Reproductive ecology of the mourning dove: large-scale patterns in recruitment, breeding endocrinology, and developmental plasticity

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Reproductive ecology of the mourning dove: large-scale patterns in recruitment, breeding endocrinology, and developmental plasticity

by

David Andrew Miller

A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Ecology and Evolutionary Biology

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Iowa State University
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CHAPTER 1. INTRODUCTION

This dissertation examines multiple aspects of the reproductive ecology of mourning doves (*Zenaida macroura*). The work builds on a long tradition of research on their reproductive ecology (McClure 1943, Hanson and Kossack 1963), techniques for large-scale monitoring of reproduction (Ruos and Tomlinson 1967), and endocrinology of Columbids (Riddle 1933). I have expanded this body of knowledge in a way that hopefully will make worthwhile contributions to knowledge of 1) techniques for monitoring reproduction, 2) geographic and weather related variation in annual recruitment, 3) endocrinology during breeding, and 4) the role of developmental plasticity in response to stress early in life.

The mourning dove is an important migratory game bird in the United States where more than 20 million birds are harvested annually. Its importance as a game species has been the impetus for a coordinated effort by state and federal agencies to improve harvest management for the species. A national strategic harvest management plan has been developed that emphasizes the use of population models to develop an informed long-term strategy for harvest (Anonymous 2004). Establishing monitoring programs for population vital rates is a critical component of the plan and priorities include instituting a large-scale operational program for monitoring reproductive rates. Large-scale studies for mourning doves between the 1950’s and 1980’s determined migration patterns (Kiel 1959), survival and harvest rates (Hayne 1975, Dunks et al. 1982, Tomlinson et al. 1988), and recruitment rates (Ruos and Tomlinson 1967, Geissler et al 1987). However, more recent monitoring of mourning dove populations has been based solely on the Call Count Survey, an annual roadside index to dove abundance (Anonymous 2004), until a large-scale banding effort was resumed in 2003 (Otis et al. 2008). A program to monitor recruitment rate will be an important complement to banding to generate estimates of population vital rates.

In 2005, with the cooperation of 22 state agencies and US Fish and Wildlife Service personnel and funding from the Webless Migratory Gamebird Research Grant program, I organized a pilot harvest parts collection program aimed at developing a
national program for monitoring dove recruitment rates. I used wings collected from this program during 2005-2008, in addition to wings collected in parallel as part of a national mail survey by the US Fish and Wildlife Service in 2007 and 2008, in analyses in Chapter 2 and 3, which make up the first section of my dissertation. I developed statistical techniques to calibrate age ratios from collected wings and to estimate population age ratios (Chapter 2 – Calibrating recruitment estimates for mourning doves from harvest age ratios). I also use these data to determine how reproduction varies geographically and how annual variation correlates with variation in weather (Chapter 3 – Range-wide estimates of mourning dove recruitment and their relationship to annual weather variation). These chapters serve as a basis for the development of a long-term operational program for monitoring mourning dove recruitment.

In addition to work on large-scale monitoring of recruitment, during the summers of 2005-2007, I initiated work with local breeding doves in central Iowa. Mourning doves offer an ideal model to examine hypotheses about parental effects and developmental plasticity as they relate to the growth and development of young. Mourning doves have an extended range both in geographical extent and across a range of habitats (McClure 1943, Hanson and Kossack 1963, Otis et al. 2008). They have a determinant clutch size of 2 eggs and one of the most protracted nesting seasons among North American birds, during which multiple nesting attempts occur. In my study areas in central Iowa during 2005-2007, nest initiations range from Mar 20 to Sept 15. Plasticity in parental effects and in growth and development of young are likely to be important for successfully breeding across the wide gradient of environmental conditions within their breeding range to which they are exposed. The work on breeding ecology presented in my dissertation is focused on two areas. First, I examined the relationship of prolactin and corticosterone levels, two important hormones affecting behavior during reproduction, to parental effort during the nestling period (Chapter 4 – Individual variation in baseline and stress-induced corticosterone and prolactin levels predicts parental effort by nesting mourning doves). Second, I examined patterns in growth and development as they related to developmental stress with a particular emphasis on the role of plasticity in affecting flight ability of juvenile doves. I focused on fledging
ability, which initiates an important life history transition from nestling to fledgling stages for doves (Chapter 5 – *Morphological plasticity reduces the effect of poor developmental conditions on fledging age in mourning doves*) and on take-off speed as well as growth in weight and size during the post-fledging period up to 90 d of age (Chapter 6 – *Immediate versus delayed effects of early nutritional stress on growth and flight ability of juvenile mourning doves*).

**Literature Cited**


CHAPTER 2. CALIBRATING RECRUITMENT ESTIMATES FOR MOURNING DOVES FROM HARVEST AGE RATIOS

A paper submitted to the Journal of Wildlife Management

David A. Miller and David L. Otis.

ABSTRACT The national strategic management plan for the mourning dove calls for the implementation of an operational monitoring program of recruitment rates that is national in scale. Age ratios estimates, i.e. juveniles per adult, generated from harvest wing collections are a potentially efficient method for large-scale monitoring of recruitment for the species. Generating unbiased estimates of recruitment from harvest age ratios requires calibration of estimates to account for wings of unknown-aged birds in the sample and for differential vulnerability of the age classes to harvest. We present results from the first national-scale effort to estimate dove age ratios while addressing the need to develop a simple, efficient, and generalizable methodology for calibrating estimates. Our method predicts age classes of unknown-age wings based on backward projection of molt distributions from fall harvest collections to late-summer banding. Estimated parameters are 1) the proportion of late molt individuals that belong to each age class and 2) molt rates of juvenile and adult birds. Monte Carlo simulations demonstrate that the estimator is minimally biased. We estimated model parameters using 96,811 wings collected and 42,189 birds banded from 68 collection blocks in 22 states during the 2005-2007 hunting seasons. Estimates were also used to derive a correction factor based on latitude and longitude of samples that can be applied to future surveys. In addition, we estimated differential vulnerability of the age classes to harvest using data from banded birds and applied this to harvest age ratios to estimate population age ratios. Using harvest age ratios from an independent sample of 41,084 wings collected from random hunters in 2007 and 2008, we found that the average uncorrected
age ratio of known-age wings for states that allow hunting = 2.25 (sd = 0.85) juveniles:adult and the average corrected ratio = 1.91 (0.68). We used an independent estimate of differential vulnerability to adjust corrected harvest age ratios, and estimated the average population age ratio = 1.45 (0.52), a direct measure of recruitment rates. Average annual recruitment rates were highest in the east of the Mississippi River and in the northwest part of their range with lower rates in between. Our results demonstrate a robust methodology for calibrating recruitment estimates for mourning doves and represent the first large-scale estimates of recruitment for the species. Methods can be used by managers to correct future harvest survey data to generate recruitment estimates that will inform harvest management strategies.

KEY WORDS Age-ratio, detection, differential vulnerability, harvest survey, *Zenaida macroura*.

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The mourning dove (*Zenaida macroura*) is an important migratory game bird in the United States, where more than 20 million birds are harvested annually. As part of an effort to improve harvest management for the species, a national strategic harvest management plan has been developed that emphasizes the use of population models to develop an informed long-term strategy for harvest (Anonymous 2004). Establishing monitoring programs for population vital rates is a critical component of the plan and priorities include instituting a large-scale operational program for monitoring reproductive rates. Large-scale studies for mourning doves between the 1950’s and 1980’s determined migration patterns (Kiel 1959), survival and harvest rates (Hayne 1975, Dunks et al. 1982, Tomlinson et al. 1988), and recruitment rates (Ruoz and Tomlinson 1967, Geissler et al. 1987). Recent monitoring of mourning dove populations has been based solely on the Call Count Survey (Anonymous 2004) until a large-scale banding effort was resumed in 2003 (Otis et al. 2008). A program to monitor recruitment rate will be an important complement to banding as part of the broader effort to generate estimates of vital rates for the population (Braun et al. 1993, Tomlinson et al. 1994, Otis 2003).
Use of age ratios from harvest wing collections is a potential cost-effective and
time-efficient method for generating recruitment estimates which can be used for harvest
population models (Martin and Carney 1977, Runge et al. 2002). For doves, harvested
wings can be aged as juveniles or adults (≥ 1 yr) to generate harvest age ratio estimates,
i.e. ratios of juveniles to adults in the harvest population (Ruos and Tomlinson 1967).
Based on estimates of age specific vulnerability, harvest age ratios can then be used to
generate estimates of recruitment, defined in this study as the population age ratio.
Recruitment estimates of this type can be directly integrated into simple population
models that can be used as part of a harvest management program (Runge et al. 2002).
Implementing such a program for mourning doves requires development of methods to
calibrate harvest age ratio estimates to obtain unbiased estimates of recruitment. For
doves this involves accounting for wings from unknown-aged birds in the harvest sample
(hereafter, unknown-age wings; Ruos and Tomlinson 1967, Haas and Amend 1979) and
for differential vulnerability of age classes to harvest (Martin and Carney 1977).

The occurrence of unknown-age wings in harvest samples are a specific challenge
to calibrating age ratio estimates for mourning doves (Ruos and Tomlinson 1967). Wings
are assigned to an age class based on presence of buffy margins on primary coverts
(Mirarchi 1993). Mourning doves progressively molt primary feathers throughout the
summer and fall and they lose the last of their primary coverts around the time the 8th
primary feather is molted. For this reason a substantial portion of the wings collected
from harvest surveys cannot be aged. If the age ratio in the unknown sample differs from
the age ratio of known-age wings, the resulting estimates based on only the known-age
sample will be biased. Predicting the proportion of unknowns from each age class will be
important for producing unbiased estimates of harvest age ratios.

Harvest age ratios must also be corrected for potential bias caused by differential
vulnerability of juveniles and adults to harvest. Differential vulnerability can be
estimated by the ratio of direct recovery rates of juveniles to adults banded just prior to
harvest (Nichols and Tomlinson 1993, Runge et al. 2002). The national banding program
which began in 2003 (hereafter, late-summer banding; Otis et al. 2008) provides data that
can be used to update prior estimates of differential vulnerability (Hayne 1975, Dunks et al. 1982, Tomlinson et al. 1988).

We present results from the first national-scale effort to estimate dove age ratios while addressing the need to develop simple, efficient, and generalizable methodology for adjusting harvest age ratios to estimate recruitment. From 2005-2007, we coordinated a harvest wing collection program for mourning doves in cooperation with 22 state wildlife agencies. Our objective was to investigate the feasibility of large-scale collections of harvested wings and to develop methodology to estimate recruitment in the fall dove population based on harvest age ratios. We used paired samples of molt distributions in summer and at the time of harvest to develop a statistical method for estimating the proportion of unknown wings in the harvest sample that belong to each age class. We used our technique to develop a predictive equation that can be used to correct age ratios from future wing surveys. We applied standard techniques to estimate differential vulnerability for the 2 age classes from bands reported by hunters (Runge et al. 2002). We applied our methodology to data from an independent national mail survey of randomly chosen dove hunters.

METHODS

Data Collection

Harvest wing collections were conducted during the 2005-2007 hunting seasons by 22 state wildlife agencies. Wing collection sites were matched to areas where birds were banded as part of the late-summer banding program. Participating states were asked to collect at least 400 wings from sites within 1 by 1° (latitude and longitude) blocks where at least 200 birds had been banded during the summer. Each state collected wings from between 1 and 6 degree blocks annually for a total of 68 unique blocks where sampling occurred for at least 1 year.

