be to prioritize wing growth relative to other body parts to minimize the effects of poor developmental conditions on fledging age. Consistent with this prediction, individuals from larger broods had greater wing area relative to overall size than those from smaller broods. Based on size alone, I predicted that young from three-nestling broods should have taken 26 per cent longer to fledge but the observed difference was 9 per cent longer. Much of this reduction could be explained by plasticity in wing growth which accounted for an estimated 11 per cent reduction.

Evidence for a plastic response that has evolved under natural selection may be inferred when the response shows a high degree of complexity (Gotthard & Nylin 1995). This argument has been used to infer that morphological responses to predator presence that are complex and integrated are evolved adaptations (e.g. Lively 1986; Crowl & Covich 1990). Schew & Ricklefs (1998) similarly argued that adaptive developmental responses to stress that involve preferential allocation among body parts rather than overall slowing of growth are stronger evidence of adaptation. Preferential allocation to wing growth in a manner that directly impacts fledging time is consistent with this line of evidence. Further support would be derived from a more thorough examination of the degree of integration in the response and comparisons among species where selective pressure to reduce fledging age is likely to differ (Gotthard & Nylin 1995). Specifically, testing whether plastic responses are integrated across components within individuals (e.g. preferential allocation in growth of skeletal, feather and muscular components of the wing) would provide insight into the complexity of the response observed in this study.

Increased environmental stress in the nest environment has been associated with reductions in fledging age in other species. Badyaev *et al.* (2006) found that in nests with high parasite loads, male house finch (*Carpodacus mexicanus*) nestlings fledged at younger ages, presumably an adaptation to reduce the time they were exposed to parasites in the nests. Bize *et al.* (2003) found that wing growth was directly related to parasite load in alpine

swifts (*Apus melba*); however, they did not examine wing growth relative to other structures to determine whether the relationship was due to changes in overall growth rate or differential allocation. Raihani & Ridley (2007) found that fledging age in pied babblers (*Turdoides bicolor*) decreased with increased group size, which was strongly associated with predation rates of nestlings. Morphological plasticity is a potential mechanism by which fledging age might have been adjusted in all of these populations.

Developmental plasticity can have both short-term and long-term effects. Plasticity has the greatest potential to be adaptive for immediate and therefore predictable conditions (DeWitt *et al.* 1998). Thus, developmental plasticity is likely to be especially important in adapting organisms to their current conditions experienced during ontogeny rather than potential future conditions that will be experienced in later life stages. My results are consistent with other studies of invertebrates (Crowl & Covich 1990; Gotthard 2008) and anurans (Newman 1992; Lind & Johansson 2007) which show that morphological plasticity has a near-term effect of reducing time to life-history transitions when environmental cues signal that fitness will be maximized by an earlier transition.