Wings were collected during the first week of the harvest season from check stations at public and private hunting areas, wing barrels placed at entrances to hunting areas, and direct hunter solicitation by state employees. Collections were limited to the first week of the harvest season to minimize the proportion of unknown-age wings in the sample and to maximize the extent to which the harvest sample was representative of
local birds and of birds from the same population as the late-summer banding sample. In most states the harvest season began on September 1st.

Wings collected as part of harvest surveys were assigned an age class and molt class by personnel from state and federal agencies using a standardized protocol during an annual event hosted by the Missouri Department of Conservation. Molt class was defined as the last primary feather lost as part of the molt process (ranged from 0, not started, to 10, all feathers lost). Molt class was assumed to be assigned without error for all wings. For wings in molt class 0 to 7, age class was assumed to be assigned without error. Because wings in molt class 8 to 10 could not be aged in most cases they were considered unknown age. These late molt wings were the cohort of interest in assigning unknown-age wings to an age class.

Birds banded as part of the late-summer banding program were also assigned to an age class and a molt class by agency personnel doing the banding. The banding period began on July 1st and ended in mid-August. The majority of birds were banded during the month of July when the proportion of unknown-age birds was minimal.

**Technique for Assignment of Unknown-age Wings**

We developed a technique to estimate the proportion of unknown-age wings that belong to each age class from harvest wing collections. The method relied on samples of molt classes of wings from the harvest sample and the late-summer banding sample. We took advantage of the fact that molt class was ordinal (i.e., the molt progression is linear from primary 1 to 10) to model how the population distribution of molt classes changed with time. We assigned unknown-age wings in molt class 8, 9, and 10 to an age class by jointly estimating the proportion of unknown-age wings from each age class and the intervals at which primaries were molted. We used estimates that produced the best fit between molt distributions for the harvest sample projected back to the time of banding, and the observed molt distributions from the banding data.

The technique is briefly summarized by 4 steps: 1) assign unknown-age wings at the time of harvest into each of the age classes; 2) convert the harvest distribution of discrete molt classes into a predicted continuous distribution on a scale defined by days since molt started; 3) project this distribution back to the time of late-summer banding;
and, 4) assess the fit of the predicted proportion to the true number in the late-summer banding sample for each molt class treating it as a multinomial likelihood. Estimated values for molt intervals and proportions of unknown-age wings in each age class that maximized the likelihood were then determined using standard optimization routines.

In developing our model we made the following assumptions. We assumed that birds molt feathers at regular intervals, with an equal number of days for each feather for adults and unequal number of days for each feather for juvenile birds. Molt rates were assumed to be the same for all individuals in samples being compared. Birds from the harvest collections were assumed to come from the same population as birds banded in the same degree block as part of the late-summer banding program. To test this assumption that migration was minimal between samples, we used band recoveries to determine the distribution of distances between banding sites and where birds were harvested during the first week of harvest (see section on differential vulnerability for detailed description of the data set used).

**Notation**

*Data.* 

\[ B = \{b_{ijk}; i = J (juvenile), A (adult); j = 1, 2, \ldots, 68; k = 0, 1, \ldots, 10\}; \]  
The number of doves in the \(i\)th age class, banded the \(j\)th day before harvest (68 days from 1 July to 7 September), in the \(k\)th molt class.

\[ H_\ast = \{h_{ik}; i = J, A, U (unknown); k = 0, 1, \ldots, 10\}; \]  
The number of doves from the harvest sample in the \(i\)th age class and \(k\)th molt class. If \(k \geq 8\), then \(i = U\).

*Estimated Parameters and Distributions.* 

\[ f_\ast (k); \{i = J, A; k = 0, 1, \ldots, 10\}; \]  
discrete probability distribution function (pdf) for the probability that a wing in the \(i\)th age class from the harvest sample was in the \(k\)th molt class.

\[ f(T); \]  
continuous pdf defining a latent distribution for time in days, \(T\), since the molt process began, \(T_0\), for wings from harvest samples in the \(i\)th age class.

\[ F_\ast (T); \]  
cumulative distribution function (cdf) of \(f(T)\).

\[ \alpha_{ik}; \]  
age (days) at which doves from \(i\)th age class, molt the \(k\)th primary feather. (hereafter referred to as molt intervals).
\( \rho_{ik}; \{ k = 8, 9, 10 \}; \) proportion of unknown-age wings in the \( k \)th molt class, that came from age class \( i \).

**Estimation Procedure**

We defined \( p_{ijk} \) as the probability a bird caught during late-summer banding came from the \( k \)th molt class, given that it is from the \( i \)th age class and banded on the \( j \)th day prior to harvest. Then the data from banded birds, \( \{ b_{ijk} \} \), were assumed to come from a multinomial distribution, with corresponding likelihood function proportional to:

\[
L(F_i[T], \alpha, \rho | B) = \prod_i \prod_j \prod_k (p_{ijk})^{b_{ijk}}, \text{ where} \tag{1}
\]

\[
\sum_i p_{ijk} = 1, \text{ and} \tag{2}
\]

\[
p_{ijk} = g(F_i[T], \alpha_{ik}, \rho_{ik}) \tag{3}
\]

Values for \( \hat{F}_i(T) \), the estimated continuous cdf for the time in days (\( T \)) elapsed since the onset of the molting process at the time of harvest, were derived as described below. The frequencies of harvested wings for each age class, \( \{ h_{ik} \} \), were used to generate the empirical discrete pdfs, \( f_j^*(k) \) and \( f_A^*(k) \), representing the probabilities individuals were in the \( k \)th molt class at the time of harvest. These were used to construct the estimated latent continuous distributions, \( f_j(T) \) and \( f_A(T) \) for the continuous variable \( T \).

Approximating this latent distribution was a necessary step to project the distribution across time and therefore necessary to compare late-summer and harvest molt distributions. The estimated latent distribution was expressed with respect to time, which allowed us to project the distribution by shifting the distribution by the number of days prior to harvest at which the banding sample was taken. In addition, the estimated distribution was smoothed as compared to the discrete molt distribution, better approximating what we believed would be a relatively continuous distribution in the timing of molt commencement. First, we generated \( f_j^*(k) \) and \( f_A^*(k) \) conditional on the values of \( \hat{\rho}_{ik} \), which were used to assign unknown-age wings from molt class 8, 9, and 10 to an age class. Then, we approximated a functional form for \( f_j(T) \) and \( f_A(T) \) as defined based on the following rules. 1) the estimated pdf changed linearly between the midpoints of each molt class; 2) the estimated pdf was uniform from the midpoint of the
first molt class to day 0 and from the midpoint of the final molt class to the last day for individuals in the final molt class; and, 3) the estimated proportion of wings in each molt class was equal to the original proportion of wings collected in that molt class. Refer to Appendix A for details of the estimation of the latent distribution, \( f(T) \).

The cumulative distribution function, \( F_i(T) \), was used to estimate the probabilities for the likelihood in Eq 1-3. Because \( F_i(T) \) was on a continuous temporal scale we were able to generate the estimated molt distribution for any day a bird was captured as part of the late-summer banding period by simply shifting the distribution to the left by the number of days before harvest, \( j \), the individual was sampled. The probability of trapping a bird during banding in the \( k \)th molt class conditional on being in the \( i \)th age class \( j \) days prior to harvest was estimated based on the cdf, \( F_i(T) \). Probabilities were based on subtracting \( F(T) \) at the ending age from \( F(T) \) at the starting age of a molt class and then dividing by the sum of probabilities for all molt classes where age was known. The proportion of individuals in molt class 8, 9, and 10 was assumed to be minimal at the time of banding and the distribution was right truncated at the start of molt class 8. We accounted for the significant proportion of juvenile birds from the harvest sample that were not available for capture at the time of banding (too young or not hatched) by left truncation of the distribution at the start of molt class 0.

\[
\hat{p}_{ijk} = \frac{\hat{F}_i(\hat{\alpha}_{k+1} + j) - \hat{F}_i(\hat{\alpha}_k + j)}{\hat{F}_i(\hat{\alpha}_8 + j) - \hat{F}_i(\hat{\alpha}_0 + j)}
\]  

We generated maximum likelihood estimates of \( \hat{\rho} \) and \( \hat{\alpha} \) using optimization routines in the R statistical package (v.6.2.1). Estimates of age ratios for the harvest sample were derived by assigning unknown-age wings to an age class based on values of \( \hat{\rho}_{ik} \), and then calculating the ratio \([\text{known} + \text{assigned juveniles}] / [\text{known} + \text{assigned adults}]\).

**Monte Carlo Simulation of Estimator**

To evaluate bias and variance for the corrected age ratio estimator, we conducted Monte Carlo simulations for a set of scenarios in which we varied the true age ratio and the molt distribution of the population. If we were able to age all wings at the time of harvest under an “ideal” scenario, we would be able to generate unbiased estimates of harvest age ratio and associated variance based on the binomial MLE for the proportion of wings in
each of the 2 age classes. Given that the expected variance for a ratio of 2 random variables \( M \) and \( N \) is:

\[
Var\left( \frac{M}{N} \right) = E^2[M] \left[ Var[M] - \frac{2 * Cov[M,N]}{E[M]*E[N]} + Var[N] \right],
\]

(Stuart and Ord 1998) the expected variance for our age ratio estimator based on Eq 5 was:

\[
Var(R) = \frac{p}{n(1-p)} + \frac{2p^2}{n(1-p)^2} + \frac{p^3}{n(1-p)^3},
\]

where, \( p \) is the binomially distributed proportion of juvenile birds and \( n \) is the sample size. This served as a baseline estimate to gauge the relative loss of efficiency due to unknown-age wings when estimating age ratios. Our estimator will have a greater MSE (mean square error; variance + bias\(^2\)) than the ideal estimator due to statistical uncertainty in the proportion of unknown-age wings from each age class and potential bias in the estimates.

We varied 2 parameters among simulation sets while constraining other parameters to remain the same across different sets of simulations. We simulated age ratios that were typical of what we expected in actual mourning dove populations, using ratios of 1, 3, or 6 juveniles per adult. Age class of simulated individuals came from a binomial distribution defined by one of these age ratios. We generated 2 frequency distributions of molt class for juvenile birds and 2 for adult birds (Fig. 1). For juvenile birds we assumed a latent beta distribution, allowing for a skewed distribution and for variability in the length of time over which fledging occurred. For adults the latent distribution was generated from a normal distribution because molt class distributions from summer banding program suggested a relatively symmetrical distribution. The expected proportions of unknown-age wings (molt class \( \geq 8 \)) were 0.210 and 0.085 for the two juvenile distributions respectively, and 0.208 and 0.263 for the two adult distributions respectively. We simulated all combinations of age ratios and each of the 2 molt distributions for a total of 12 scenarios.

Additional parameters were consistent across scenarios. We chose values for \( \alpha_{ik} \) based on previous estimates in the literature that indicate that adults molt feathers at
consistent intervals while juvenile molt intervals increase through the molt process (Swank 1955a, Allen 1963, Sadler et al. 1970, Haas and Amend 1976, 1979, Morrow 1983, Morrow et al. 1985, Johnson 1989). We constrained adults to molt primaries at a rate of 1 every 15 d and juveniles to differ in the molt interval between primaries, with the number of days per feather increasing as molt progressed (Fig. 1). For the banding sample the number of days before harvest at which a bird would have been sampled was drawn from a uniform distribution between 16 and 45 d. The sample size for the harvest and banding samples were each 1000 birds.

Data were generated as follows: For harvest data the age of each individual was assigned by a draw from a binomial distribution and then molt class was assigned by a draw from the age specific molt class frequency distribution. All individuals with molt class 8, 9, or 10 were then reassigned to be of unknown age. For the banding data we assigned the number of days before harvest by a draw from the uniform distribution and the age class again from a binomial. Then molt class was assigned by drawing from the age specific molt distribution shifted backward in time by the number of days before harvest. The resultant harvest data, $H^*$, and banding data, $B$, were then used to estimate the corrected age ratio of the harvest distribution.

For each of the 12 scenarios we simulated 1000 data sets and calculated the mean, variance, bias, and MSE of the corrected age ratio estimates. In estimating molt intervals, we constrained adult molt intervals to be the same for all primaries while allowing juvenile molt intervals to vary among primaries. We compared simulated means to true age ratios and compared simulated variances to expected variances assuming all ages were known (Eq 6).

**Estimating Corrected Age Ratios**

We analyzed data from harvest wing collections and late-summer banding collected by state wildlife agencies using our estimator. Data came from numerous blocks and we chose to constrain some parameters to be equal across multiple blocks while others were estimated separately for each block. In specifying the likelihood, we treated each combination of block and year separately for calculated harvest molt distributions ($f[T]$) and estimated the unknown proportion of wings in each age class ($\rho_k$) separately for
each block/year combination. We constrained adult molt intervals to be the same for all primaries while allowing juvenile molt intervals to vary among primaries. Molt intervals ($\alpha_{ik}$) were constrained to be equal within each of 11 sub-regions for all blocks and years (see Otis et al. 2008 for definition of sub-regions).

We were unable to efficiently estimate sampling variances directly from the likelihood information matrix because the parameters of interest, correction factors and corrected age ratios, were derived from estimated parameters. Indirect estimation from bootstrap resampling was not possible due to computing constraints, as computing time for a single iteration took 3-4 d to run. Instead we present empirical variances in parameters among independent sample units (i.e., block-years for age-ratios and unknown proportions, and sub-regions for molt rates). Standard deviations of estimates are calculated; however, this measure of precision includes both sampling variance and spatial and temporal process variation in estimates.

**Estimating Recruitment**

We also needed to correct for differential harvest vulnerability of age classes to adjust the estimate of the harvest age ratio to an estimate of population age ratio at the time of harvest, our measure of recruitment. We used data from late-summer banding in 2003-2007, in combination with band recovery data from the USGS-Bird Banding Laboratory (BBL), to estimate relative rates of vulnerability of juveniles and adult mourning doves to harvest. We filtered recoveries to include only direct recoveries (those recovered in the same year they were banded) from the first week of the harvest season (Sept. 1 – Sept. 7). By limiting recoveries to only the first week the sample matched the sample population for the harvest wing survey and potential bias due to seasonal shifts in the harvest population was minimized.

We estimated differential age vulnerability to harvest using the ratio of direct recovery rates for juveniles and adults. This correction assumes mortality rates do not differ between the age classes from the time of banding and harvest. We estimated the proportion of banded birds directly recovered from each age class. The ratio of estimated juvenile to adult direct recovery rates was used as an estimate of differential
vulnerability. Harvest age ratio estimates were divided by this value to generate estimates of recruitment.

**Predictive Correction Factor for Unknown-age Wings**

The data collection protocol used to develop our estimation technique to assign unknown-age wings does not fit a future envisioned program where wings are collected from randomly chosen hunters in a mail survey, similar to the waterfowl part collection survey (Runge et al 2002). Therefore, we developed a predictive correction model that could be used to generate correction factors for future surveys based on geographic location. In developing the correction factor we limited our sample to blocks where the harvest season began in the first week of September, because the proportion of unknowns will be dependent on date. All or some of the blocks in Alabama, Florida, and Texas for this part of the analysis because hunting seasons began in late September or early October.

We identified 3 potential parameters that result from our estimates for correcting age ratio estimates. We could correct estimates using 1) the proportion of unknowns that were juveniles \(P(U_J)\); this statistic is equivalent to \(P(U_A)\) because \(P(U_A) = 1 - P(U_J)\), 2) the proportion of adults that were of unknown age \(P(A_U)\), 3) or the proportion of juveniles that were of unknown age \(P(J_U)\). We developed geographically specific correction equations based on latitude and longitude for each of these estimators and chose the method that minimized the squared error between corrected age ratios that came directly from our estimation model and estimates derived based on the correction factor equations.

We assumed that spatial variation would occur in each of our potential correction factors. Therefore we constructed a prediction formula based on latitude and longitude of sample locations. We calculated values for \(P(U_J)\), \(P(A_U)\), and \(P(J_U)\) for each combination of block and year based on the results from our estimation model. We then fit a generalized linear model with a logit-link function, using each predictor as the response variable and latitude, longitude, and their interaction as explanatory variables. Because our response consisted of proportions rather than binomial outcomes, we assumed the variance of the response was quasi-binomial with binomial variance multiplied by a positive scalar (Agresti 2002). In addition, estimates of the response variable included
sampling error that likely differed among blocks with respect to sample size used to estimate the values. We accounted for this by weighting values by the sample size for the block.

Thus, our model had 2 random error components, the first expressed as a quasi-binomial and shared by all sample units, and the second expressed as a weight proportional to the expected sampling error used to produce each individual estimate. The generalized models were fit using the glm routine in the R-Statistical Package (version 2.6.1).

**Example Data Set**
We demonstrate the use of correction factors for unknown-age wings and differential vulnerability for an independent data set. In 2007 and 2008 the US Fish and Wildlife Service conducted a mail survey to collect mourning dove wings from randomly chosen hunters in all states that permitted hunting. We used this data set to demonstrate the application of our methods to assign unknown age wings and correct for harvest age ratios for differential vulnerability to generate recruitment estimates.

**RESULTS**

**Simulations**
Simulated relative bias was <0.05 for all scenarios, suggesting that bias in our estimator was minimal (Table 1). Bias had a small contribution to overall MSE of estimates. MSE for all the scenarios was 2-3 times greater than the ideal scenario where all wings can be aged at the time of harvest. The relative loss in efficiency was greatest for small age ratios and would likely increase as the proportion of unknown-age wings increased. The CV was consistent across all of the scenarios tested, ranging between 0.095 and 0.136 (Table 1).

**Field Data**
We collected wings in 22 different states, within 68 unique degree blocks, during the 3 year period. Not all blocks were used for all 3 years, so we had 155 unique combinations of year and degree block. We collected 96,811 wings during harvest and molt classes were recorded for 42,189 birds during banding. Wings collected in 68% of the block-years met or exceeded the 400 wing goal ($\bar{x} = 625$ wings). Birds for which molt classes
were recorded during late-summer banding period in 61% of the block-years met or exceeded the 200 wing goal (\( \bar{x} = 272 \)). Both goals were met in 65 block-years (42%).

Band recoveries confirmed that migration was minimal between banding and harvest and supported the assumption that samples came from the same population for both periods. The median recovery distances for juveniles (n = 2599) and adults (n = 1562) respectively were 11.1 and 8.9 km. We found that 90.0 and 91.2% of direct recoveries of juveniles and adults respectively were within 100 km of the banding site. This is consistent with the harvest age ratio being representative of local recruitment rates and late-summer and harvest samples coming from the same population.

**Parameter Estimates and Prediction Equation**

Estimates of adult molt rate averaged 17.9(sd = 3.34) d per feather for all sub-regions, and we estimated that juvenile birds took an average of 83.7(25.2) d between molting their first and eighth primary. Age ratios based on the uncorrected ratio of juvenile wings per adult wing averaged 3.31 (sd = 2.61) for all blocks; after correction for unknown-age wings the average was 2.67 (1.88) indicating that uncorrected age ratios were generally biased towards juveniles. After accounting for differential vulnerability, estimates of recruitment averaged 2.02 (1.42). In general age ratios declined when moving from eastern sites to western sites. In blocks where wings were sampled in all 3 years, pairwise correlations for estimated block-level age ratios among years were \( r = 0.56, 0.66, \) and 0.62 for 2005 vs. 2006, 2005 vs. 2007, and 2006 vs. 2007, respectively. Thus age ratios for a given location were moderately repeatable among years.

The direct recovery rate for juvenile mourning doves was 2.41 % and for adults was 1.76 %, which produced an estimate of 1.32 for differential vulnerability. We calculated estimates of recruitment by dividing corrected harvest age ratios by 1.32.

The mean sum of squares error between the estimated age ratio from our estimation model and that predicted using each of the 3 correction factors was 3.19, 1.16, and 4.59, for \( P(U_J) \), \( P(A_U) \), and \( P(J_U) \), respectively. Therefore, the proportion of unknown-age adults had the strongest support as a correction method for future surveys. Our estimating equation for the proportion of unknown-age adults in the harvest survey during the first week of September, as a function of latitude (lat) and longitude (lon) was:
logit\left( P[A_u] \right) = -23.00508 + 0.68509 \times \text{lat} + 0.25552 \times \text{lon} - 0.007825 \times \text{lat} \times \text{lon} \quad (7)

The equation predicts the highest proportion of adults in late molt classes in the southeastern region of the breeding range and the lowest proportion in the northwest.

**Example Data Set**

We applied corrections for unknown-age wings and differential vulnerability to 41,084 wings collected as part of the national mail survey in 2007 and 2008. Overall spatial pattern in recruitment was similar to those from our data set, although estimates were generally smaller. The average uncorrected age ratio of known-age wings for all states was 2.25 (sd = 0.85). After applying the correction factor for unknown-age wings the average was 1.91 (0.68), indicating that unknown-age wings were biased towards adults. When differential vulnerability was taken into account, the average state recruitment rate was 1.45 (0.52). Recruitment rates were highest in eastern states and in the northwest with lower average recruitment in the areas in between and patterns were consistent between years (Fig. 2). The average state recruitment rate for each of the dove management units was 1.75 (0.52), 1.14 (0.31), and 1.22 (0.38) for the eastern, central, and western management units, respectively.

**DISCUSSION**

Management strategies for both game and non-game species increasingly rely on the integration of data-driven population models coupled with empirical predictions of the effects of management actions to judge the efficacy of different management scenarios (Williams et al. 2002). This mechanistic approach to addressing management questions inherently relies on accurate and unbiased estimates of population dynamics and the underlying vital rates that drive the dynamics. The national strategic harvest management plan for mourning doves adopts this mechanistic approach for assessing and setting future harvest regulations (Anonymous 2004). A key component of the plan is the development of an operational monitoring program that is national in scope to generate annual estimates of recruitment. We demonstrated a comprehensive methodology that addressed both the specific concerns for generating estimates of fall population age ratios based on samples of wings from harvested mourning doves and contributes to the general methodology used for estimating recruitment based on sampled age ratios.
The simulation results and empirical analyses support the contention that our technique for estimating the age composition of unknown-age wings performed well. Simulations showed that when assumptions are met, the technique is minimally biased and can be used to generate age ratio estimates that incorporate unknown-age wings. However, there was a loss of precision due to uncertainty in classifying unknown-age wings. Any effort that increases the proportion of wings that can be classified to an age class would reduce variance of future estimates. Therefore, any improvement in traditional aging techniques that allowed for late-molt birds to be directly aged would improve estimates over our indirect classification technique.