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REFERENCES

- Altwegg, R. 2002 Predator-induced life-history plasticity under time constraints in pool frogs. *Ecology* **83**, 2542–2551.
- Badyaev, A. V. 2005 Stress-induced variation in evolution: from behavioral plasticity to genetic assimilation. *Proc. R. Acad. B* **272**, 877–886.
- Badyaev, A. V., Hamstra, T. L., Oh, K. P. & Acevedo Seaman, D. A. 2006 Sex biased maternal effects reduce ectoparasite-induced mortality in a passerine bird. *Proc. Natl Acad. Sci. USA* **103**, 14 406–14 411. (doi:10.1073/pnas.0602452103)
- Benowitz-Fredericks, Z. M., Kitaysky, A. S. & Thompson, C. W. 2006 Growth and allocation in captive common murre (*Uria Aalge*) chicks. *Auk* **123**, 722–734. (doi:10.1642/0004-8038(2006)123[722:GAICCC]2.0.CO;2)
- Bize, P., Roulin, A., Bersier, L.-F., Pflüger, D. & Richner, H. 2003 Parasitism and developmental plasticity in Alpine swift nestlings. *J. Anim. Ecol.* **72**, 633–669. (doi:10.1046/j.1365-2656.2003.00734.x)
- Blockstein, D. E. 1989 Crop milk and clutch size in mourning doves. *Wilson Bull.* **101**, 11–25.
- Bosque, C. & Bosque, M. T. 1995 Nest predation as a selective factor in the evolution of developmental rates in altricial birds. *Am. Nat.* **145**, 234–260. (doi:10.1086/285738)
- Burnham, K. P. & Anderson, D. R. 1998 *Model selection and inference: a practical information-theoretic approach*. New York, NY: Springer.
- Crowl, T. A. & Covich, A. P. 1990 Predator-induced life-history shifts in a freshwater snail. *Science* **247**, 949–951. (doi:10.1126/science.247.4945.949)
- DeWitt, T. J., Sih, A. & Sloan, D. S. 1998 Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.* **13**, 77–81. (doi:10.1016/S0169-5347(97)01274-3)
- Dinsmore, S. J., White, G. C. & Knopf, F. L. 2002 Advanced techniques for modeling avian nest survival. *Ecology* **83**, 3476–3488.
- Efron, B. & Tibshirani, R. J. 1994 *An introduction to the bootstrap*. New York, NY: Chapman and Hall.
- Geissler, P. H. *et al.* 1987 Mourning dove nesting: seasonal patterns and effects of September hunting. *US Fish and Wildlife Resource Publication* 168.
- Gil, D., Bulmer, E., Celis, P. & López-Rull, I. 2008 Adaptive developmental plasticity in growing nestlings: sibling competition induces differential gape growth. *Proc. R. Soc. B* **275**, 549–554. (doi:10.1098/rspb.2007.1360)
- Gotthard, K. 2008 Adaptive growth decisions in butterflies. *Bioscience* **58**, 222–230. (doi:10.1641/B580308)
- Gotthard, K. & Nylin, S. 1995 Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos* **74**, 3–17. (doi:10.2307/3545669)
- Grand, J. B., Hitchcock, R. R. & Mirarchi, R. E. 1984 Mortality of nestling and fledgling mourning doves in east-central Alabama. *J. Ala. Acad. Sci.* **55**, 131.
- Hanson, H. C. & Kossack, C. W. 1957 Methods and criteria for aging incubated eggs and nestlings of the mourning dove. *Wilson Bull.* **69**, 91–101.
- Hitchcock, R. R. & Mirarchi, R. E. 1984 Duration of dependence of wild fledging mourning doves on parental care. *J. Wildl. Manage.* **48**, 99–108. (doi:10.2307/3808457)
- Holcomb, L. C. & Jaeger, M. 1978 Growth and calculation of age in mourning dove nestlings. *J. Wildl. Manage.* **42**, 843–852. (doi:10.2307/3800774)
- Lepczyk, C. A. & Karasov, W. H. 2000 Effect of ephemeral food restriction on growth of house sparrows. *Auk* **117**, 164–174. (doi:10.1642/0004-8038(2000)117[0164:EO EFRO]2.0.CO;2)
- Lind, M. I. & Johansson, F. 2007 The degree of adaptive phenotypic plasticity is correlated with the spatial environmental heterogeneity experienced by island populations of *Rana temporaria*. *J. Exp. Biol.* **20**, 1288–1297.
- Lively, C. M. 1986 Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. *Evolution* **40**, 232–242. (doi:10.2307/2408804)
- Martin, T. E. 1995 Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* **65**, 101–127. (doi:10.2307/2937160)
- Moran, N. A. 1992 The evolutionary maintenance of alternative phenotypes. *Am. Nat.* **139**, 971–989. (doi:10.1086/285369)
- Newman, R. A. 1992 Adaptive plasticity in amphibian metamorphosis. *Bioscience* **42**, 671–678. (doi:10.2307/1312173)
- Nilsson, J.-Å. & Gårdmark, A. 2001 Sibling competition affects individual growth strategies in marsh tit, *Parus palustris*, nestlings. *Anim. Behav.* **61**, 357–365. (doi:10.1006/anbe.2000.1602)
- Øyan, H. S. & Anker-Nilssen, T. 1996 Allocation of growth in food stressed Atlantic Puffin chicks. *Auk* **113**, 830–841.
- Raihani, N. J. & Ridley, A. R. 2007 Variable fledging age according to group size: trade-offs in a cooperatively breeding bird. *Biol. Lett.* **3**, 624–627. (doi:10.1098/rsbl.2007.0435)
- Remeš, V. 2007 Avian growth and development rates and age-specific mortality: the roles of nest predation and adult mortality. *J. Exp. Biol.* **20**, 320–325.
- Remeš, V. & Martin, T. E. 2002 Environmental influences on the evolution of growth and developmental rates in passerines. *Evolution* **56**, 2505–2518.
- Ricklefs, R. E. 1968 Patterns of growth in birds. *Ibis* **110**, 419–451. (doi:10.1111/j.1474-919X.1968.tb00058.x)

- Rising, J. D. & Somers, K. M. 1989 The measurement of overall body size in birds. *Auk* **106**, 666–674.
- Roff, D. A., Remeš, V. & Martin, T. E. 2005 The evolution of fledging age in songbirds. *J. Evol. Biol.* **18**, 1425–1433. (doi:10.1111/j.1420-9101.2005.00958.x)
- Schew, W. A. & Ricklefs, R. E. 1998 Developmental plasticity. In *Avian growth and development* (eds J. M. Starck & R. E. Ricklefs), pp. 288–304. New York, NY: Oxford University Press.
- Smith-Gill, S. J. 1983 Developmental plasticity: developmental conversion versus phenotypic modulation. *Am. Zool.* **23**, 47–55.
- Tobón, E. & Osorno, J. L. 2006 Chick growth variability and parental provisioning in the magnificent frigatebird. *Condor* **108**, 612–622. (doi:10.1650/0010-5422(2006)108[612:CGVAPP]2.0.CO;2)
- West-Eberhard, M. J. 1989 Phenotypic plasticity and the origins of diversity. *Ann. Rev. Ecol. Syst.* **20**, 249–278. (doi:10.1146/annurev.es.20.110189.001341)
- West-Eberhard, M. J. 2003 *Developmental plasticity and evolution*. New York, NY: Oxford University Press.
- Westmoreland, D. & Best, L. B. 1987 What limits mourning doves to a clutch of two eggs? *Condor* **89**, 486–493. (doi:10.2307/1368638)
- Westmoreland, D., Best, L. B. & Blockstein, D. E. 1986 Multiple brooding as a reproductive strategy: time-conserving adaptations in mourning doves. *Auk* **103**, 196–203.