Our estimation technique requires the estimation of the rate of feather molt of juvenile and adult birds. Comparisons of estimates from our model with independent estimates of molt rate serves as an independent check on our methods. Our ability to assign unknown-age wings to an age class relied on projecting fall molt distributions backward to the late-summer distributions based on accurately estimated molt rates. Previous studies of juvenile molt rate reported that it took between 70 and 76.4 d from the time the 1st primary was molted until the 8th primary was molted ($n = 4$; Swank 1955a, Allen 1963, Haas and Amend 1976, Morrow 1983) compared to 83.7 d in this study. Swank (1955b) and Morrow et al. (1985) found that when estimated molt rates were used to project harvest molt distributions back to determine a hatching distribution, the predicted distributions were skewed to later dates than the actual hatching distribution. This indicates that field estimates of juvenile molt rate may underestimate the amount of time molt takes late in the season when measured from harvest rather than during mid-summer when the above molt rates were estimated. This would be consistent with our somewhat higher estimate for the total time to molt primary feathers in juveniles.

Previous estimates for adult molt rate range from 13.7-14.3 and 15.5-16.5 d feather$^{-1}$ for birds in North and South Carolina (Haas and Amend 1979, Johnson 1989) and in Missouri (Sadler et al. 1970), respectively. Our comparable estimates were 16.3 and 17.4 d feather$^{-1}$ for the respective sub-regions where the previous studies occurred.
The general pattern in the proportion of adults that are of unknown age is consistent with the conclusions of Haas and Amend (1979) that a greater proportion of molt complete birds will be found in southern states. This pattern is driven by the timing of the onset of molt by adults, where the mean observed molt class during the late-summer banding period decreases from the southeast to the northwest. This distinct geographic trend and the consistency in the molt distribution among years likely explain why we found that the proportion of adults of unknown age worked best as a correction factor.

Examination of direct recoveries during the first week of September for mourning doves supported our assumption that within blocks late-summer banding and fall harvest molt samples came from the same local populations. In a broader context the local scale of age ratio samples has both benefits and drawbacks for study design and interpretation. Harvest wing surveys offer an opportunity to examine small scale variation in recruitment rates and to scale up as management or research objectives dictate. In addition, long-term and large-scale monitoring of recruitment has the potential to make important contributions to the understanding of the mechanisms that structure local variation in realized life history strategies across the broad geographic range of a single bird species. For survey design, a consequence of the local age ratio samples was that collecting wings from a relatively small number of geographic locations was unlikely to be representative of the variation in the population as a whole. This design constraint could be addressed by maximizing the number of local sites at which wings are collected or by collecting wings directly from random hunters as done with the mail survey data used here to demonstrate our methodology.

Our estimate of differential harvest vulnerability of juveniles relative to adults is consistent with previous estimates for mourning doves. Our estimate that juveniles were 1.32 times more likely to be harvested than adults was intermediate to estimates based on banding studies in the 1960’s and 1970’s when the ratio was estimated as 1.30 for the Western Management Unit (Tomlinson et al. 1988), 1.30 for the Central Management Unit (Dunks et al. 1982), and 1.42 for the Eastern Management Unit (Hayne 1975).
Our recruitment estimates were similar to previous predictions for recruitment necessary to balance estimated mortality rates. Previous estimates of necessary recruitment rates for the Western and Central Management Units respectively were 2.8 and 2.2 juveniles per pair (Dunks et al. 1982, Tomlinson et al. 1988). If we assume a 1:1 sex ratio, then our comparable estimates are 2.43 and 2.29 for these 2 management units.

The spatial pattern in state collected and mail survey samples were similar and patterns between the two years in the mail survey were similar, with the highest recruitment rates observed in the eastern half of the range. The high repeatability of age ratios among years within blocks and between collection methods indicate that estimated spatial variation in age ratios was representative of true spatial dependence in rates and not just sampling error. The estimates we present represent the first large-scale estimates of dove recruitment and can serve as a baseline for integrating recruitment into models of mourning dove population dynamics.

An additional source of potential bias in recruitment estimates from wing surveys was that reproduction for mourning doves continues into the early fall for mourning doves. Any dove less than ~ 25-d old at the time of harvest, around the age when juveniles become independent of adult feeding and begin making larger movements from their nest site to feed on their own (Hitchcock and Mirarchi 1984), are unlikely to be available for harvest when wing collections occur. Geissler et al. (1987) summarized results from a large-scale study of breeding by mourning doves and concluded that nationally, 10% of mourning doves did not fledge until after 1 Sept. This proportion is closer to 18% if a cut-off of 25 d is used for juveniles becoming vulnerable to harvest (based on Figure 5 in Geissler et al. 1987). Thus the population age ratio of independent birds at the time of harvest can underestimate overall annual recruitment rates.

MANAGEMENT IMPLICATIONS
Mourning doves offer an important recreational opportunity across the U.S. with participation in harvest by more than 1 million hunters annually in the United States (Anonymous 2004). It is conspicuous then that until recently little unified effort has gone into monitoring of population vital rates. This study complements recent efforts that have focused on implementing an operational banding program (Otis et al. 2008) and
preliminary efforts at developing population models that can be used for harvest (Otis 2006). Taken in combination and maintained long-term, the efforts are an important part of an informed management strategy that can improve the harvest regulation process while increasing our knowledge of the population dynamics for the species (Williams et al. 2002). In addition to immediately informing management decisions, the local nature of estimates of age ratios from this monitoring program offers a unique opportunity to examine how local patterns in population dynamics vary spatially across the range of a species, adding to our knowledge of avian population ecology. Both these efforts are dependent on generating accurate and unbiased estimates of age ratios. Biases for uncorrected harvest age ratios are likely to be spatially dependent making it impossible to sort out patterns of variation in true age ratios from bias without calibration of estimates. Thus correcting age ratio estimates is important for any effort that uses wing collections to study this species.

We presented a generalizable method that can be used in future efforts to monitor mourning dove recruitment based on harvest wing collections. Our method is simple to use, depending only on a sample of aged harvest wings and the latitude and longitude of the collection site (Eq 7). For areas of moderate geographic size (e.g., a county or state) we suggest correcting estimates based on the latitude and longitude of the centroid of the area and correcting based on weighting of smaller subsets for estimates for areas at larger scales (e.g., sub-region or management unit).

ACKNOWLEDGMENTS

Funding for this work was provided by the U.S. Fish and Wildlife Migratory Gamebird Research Grant Program, along with in-kind contributions from 22 state wildlife agencies. Special thanks to D. Dolton, K. Richkus, P. Padding, and J. Schulz who assisted with logistics and development of the pilot program. J. Flemming provided invaluable assistance with data entry and database development and management. The Missouri Department of Conservation hosted Wing Bees in all years. The U.S. Fish and Wildlife Service Harvest Survey Branch provided additional logistical support and mail survey data. P. Dixon provided useful comments on an earlier draft of this manuscript.
LITERATURE CITED


Table 1. Results from Monte Carlo simulations to test the efficiency of the estimation model to correct Mourning Dove age ratios for unknown-age wings. Two sets of distributions for both juvenile and adult birds and 3 different age ratios were used to generate 100 simulated data sets for each scenario. Relative bias (\((\text{estimated age ratio} - \text{true age ratio}) \times \text{true age ratio}^{-1}\)) was minor with a slight tendency to over-estimate age ratios. Bias contributed little to mean square error (MSE) as compared to sampling variance (VAR). Relative uncertainty was consistent across scenarios as measured by the coefficient of variation (CV; sqrt[MSE]*[Age Ratio]^{-1}). MSE was greater for estimated age ratios based on assigning unknown-age wings to age classes than expected MSE based on the ideal case in which all wings are correctly identified to age class.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Age Ratio</th>
<th>Relative Bias</th>
<th>VAR</th>
<th>MSE</th>
<th>CV(^a)</th>
<th>Ideal MSE</th>
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<td>0.012</td>
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<td>0.120</td>
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<tr>
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<td>0.011</td>
<td>0.011</td>
<td>0.105</td>
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<tr>
<td>Adult - 2</td>
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<td>0.103</td>
<td>0.107</td>
<td>0.048</td>
</tr>
<tr>
<td></td>
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<td>0.669</td>
<td>0.136</td>
<td>0.294</td>
</tr>
<tr>
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<td>0.009</td>
<td>0.009</td>
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\(^a\) CV = sqrt[MSE]*[Age Ratio]^{-1}
Figure 1. Probability distributions for molt class used in Monte Carlo simulations. Two distributions were generated for both juvenile (A, B) and adult birds (C, D). Vertical grid lines represent simulated timing of feather molt for primary feathers 1 to 10. Sampled observations for molt class used in simulations were generated from the cumulative distribution for the period between the molting of 2 feathers. The proportion of birds that were molt class 8 or greater and therefore classified as unknown age was 0.085 and 0.215 for the juvenile distributions (A and B) and 0.219 and 0.264 for the adult distributions (C and D).

Figure 2. Estimated recruitment rates of mourning doves, i.e., the ratio of juveniles to adults in the fall population, corrected to account for unknown-age wings and differential vulnerability. Estimates are based on wings solicited from random hunters by mail survey during the 2007 and 2008 hunting seasons. All states permitting hunting were included in the survey and all wings collected during the first two weeks of September are used to generate estimates. Each symbol represents an age ratio estimated by combining all wings in the 5 by 5° latitude and longitude block and corrected for unknown-aged wings using a correction equation we developed and for differential harvest vulnerability of the age classes. We excluded blocks with < 50 wings were collected in either year.
Figure 1

A

B

C

D

Probability

T (d)

T (d)
APPENDIX A.

**Estimating the latent molt distribution with respect to days since molt began (T)**

Fig. A.1 demonstrates the resulting estimate of \( f(T) \) for an example set of values of \( f^*(k) \) and \( \hat{\alpha}_k \). The solution is uniquely defined by the rules defined in the main text. We determined values by solving for the probabilities at the midpoint age of molt class based on a set of linear equations. Fig. A.2 graphically illustrates parameters used to fit the distribution. First, we defined \( A_k = \hat{\alpha}_{k+1} - \hat{\alpha}_k \), the estimated number of days a bird stays in \( k \)th molt class; \( R_k = (f^*[k])/A_k \), the mean density day\(^{-1}\) for birds occurring in the \( k \)th molt class; and, the unknown parameter \( \sigma_k \), the difference between the value of \( R_k \) and the estimated probability at the mid point of the \( k \)th molt class for the estimated distribution \( f(T) \). We defined the slope of the line connecting the midpoint of molt class \( k-1 \) to \( k \) to be \( S_k \), where,

\[
S_k = \begin{cases} 
0 & \text{for } k = 0,11 \\
\frac{(R_k + \sigma_k) - (R_{k-1} + \sigma_{k-1})}{0.5(A_k + A_{k-1})} & \text{for } 1 \leq k \leq 10
\end{cases}
\]  

(A.1)

Based on the constraints implied by assumptions 1 and 2 for our distribution, we defined \( f(T) \) from the midpoint of the \( k \)th molt class to the next as:

\[
f(T) = (R_k + \sigma_k) + S_k(T - 0.5(\hat{\alpha}_{k-1} + \hat{\alpha}_k)) \quad \text{for } 0.5(\hat{\alpha}_{k-1} + \hat{\alpha}_k) \leq T \leq 0.5(\hat{\alpha}_k + \hat{\alpha}_{k+1}),
\]

(A.2)

where \( T \) was the time in days since the molt process started.

Then based on our 3rd assumption of no change in the sum probability of occurring in a molt class we defined an integral representing the area under the function for 2 half triangles to equal 0 (see Fig A.2 for a graphical demonstration of the equation):

\[
0 = \int_0^{0.5A_k} \sigma_k + S_{k+1} t \, dt + \int_0^{0.5A_k} \sigma_k - S_k t \, dt
\]

(A.3)

Solving the equation, we were left with a set of linear equations, one for each molt class with the \( \sigma_k \)’s as the only unknowns to solve for. The linear equations were defined by substituting the slope estimates from Eq. A.1 into the re-expression of Eq. A.3:

\[
0 = \sigma_k A_k + \frac{(S_{k+1} - S_k)A_k^2}{8} \quad \text{for } k = \{0,1,...,11\},
\]

(A.4)
and solving for the unique values of $\sigma$ that were then used in Eq. A.2 to generate the estimates of $f_i(T)$.
Figure A.1. The observable harvest distribution of mourning dove molt classes was used to estimate a latent distribution representing the time since the molt process started measured in days. Points represent average probability a wing comes has a given molt class based on the distribution of harvested wings and the proportion of unknown-age wings molting the 8th to 10th primaries assigned to the age class. Vertical gray lines represented the estimated ages at which each primary is molted and define the endpoints for each molt class. The solid black line is the latent continuous distribution on the age scale that was calculated for the set of observed average molt class probabilities represented as points. Rules used to build the continuous distribution include that the sum probability of occurring in a molt class in the estimated distribution is the same as the true proportion in the sample and that the distribution changes linearly between midpoints of molt classes. The distribution is calculated by a set of linear equations defined in this appendix.

Figure A.2. Graphical demonstration of the technique used to estimate a latent continuous distribution defined by the number of days since molt began from the observed empirical distribution of molt classes collected at harvest for mourning doves. Shown are 1) the distribution assuming uniform probability for all days within a molt class (solid lines) and 2) the estimated continuous distribution function in which probabilities changed linearly between the midpoints of molt classes (dashed lines). Parameters defined in the figure are: $\alpha_k$ – days since molt began to the time that the feather $k$th feather was molted; $A_k$ – days a bird stays in molt class $k$; $R_k$ – average probability per d of being in molt class $k$; $\sigma_k$ – difference between $R_k$ and the probability at the mid point of molt class $k$ of the estimated distribution; $S_k$ – slope of estimated linear function between the mid-point of molt class $k$ and $k+1$. A closed form unique solution for the estimated function was derived based on the assumption that the probability of occurring anywhere within molt class $k$ was the same for the estimated function as for the true data set. As a result the area of the shaded region X must be equal to the areas of shaded regions Y and Z. This was done by equating the integrals for the equations of the 2 lines with slope $-S_k$ and $S_{k+1}$ and intercept $\sigma_k$ within the region $\alpha_k$ to $\alpha_{k+1}$ to equal 0.
Figure A.1

![Graph showing probability distribution over T (d)]
Figure A.2
CHAPTER 3. RANGE-WIDE ESTIMATES OF MOURNING DOVE RECRUITMENT AND THEIR RELATIONSHIP TO ANNUAL WEATHER VARIATION

A paper to be submitted to the Journal of Animal Ecology

David A. Miller and David L. Otis

Abstract

1. The effects of annual weather variation on avian reproduction have important consequences for large-scale population dynamics by synchronizing regional variation in recruitment.

2. 166,412 doves were aged as juveniles or adult from two surveys of post-breeding age ratios of mourning doves (*Zenaida macroura*) during 2005-2008. Samples were collected from sites throughout the species’ range in 570 1°-latitude by longitude blocks. We estimated the relationship of the proportion of juveniles in the harvest wing sample to 1) annual variation in winter precipitation, 2) early breeding season temperature, and 3) a composite measure of summer precipitation and temperature (dry-heat index). In addition, we modeled the proportion of juveniles varied across the range of the species.

3. Annual variation in the proportion of juveniles was positively related to all three weather variables with the strongest relationship to the dry heat index, then early season temperature, with weaker support for an effect of winter precipitation.

4. There was some support for systematic variation in weather effects across the range. Early season temperature had the strongest positive relationship to reproduction in the northwest and weakest in the southwest. There was weak support for a relationship between early season temperature and of winter precipitation varying across a climatic gradient. Correlation was strongest in the cooler and dryer climates, respectively.
5. Mean reproductive rates varied systematically across the breeding range.
   Reproductive rates were highest in the east. Latitudinal gradients differed across longitudinal regions with highest age ratios in northern latitudes in the west, in mid-latitudes in central sites, and in southern-latitudes in the east.

6. Our results demonstrate that variability in both temperature and precipitation is related to reproduction for mourning doves and that significant but predictable variation in mean reproductive rates occur within the species’ range. Increased sample size and use of information from other data sources will help to improve estimates of these relationships and improve understanding of how they vary across the species’ range.

**Keywords:** avian reproductive rate, climate change, harvest management, mourning dove, population dynamic.

**Introduction**

Annual variation in vital rates is an important component of population dynamics (Sæther and Bakke 2000, Gaillard et al. 2000). Weather, e.g., short-term variation in temperature and precipitation, can be an especially important causal factor in determining annual population variability because of its primary role in determining the environmental conditions that influence survival and reproduction. In addition, annual variation in weather may simultaneously influence variation in recruitment across large-scales, synchronizing annual dynamics of populations, unlike other sources of local variation that are often averaged out at regional scales (Moran 1953, Grøtan et al. 2005). As a result, mechanistic models that incorporate annual variation in weather conditions have many applications, including population viability analysis for threatened populations (Lande 1993, Franklin et al. 2000), determining annual surplus of harvested species (Gordon et al. 2004), and in predicting the effect of global climate change on populations (Sillett et al. 2000, Kausrud et al. 2008).

The effects of weather on large-scale avian demography in regards to phenology and abundance have received intense focus in recent years. Shifts to earlier breeding and migratory phenology of birds in response to warming climates are well documented (Both et al. 2004, 2006). Likewise, annual variability in population abundances has been
shown to vary in response to annual variation in weather across species’ ranges (Grøtan et al. 2005, Anders and Post 2006, Both et al. 2006). Examination of both of these phenomenal measures benefit from long-term data sets collected at numerous sites. Local effects of weather have been demonstrated on survival (e.g., Grosbois et al. 2008) and reproduction (e.g., Franklin et al. 2000), but less is understood about survival and reproduction and how they are affected by variability in weather across large spatial scales. Important improvements in estimation of current and prediction of future population dynamics can be realized by understanding the mechanistic relationships between vital rates and variation in weather.

Models that incorporate variation in dynamics across geographic and climatic gradients are necessary for predicting the effects of climate change because the effects of weather may vary within species’ ranges. The effect of weather on population dynamics predictably vary across ranges of a species (Sæther et al. 2003, Anders and Post 2006, Both et al. 2006, Balbontín et al. 2009). The effects of warmer seasonal weather, for example, is likely to be very different for a population at lower latitudes within a temperate species’ range where individuals may be near the maximum physiological threshold for temperature than at higher latitudes where warmer temperatures may improve fitness. Likewise, annual variation in weather near the upper or lower extremes of the climatic gradient in which a species occurs may force conditions that are outside of a species’ climatic niche, and thus the effects of annual variation on population dynamics may be greater.

In 2005, a large-scale program was initiated to monitor reproduction of mourning doves (Zenaida macroura) based on fall age-ratios (Miller and Otis In review). The sampling design resulted in local estimates of reproduction across much of the breeding range of this species. This monitoring program provided an opportunity to examine how annual variation in weather is associated with reproductive output across the range of the species and across the climatic gradient within the species’ range. We also benefited from a long history of research on mourning doves with which to make predictions about how weather would impact reproduction (e.g., McClure 1943, Hanson and Kossack 1963). Our strategy was to develop a small set of weather covariates that parsimoniously
described seasonal variation in temperature and precipitation and their predicted relationships to reproduction. We determined whether inter-annual variation in local recruitment rates was correlated with inter-annual variation in weather variables and whether relationships varied systematically among geographic regions or across the climatic gradient of the mourning dove’s range. We also determined how mean annual reproductive output varied across the species’ range and whether it followed predictable geographic patterns.

**Methods**

**Age Data**

We estimated the annual proportion of hatch-year birds in the post-breeding population of mourning doves using samples of wings collected annually from harvested birds in the U.S. between 1 Sept and 14 Sept. Data came from two sources. During the fall of 2005-2008 wings were collected by state wildlife agencies from designated 1 by 1° (latitude and longitude) blocks during the first two weeks of the hunting season (hereafter, state survey; see Miller and Otis *In review*). In addition, during the fall of 2007 and 2008 wings were solicited from randomly selected hunters from all states that allow dove hunting (hereafter, mail survey). Analysis of band recovery data demonstrated that >90% of sampled juveniles and adults are produced or breed locally within a radius restricted within the block size (Miller and Otis *In review*). Wings from both samples were aged annually at a central location by personnel from state agencies. Samples included unknown-age wings due to completion of wing molt and these wings were assigned to an age class based on a previously developed correction factor (Miller and Otis *In review*). State survey data were characterized by larger sample sizes for a limited set of local areas while the mail survey provided greater geographic coverage.

Wings from the state survey were collected from check stations, wing barrels, and direct solicitation of hunters. Within a given degree block, wings were collected from one or more sites, thus blocks with multiple sites provided information about local scale variation that was accounted for in analyses. Geographic locations for state survey data, i.e., latitude and longitude, were assigned based on the latitude and longitude of the block centroid (Figure 1A).
In the mail survey, individual hunters were contacted by the U.S. Fish and Wildlife Service to solicit wings from birds harvested during the first week of the hunting season. Hunters were also asked to provide information about the county in which wings were collected. Geographic locations of sampled wings were assigned based on the county centroid. Samples from counties were then aggregated into 1 by 1° blocks similar to the state survey data (Figure 1B). Unlike the state survey in which large samples occurred at distinct geographic locations, we assumed wings from this sample represented a single random sample of harvested birds from within the block.

Weather Data

Weather data were acquired from databases compiled by the National Climatic Data Center, Asheville, North Carolina, USA. We used individual weather station data compiled in monthly increments in the DSI-3220 dataset, accessed in June 2009 at http://www7.ncdc.noaa.gov/CDO/dataproduct. Monthly summaries of weather covariates were used from weather stations throughout the study range. Values of weather covariates were averaged for all weather stations within a degree block in which wings were collected to generate block level weather covariates. The mean number of weather stations in a block for temperature variables was 5.8 (range 1-20) and for precipitation variables was 7.9 (range 1-25). For < 1% of blocks weather station data were not available for all years, in which case data were imputed using the mean weather covariate value for all years with data.

We initially developed 4 covariates that related to annual differences in temperature and precipitation. Covariates were chosen that we predicted would influence the number of nesting attempts, success of the nesting attempts, or early juvenile survival, all of which would influence the proportion of juveniles in the fall population. Examination of temporal correlations in the weather covariates within blocks, i.e., the correlation between residuals when adjusted for respective block level means across all years, revealed that two of our variables were strongly correlated (r = -0.79; see below). We subsequently combined these into a composite measure. Justification and calculation
of each of the covariates was as follows:

1) **Mean Minimum Daily Temperature for April and May (MMTAM)**; Mourning doves have an extended nesting season with multiple nesting attempts that begins in late-March and April in most regions and continues through September and later (Geissler et al. 1987). It has been previously suggested that temperatures during the early part of the nesting season determine the onset of nesting effort in doves (Hanson and Kossack 1963) and that length of the nesting season would be a determinant of total annual production (Otis 2005). Thus, we predicted that MMTAM would be positively related to annual variation in age ratios based on the prediction that warmer springs would lead to longer nesting seasons and therefore a greater number of nesting attempts.

2) **Total Precipitation for January through March (TPJM)**; Higher availability of seeds, the main diet of mourning doves (Lewis 1993), early in the season and throughout the summer is likely to positively affect reproduction. Winter precipitation can have large impacts on productivity (Polis et al. 1997) increasing food ability for nesting birds by promoting early season seed productivity. Thus we predicted that TPJM would be positively related to annual variation in age ratios.

3) **Dry Heat Index (DH)**; This covariate was a composite measure of the Total Precipitation for April through August (TPAA) and the number of days in June, July, and August when the high temperature was $> 90^\circ$ F (D90JA). We predicted that precipitation during nesting would be negatively related to reproduction by reducing time spent foraging and by making foraging less efficient in preferred feeding sites on the ground in open areas (Lewis 1993). Similarly, we hypothesized that high summer temperature would improve feeding conditions by creating dry, bare ground, but that extremes in thermal conditions, especially in hotter climates, would also have negative physiological effects on nesting adults (Bartholomew and Dawson 1954, Webster and Bernstein 1987). Inter-annual variation within blocks for the two covariates was strongly negatively correlated and therefore we chose to create a single composite measure. The Dry Heat Index (DH) was proportional to the first principal component of the correlation matrix of the two measures and loaded positively for D90JA and negatively for TPAA. Thus higher values occurred in years when summers were hotter and drier than average.
predicted that DH would be negatively related to annual age ratios in climates that were extremely hot and dry because of negative physiological effects and positively related in wetter and cooler climates by positively affecting feeding conditions.

For each of the three variables we scaled values by dividing by the standard deviation of annual variation in the variable. Thus, our regression models were scaled so that the estimated coefficients were equal to the expected change in the proportion of juveniles in years when the variable was one standard deviation above average.

**Statistical approach**

We were interested in modeling 1) variation within blocks among years and 2) variation among blocks in mean annual age ratios, to estimate weather and geographic relationships, respectively. The first model addressed temporal variation in rates within sites while the second model addressed spatial variation in rates among sites. Statistical models were developed for each of these objectives to properly account for the sampling design and the probability distribution of the response variable.

The response variable in all models was the proportion of hatch-year, i.e., juvenile, birds in a wing sample \(PHY\), corrected for unknown-age wings following the methodology of Miller and Otis (In review). Using \(PHY\) of harvested wings rather than an estimate of a population age ratio meant that our measure was an index to annual recruitment, because it does not account for differential harvest vulnerability of the 2 age classes. Juveniles are generally more vulnerable to harvest than adults mourning doves (Otis et al. 2008), which results in a positive bias in \(PHY\) of the harvested population.

Values were indexed by block, year, and site so that \(PHY_{ijk}\) was the proportion of juveniles in the \(i^{th}\) block, in the \(j^{th}\) year, and the \(k^{th}\) site. We chose to estimate relationships using weighted mixed models regression (PROC MIXED, SAS) to incorporate the hierarchical nature of the data structure. We fit mixed models by maximum likelihood so that we could compare model fits using Akaike’s Information Criterion (AIC, Burnham and Anderson 1998).

The statistical models accounted for our multi-stage sampling design with repeated measures among years and unequal sampling error among sites due to differences in sample sizes. In our model notation, we used \(\alpha\) to denote fixed categorical
effects, $\beta$ to denote fixed continuous effects, $\varepsilon$ to denote sampling error in the response variable proportional to the expected binomial sampling error, and $\delta$ to denote additional random effects.

For graphical presentation of results, we transform PHY estimates to age ratio estimates using the transformation $\text{PHY}/(1 – \text{PHY})$. Age ratio estimates are more directly interpretable as a demographic vital rate and thus are more meaningful in the context of analysis of population dynamics. Confidence interval bounds for age ratios were obtained by back-transformation of confidence interval bounds for PHY estimates.

Weather Models

We used data from both state and mail surveys to fit weather models. Although collection methods differed between the state and mail survey and among blocks within the state survey, we controlled for block differences and therefore any consistent biases in estimates associated with collection methods. Estimated relationships were between annual PHY minus the mean PHY for all years versus annual weather covariates minus the mean weather covariate for all years in a single block.

For modeling within-block inter-annual variation as a function of weather covariates we used the mixed model,

$$
\begin{align*}
X_{ij} = \alpha_i + \beta X_{ij} + \delta_{ij} + \sigma_{ijk} + \epsilon_{ijk}
\end{align*}
$$

We estimated different intercepts for each block and a common slope to explain the relationship between the weather covariate measured separately for each block during each year ($X_{ij}$) and annual variation in PHY within a block. Thus, the structure allowed us to examine only temporal variation with respect to our continuous covariates while controlling for spatial variation in mean reproductive rates among blocks. The model assumes three normally distributed random components:

$$
\begin{align*}
\delta_{ij} & \sim N(0, \sigma^2_{\text{block-year}}) \\
\sigma_{ijk} & \sim N(0, \sigma^2_{\text{site}}) \\
\epsilon_{ijk} & \sim N(0, \omega_{ijk} \sigma^2) \\
\text{where } \omega_{ijk} & = \frac{\text{PHY}_{ijk} (1 – \text{PHY}_{ijk})}{n_{ijk}}
\end{align*}
$$

(2)
The random effect, $\delta_{ij}$, represents variation among each unique combination of block and year. Two random effects, $\varepsilon_{ijk}$ and $\delta_{ijk}$, were used at the site level to account for 1) binomial sampling error by weighting by $w_{ijk}$ where $n_{ijk}$ is sample size for a site and 2) process variation among sites within a block that should not be proportional to $w$ but assumed to be equal for all sites.

We first fit models using Eq. 1 where slopes for each weather covariate were the same for all blocks. We then fit models that allowed variation in slopes among geographic regions and across climatic gradients. We defined 6 geographic regions for determining regional differences. Regions were divided between north and south at 39° latitude and between east, central, and west at -92° and -109° longitude, the approximate boundaries between traditional dove management units designated based on distinct migratory routes of the populations (Kiel 1959). In addition, for each of the covariates we divided blocks into low, medium, and high categories based on ranked block averages of the variable (25%, 50%, and 25% of samples, respectively). We expected that covariate effects would differ among categories across the gradient and that largest effects would occur in blocks nearer to the extreme. For example, we predicted that in the blocks with the lowest 25% for mean DH, i.e., the coolest and wettest blocks, that the effect of DH should be most positively correlated with PHY.

We used AIC model selection procedures to evaluate weather covariates for global effects, regional effects, and climatic gradient effects. Candidate model sets were derived sequentially. The first model set was constructed by using all combinations of covariates with slopes for covariates constrained to be equal for all blocks. Using the best model from the first comparison, for each of the three variables we developed and compared models that also included regional slope parameters for each of the covariates to evaluate support for regional variation in relationships. A third model set for evaluating variation among climate categories was constructed in a similar manner so that models included differing slope parameters for low, medium, and high blocks for each covariate.
Geographic Models

We used mail survey data to examine large-scale spatial patterns in mean annual age ratios. In addition to a more spatially comprehensive coverage of the species’ range, the mail survey used consistent sampling methods across all blocks. To better visualize raw geographic variation in age ratios, we estimated mean age ratios for 5 by 5° areas and mapped estimates. We modeled age ratios from each 1 by 1° block as a function of latitude and longitude of the sample locations to determine whether variation varied systematically throughout the sampled range. In both cases we used mixed effects models similar to the weather analysis to incorporate the multi-level sampling design used to collect data.

For modeling among block spatial variation we used the mixed model,

\[ PHY_{ij} = \alpha + \beta X_i + \gamma_i + \delta_{ij} + \epsilon_{ij} \]  

Fixed effects were used to explain variation among blocks for mean PHY for all years which included categorical effects, \( \alpha \), and continuous effects unique to each block, \( \beta \). In comparison to the within block model (Eq. 1), the among block model also included an additional error term, \( \gamma_i \sim N(0, \sigma_{\text{block}}^2) \), to account for common variance among years within a single block. The site-level random effect was removed because for the mail survey samples from each block for each year were treated as coming from a single “site”. The random effects structure accounted for common variation within blocks among years (\( \gamma_i \)), weighted sampling error (\( \epsilon_{ijk} \)), and process error within blocks for a given year (\( \delta_{ij} \)).

First, we estimated age ratios for 5 by 5° areas throughout the sampling range to create an unconstrained map for visualizing geographic variation in age ratios. We chose areas of this size to create areas that were geographically limited but large enough to have sample sizes that limited estimation error. We did this by fitting a model with a fixed intercept for each 5 by 5° area, \( \alpha_h \), and the random effect structure used in Eq 3.

We then determined whether consistent patterns in recruitment occurred across latitude and longitude. We created three longitudinal strata by using the east, central, and west regional boundaries used in the weather analysis. We treated latitude as a continuous variable and created two polynomial models, a linear trend and a quadratic
trend including first and second order terms. We compared models based on AIC values that included our latitude and longitude covariates to determine the best fitting structure for spatial patterns. Longitudinal differences were modeled as separate intercepts for the $k^{th}$ region ($\alpha_k$) and latitudinal effects as continuous covariates ($\beta$). The model set included models with each effect singly, the additive combination of the longitudinal categories and each of the latitude models, as well as models with both additive effects and an interaction between latitude and longitude effects (i.e., slopes for the latitudinal gradient were allowed to differ among west, central, and east regions).

**Results**

We collected 125,328 wings 455 sites in 76 unique blocks from the state wing collection program during 2005-2008 (Figure 1A). We also collected 41,084 wings from 494 unique blocks from the mail survey collection program during 2007 and 2008 (Figure 1B). All 494 blocks provided information for estimating spatial patterns and the 250 blocks where wings were collected in both years contributed to the estimation of the effects of weather on inter-annual variation in age ratios.

First we examined weather models in which the relationships between PHY and weather covariates were constrained to have the same slope for all blocks. The best model included all three weather covariates (Table 1). The model including DH and MMTAM fit the data nearly as well with a $\Delta$AIC < 1.0. The estimated effect size for a one standard deviation increase in the weather covariate was greatest for DH, then MMTAM, and smallest for TPJM for which the 95% confidence interval of the estimate included 0 (Table 1, Figure 2). This ordering in the importance of the parameters was apparent in the summed parameter weights for each of the weather covariates (Table 1).

There was support for regional variation in MMTAM (Table 1) due to a strong positive relationship in the northwest, weakly negative relationship in the southwest, with positive slopes in the rest of the range (Table 2). There was weak evidence for differences in slopes across climatic gradients for both MMTAM and TPJM (Table 1; $\Delta$AIC < 1.0). In both cases, differences among low, medium, and high categories were consistent with our predictions. The strongest relationship between weather and PHY occurred in blocks with low mean values for the covariate (Table 2). Winter precipitation
(TPJM) had the greatest positive effect in drier areas and spring temperatures (MMTAM) the greatest positive effect in cooler climates. In both cases, estimated confidence intervals (1.96 times the SE) for the low category did not include 0 (Table 2).

Variation in annual reproduction among blocks followed consistent geographic patterns. Mapping mean age ratios for 5 by 5° showed that strong regional patterns occurred with a strong east-west gradient and the lowest age ratios occurring in the southwest (Figure 3). Fitted models based on latitudes and longitudes of blocks are consistent with strong spatial trends. Model selection supported a model in which PHY varied among west, central, and east regions with unique quadratic relationships to latitude in each region (Table 3). Age ratios were highest at high latitudes in the west, at mid-latitudes in the central, and at low latitudes in the east (Figure 4).

**Discussion**

Our results indicate that weather may be important in driving annual variation in dove recruitment. We demonstrated evidence for differential regional effects of weather and effects that changed across a climatic gradient. In addition, we found that mean annual age ratios varied greatly across both latitudes and longitudes within their range.

Mourning dove reproduction was positively associated with low precipitation and high temperatures during the breeding season, and wet winters. This was consistent with our predictions based on the ecology of the species and suggests that weather has direct role in generating at least some of the annual variation in recruitment. Results are also consistent with the preponderance of evidence for climate having important consequences for population dynamics at both local (Franklin et al. 2000, Grosbois et al. 2008) and range-wide levels (Both et al. 2004, Anders and Post 2006). Reproductive output and juvenile survival are especially important in understanding mechanistic relationships between climate and population dynamics because of the greater annual variation in these parameters (Sæther and Bakke 2000, Gaillard et al. 2000). Our finding of strong relationships of breeding season weather to reproduction differs from results of Sæther et al. (2004) where winter weather rather than summer conditions had a stronger effect on population dynamics of northern altricial birds.
We found some support for differences in the effects of weather variation within the range of mourning doves. More data are needed to confirm results; however, the trends are consistent with predictions that weather effects will vary across the species’ range and that effects of weather, i.e., winter precipitation and early season temperatures, will be greater in more extreme environments. Higher levels of winter precipitation had the greatest effect in sites characterized by low average winter precipitation while higher temperatures in April and May had the greatest effect in sites characterized by low spring temperatures. This is consistent with other studies that show that the effects of weather on population dynamics vary across species’ ranges (Sæther et al. 2003, Anders and Post 2006, Both et al. 2006, Balbontin et al. 2009) and suggests that regional differences in recruitment-weather relationships may be predicted based on the relative location of a population within its climatic niche.

*Future refinement of recruitment models*

Our results show promise for estimating the relationship of annual variation in reproduction to important environmental covariates. The large numbers of spatial replicates in the study design were an important component of the ability to estimate relationships, mitigating for the short temporal duration of the dataset. Mourning doves are somewhat unique among migratory game birds in that harvest parts surveys to estimate recruitment can be targeted to local birds by restricting collections to the beginning of the harvest season (Miller and Otis *In review*). The local nature of estimates should speed the acquisition of knowledge from monitoring programs through spatial replication. For example, one additional year of data from 2009 will double the current degrees of freedom from the mail survey data set for estimating within block relationships in which the number of degrees of freedom is equal to the number of years of data minus one. Under the assumption that the USFWS mail survey is institutionalized as an annual monitoring program, we envision that the accumulation of spatially comprehensive age data during the next several years will allow development of increasingly useful spatially explicit predictive models of recruitment that incorporate adjustments for weather variation.
Our estimated longitudinal and latitudinal trends in recruitment are consistent with predicted longitudinal variation for reproductive rates made based on season length by Otis (2005). In combination with recent efforts to estimate survival (Otis et al. 2008) data are available to begin to investigate basic life-history strategies of doves across their range. Reproductive data indicate that the balance between reproduction and survival likely differs greatly across the mourning dove range, and therefore population dynamics may differ greatly. In addition, this variation should lead to variation in sensitivities of population growth rates to changes in vital rates (Caswell 2000), potentially leading to very different effects of harvest rates on population dynamics (Williams et al. 2003).

The development of an operational program to monitor mourning dove recruitment (Miller et al. In review) in conjunction with long-term indices of population abundance (Sauer et al. 1994) and banding efforts to estimate survival and harvest rates (Otis et al. 2008) fulfill information streams called for by the national strategic harvest plan for mourning doves (Anonymous 2004). The next step in implementing the plan is to begin to develop population models that can be used for making harvest management decisions based on these available data sets. This integration of multiple data sources offers an additional opportunity to take advantage of information from all of the monitoring programs to improve our understanding of relationships such as those examined in this study. Recent methodological advances integrate information used to estimate survival and reproduction with estimates or indices of abundance into single analyses, taking advantage of the functional relationship between vital rates and changes in abundance through time through state space modeling (Besbeas et al. 2002). Within a maximum-likelihood (Tavecchia et al. 2009) or Bayesian framework (Fonnesbeck and Conroy 2004, Hoyle and Maunder 2004), parameters and their relationships to external covariates are simultaneously estimated to determine functional relationships. This integrated approach combines the processes of parameter estimation and population model building and may be useful in improving understanding of factors influencing vital rates for mourning doves.
Literature Cited


Table 1. Model selection results for models predicted inter-annual variation within individual blocks in the proportion of hatch year mourning doves in wing samples from both state survey (2005-2008) and mail survey (2007-2008) wing collections. Random effects were used to properly control for the two-stage sampling technique and sampling error. These included effects of block-year, site, and weighted errors. Separate fixed intercepts were estimated for each block with common slopes for weather covariates used among blocks either at a global level (all blocks), or within regions or gradient categories.

<table>
<thead>
<tr>
<th>Model Selection</th>
<th>Model Parameter Estimates $^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>$k$</td>
</tr>
<tr>
<td>DH MMTAM TPJM</td>
<td>7</td>
</tr>
<tr>
<td>DH MMTAM</td>
<td>6</td>
</tr>
<tr>
<td>DH TPJM</td>
<td>6</td>
</tr>
<tr>
<td>DH</td>
<td>5</td>
</tr>
<tr>
<td>MMTAM</td>
<td>5</td>
</tr>
<tr>
<td>MMTAM TPJM</td>
<td>6</td>
</tr>
<tr>
<td>Intercept only</td>
<td>4</td>
</tr>
<tr>
<td>TPJM</td>
<td>5</td>
</tr>
</tbody>
</table>

Relative covariate importance ($\Sigma w^4$)

<table>
<thead>
<tr>
<th>Regional Models $^5$</th>
<th>Regional Models $^5$</th>
<th>Gradient Models $^6$</th>
<th>Gradient Models $^6$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$k$</td>
<td>AIC</td>
<td>$\Delta$AIC</td>
<td>$w$</td>
</tr>
<tr>
<td>DH MMTAM TPJM</td>
<td>12</td>
<td>-2008.2</td>
<td>0.0</td>
</tr>
<tr>
<td>DH MMTAM TPJM</td>
<td>7</td>
<td>-2003.9</td>
<td>4.3</td>
</tr>
<tr>
<td>DH MMTAM TPJM</td>
<td>12</td>
<td>-1999.3</td>
<td>8.9</td>
</tr>
<tr>
<td>DH MMTAM TPJM</td>
<td>12</td>
<td>-1998.8</td>
<td>9.4</td>
</tr>
</tbody>
</table>

$^1$Weather covariates are standardized so that effect size estimates are the predicted change in the proportion of hatch year birds given the weather variable is one standard deviation above the average.

$^2$Models assume a single slope for the weather effect for all blocks throughout the range. Weather parameters are: DH – Dry Heat Index, MMTAM – Mean Minimum Daily Temperature for April and May, and TPJM – Total Precipitation for January to March.

$^3$A measure of the probability that the model is the “best” model among those examined given AIC as a selection criteria: $w = e^{-0.5\Delta AIC}/\sum e^{-0.5\Delta AIC}$.

$^4$Sum of $w_i$ for models that include the parameter. A measure of parameter support.

$^5$For each of the weather covariates we included a model in which the slope of the relationship varied among regions (REG). Regions were divided north and south at 39° latitude and between west, central, and east at -109° and -92° longitude for a total of 6 regions.

$^6$For each of the weather covariates we included a model in which the slope of the relationship varied among sites depending on a gradient defined by the annual mean of the weather variable for the block. Three gradient categories (GRAD) were defined based on the lower 25%, middle 50%, and upper 25% of the ranked blocks.
Table 2. Estimated relationship of weather covariates to annual differences in the proportion of juveniles in the harvest population from models that included variation among climatic gradient categories or geographic regions.

<table>
<thead>
<tr>
<th>Weather Covariate</th>
<th>Climatic Gradient</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low SE</td>
<td>Medium SE</td>
<td>High SE</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TPJM</td>
<td>0.0205</td>
<td>0.0018</td>
<td>0.0025</td>
<td>0.0027</td>
<td>0.0022</td>
<td></td>
</tr>
<tr>
<td>MMTAM</td>
<td>0.0119</td>
<td>0.0048</td>
<td>0.0031</td>
<td>0.0001</td>
<td>0.0047</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Regions</th>
<th></th>
<th>West SE</th>
<th>Central SE</th>
<th>East SE</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>MMTAM – North</td>
<td>0.0420</td>
<td>0.0035</td>
<td>0.0039</td>
<td>0.0069</td>
<td>0.0072</td>
<td></td>
</tr>
<tr>
<td>MMTAM – South</td>
<td>-0.0035</td>
<td>0.0042</td>
<td>0.0051</td>
<td>0.0039</td>
<td>0.0042</td>
<td></td>
</tr>
</tbody>
</table>
Table 3. Model selection results for spatial models of the proportion of hatch year mourning doves in the harvest population based on mail survey data during 2007 and 2008. Samples were divided into 3 regions based on longitude (cLON), while latitude was examined as a linear and quadratic variable (LAT and LAT*LAT).

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>w</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAT*LAT *cLON</td>
<td>12</td>
<td>-1036.1</td>
<td>0.0</td>
<td>0.93</td>
</tr>
<tr>
<td>LAT *cLON</td>
<td>11</td>
<td>-1031.0</td>
<td>5.1</td>
<td>0.07</td>
</tr>
<tr>
<td>cLON</td>
<td>6</td>
<td>-1017.8</td>
<td>18.3</td>
<td>0.00</td>
</tr>
<tr>
<td>LAT + cLON</td>
<td>7</td>
<td>-1017.3</td>
<td>18.8</td>
<td>0.00</td>
</tr>
<tr>
<td>LAT*LAT + cLON</td>
<td>8</td>
<td>-1016.7</td>
<td>19.4</td>
<td>0.00</td>
</tr>
<tr>
<td>LAT*LAT</td>
<td>6</td>
<td>-960.5</td>
<td>75.6</td>
<td>0.00</td>
</tr>
<tr>
<td>Intercept Only</td>
<td>4</td>
<td>-953</td>
<td>83.1</td>
<td>0.00</td>
</tr>
<tr>
<td>LAT</td>
<td>5</td>
<td>-951</td>
<td>85.1</td>
<td>0.00</td>
</tr>
</tbody>
</table>
**Figure 1.** Locations of collection blocks for state (A) and mail (B) surveys of mourning dove harvest age ratios. Wing samples were aggregated into 1 by 1° latitude and longitude blocks.

**Figure 2.** Estimated effects of weather covariates on age ratios of mourning doves during 2005-2008. Effect sizes are based on estimates of a single slope for weather covariates for all blocks in the study. For blocks with a mean age ratio at the value denoted by the solid line, the short dashed lines represent predicted change in age ratios for ± 1 standard deviation in the weather covariate and the long-dashed line represents predicted effect size on age ratios ± 2 standard deviations in the weather covariate.

**Figure 3.** Estimated age ratios of mourning doves for 5 by 5° latitude and longitude blocks during 2007 and 2008. Three blocks with small sample sizes had 95% CI coverage on estimates of PHY that were > 0.15 in width and were not included because of the low precision. Estimates are shown at the block centers and are averages of all samples ± 2.5° in all directions.

**Figure 4.** For sites in the west U.S. (west of -109° longitude), central U.S. (between -109° and -92°), and east U.S. (east of -92°), we present the predicted mean annual harvest age ratio of mourning doves during 2007 and 2008 with respect to latitude. Dashed lines represent 95% CI’s.
Figure 1
Figure 2

- **DH**
- **MMTAM**
- **TPJM**

Predicted age ratio for annual weather variation
Figure 3
Figure 4

Latitude (degrees)

West

Central

East

Age Ratio (HY:AHY)

3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4

33 36 39 42 45 48

32 30 33 36 39 42 45 48

30 33 36 39 42

3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
CHAPTER 4. INDIVIDUAL VARIATION IN BASELINE AND STRESS-INDUCED CORTICOSTERONE AND PROLACTIN LEVELS PREDICTS PARENTAL EFFORT BY NESTING MOURNING DOVES.

A paper published in Hormones and Behavior

David A. Miller, Carol M. Vleck, and David L. Otis.

ABSTRACT
Endocrine systems have an important mechanistic role in structuring life-history trade-offs. During breeding, individual variation in prolactin (PRL) and corticosterone (CORT) levels affects behavioral and physiological processes that drive trade-offs between reproduction and self-maintenance. We examined patterns in baseline (BL) and stress induced (SI; level following a standard capture-restraint protocol) levels of PRL and CORT for breeding mourning doves (Zenaida macroura). We determined whether the relationship of adult condition and parental effort to hormone levels in wild birds was consistent with life-history predictions. Both BL PRL and BL CORT level in adults were positively related to nestling weight at early nestling ages, consistent with the prediction of a positive relationship of hormone levels to current parental effort of adults and associated increased energy demand. Results are consistent with the two hormones acting together at baseline levels to limit negative effects of CORT on reproduction while maintaining beneficial effects such as increased foraging for nestling feeding. Our data did not support predictions that SI responses would vary in response to nestling or adult condition. The magnitude of CORT response in the parents to our capture-restraint protocol was negatively correlated with subsequent parental effort. Average nestling weights for adults with the highest SI CORT response were on average 10-15% lighter than expected for their age in follow-up visits after the stress event. Our results demonstrated a relationship between individual hormone levels and within population
variation in parental effort and suggested that hormonal control plays an important role in structuring reproductive decisions for mourning doves.

*Keywords*: allostasis, capture-restraint protocol, glucocorticoid, pleiotropic effects, stress.

**Introduction**

The central theme of the study of life-history evolution has been to elucidate trade-offs among different components of fitness and to determine the environmental factors that influence these trade-offs (Stearns 1992). An important component of life-history study has been focused on understanding the physiological mechanisms that underlie trade-offs (Zera and Harshman 2001, Ricklefs and Wikelski 2002). Within this context, endocrine systems are of special interest because of the importance of hormones in orchestrating behavioral and physiological shifts between life-history stages and in structuring individual variation in investment (e.g., survival versus reproduction) within stages (Ketterson and Nolan 1992, Finch and Rose 1995).

Prolactin (PRL) and corticosterone (CORT) have been shown to have major pleiotropic functions in vertebrate physiology that include actions related to reproductive effort (Bole-Feysot et al. 1998, Sapolsky et al. 2000). Therefore, they are ideal hormones to look at in the context of structuring life-history trade-offs. Both baseline (BL) and stress-induced (SI; in response to acute stressors) levels of PRL and CORT have demonstrated central roles in behavior and physiology during avian reproduction (Silver and Cooper 1983, Horseman and Buntin 1995, Buntin 1996, Wingfield et al. 1998, Romero 2002, McEwen and Wingfield 2003, Landys et al. 2006, Anglier and Chastel 2009).

Although there is a strong body of evidence for understanding how PRL and CORT levels vary between species and among different periods within the life history of individuals (Horseman and Buntin 1995, Romero 2002), less attention has been given to individual variation within populations during a single life-history stage (Williams 2008). During reproduction individuals must balance investment in current and future reproduction (Williams 1966) and are likely to vary their reproductive effort in response
to their current state, environmental conditions, and future opportunities (McNamara and Houston 1996). Endocrine systems have the potential to play an important role in orchestrating decisions to optimize life-history decisions by assimilating input regarding current conditions and adjusting physiology and behavior to optimize investment (Finch and Rose 1995). If this is the case, we expect individuals to vary BL and SI levels of PRL and CORT in response to their current condition and in parallel with parental effort.

PRL plays an important role during reproduction for Columbiformes (i.e., doves and pigeons; Silver and Cooper 1983, Horseman and Buntin 1995) by stimulating behavioral and physiological actions involved in the crop-milk feeding of nestlings. Crop milk consists of regurgitated cells of the crop epithelium that have been transformed into a high nutrient source of food for young (Davies 1939). In mourning doves (*Zenaida macroura*), crop milk is primarily fed during the first half of the nestling period from hatch to 4-5 days of age, with the proportion of crop milk in feedings declining during the late nestling period (Mirarchi 1993). In addition to crop-milk production, during reproduction PRL has been shown to positively affect regurgitation behavior, broodiness, and other parental behaviors (Wang and Buntin 1999) and promote changes in the immune system (Barriga Ibars et al. 1997). In several bird species, PRL level has been shown to decline in response to acute stressors (reviewed in Chastel et al. 2005, Angelier and Chastel 2009). The factors affecting and the consequences of the avian PRL stress response have received little study. PRL response to stress was suppressed in breeding black-legged kittiwakes (*Rissa tridactyla*) when compared to non-breeding birds (Chastel et al. 2005), and in older individuals in a population of snow petrels (*Pagadroma nivea*) where reproductive output increases with age (Angelier et al. 2007a), indicating that modulation of the PRL stress response may be important in maintaining parental effort in birds.

Traditionally, studies of CORT have focused on BL level as an indicator of negative effects of stress. However, the concept of allostasis has emerged as a framework for structuring hypotheses based on life-history theory and endocrine processes (McEwen and Wingfield 2003, Landys et al. 2006). Allostasis is defined as
changes in physiological state that promote the maintenance of stability (i.e., homeostasis) across changing environments and conditions. Allostasis is important in maintaining energy balance across different life-history stages and will vary among individuals with respect to their current condition and to the level of reproductive investment. Glucocorticoid concentration (McEwen and Wingfield 2003, Landys et al. 2006) has been proposed to be central in allostatic processes by facilitating behavioral and physiological changes to match current energy demands of individuals.

Within this framework predictions can be made about how CORT should vary among and within life-history stages for free-living birds. BL and SI CORT levels promote different physiological states and thus are predicted to have different effects on reproductive behavior (Landys et al. 2006). Avian species show a general increase in BL CORT level during reproduction (Romero 2002) indicating that increasing BL CORT level may promote behaviors that meet the additional energetic and physiological needs associated with reproduction. Elevated BL CORT can affect physiology by increasing available energy, can affect behavior by stimulating higher feeding rates, and may play a preparative role by priming individuals for potential stressors that may occur during a life-history stage (Sapolsky et al. 2000, Romero 2002). In the ring dove (Streptopelia risoria), elevation of PRL causes a subsequent elevation in CORT, which may meet the increased physiological energy demands of crop-milk feeding as well as stimulating feeding behavior to increase available energy (Koch et al. 2002, Koch et al. 2004).

The potential for SI CORT secretion to affect the life-history trade-off between the immediate needs of an individual for survival and their investment in reproductive output has led to a focus on factors that cause individuals to modulate their stress response (Wingfield et al. 1998, Romero 2002, Wingfield and Sapolsky 2003). There is mixed evidence that birds suppress their CORT response to acute stressors during breeding (Romero 2002, Wingfield and Sapolsky 2003) or that different populations of the same species vary their response to reflect different conditions during breeding (Kitaysky et al. 2007, Shultz and Kitaysky 2008). Differences among species in reproductive value of offspring predict differences in SI CORT responses (Bokony et al.
indicating that life-history predictions may be important in driving variation in the response. An alternative approach to investigation is to examine individual variation in the stress response to determine if responses are modulated in response to life-history trade-offs (Lendvai et al. 2007, Williams 2008).

Columbiformes have served as a model for laboratory studies of avian endocrine regulation (e.g., Riddle et al. 1933, Horseman and Buntin 1995), making the taxon an ideal model for examining the relationship between endocrine function and life-history trade-offs within wild populations. Laboratory studies show that BL levels of both hormones are important in determining reproductive behavior (Horseman and Buntin 1995, Koch et al. 2002). In addition, SI changes in response to acute stressors (i.e., increases in CORT secretion and decreases in PRL level) may help mediate the immediate costs of the stress event and have indirect effects on reproductive behavior by reducing investment in current reproductive effort (Wingfield et al. 1998, Chastel et al. 2005, Angelier and Chastel 2009).

We examined whether BL and SI levels of PRL and CORT in mourning doves fit six predictions or hypotheses based on life-history theory and our current understanding of the function of both hormones during reproduction. When examining individual variation in BL level we focused on two different components of investment: adult weight as a measure of available endogenous resources and nestling weight as a measure of parental effort in the current nesting attempt. The first prediction we made was that if hormone levels were driven by adult condition, structuring prioritization of adult maintenance over reproductive output, lighter adults would suppress BL PRL because less energy would be available to transfer to feeding young, and would increase BL CORT level to meet the increased energy demands on the adult. Our second prediction was that alternatively, if CORT plays a primary role in promoting hyperphagia and weight gain as hypothesized by Koch et al. (2002, 2004), we would expect to see a positive relationship between CORT and adult weight. Our third and fourth predictions were that if reproduction was prioritized in hormone function, parental effort of adults at the same reproductive stage would be positively correlated with PRL, promoting greater
feeding of young, and that CORT level would be elevated to meet the greater energy demand of higher feeding rates.

SI CORT levels are expected to lead to a different physiological state than those typical of BL levels by mechanisms such as binding to different receptors (Landys et al. 2006) promoting an “emergency life-history stage” where self-maintenance is prioritized over reproduction (Wingfield et al. 1998). Likewise, some evidence suggests that the magnitude of decrease in PRL in response to an acute stressor may be negatively related to current and subsequent investment in breeding (Chastel et al. 2005, Angelier et al. 2007, Angelier and Chastel 2009). Therefore, our fifth prediction was that the magnitude of SI responses of both hormones would be smallest when adults were heaviest and likely to maintain their reproductive effort in the face of greater stress and when nestlings were heavier and thus parental effort had been high. Finally our sixth prediction was that the magnitude of SI responses would be inversely related to subsequent parental effort.

Methods

Data collection

Samples were collected as part of a larger study on reproductive ecology of mourning doves in central Iowa, USA between May and August of 2005 and 2006. Nests were found by systematic searches of trees and shrubs at four sites characterized by a mix of trees and grassland that were located within a matrix of intense agricultural land-use (i.e., primarily corn and soybean row-crops). Clutch size for mourning doves is two eggs. Nests were monitored on a regular basis (~3-5 days between visits, every 1-2 days near the predicted hatch date to determine hatching date) until the young either fledged or the nest was destroyed by predation or weather events. Eggs were candled to determine their age ± 1 days for all nests found during the incubation period (Hanson and Kossak 1963). Nestling age was determined based on observations of hatching and the hatch day was considered to be day 1.

We collected blood samples from adult females and males to measure plasma concentrations of PRL and CORT. Both adults contribute to the incubation and feeding of the young. Males generally take incubation and brooding duties during the day (~1000
to ~1800 h), while females are present on the nest from early evening to mid-morning (~1800 to ~1000 h the following day). Males were sampled between 1150 and 1600 h (\( \bar{x} = 1355 \)) while females were sampled from 1820 to 2030 h (\( \bar{x} = 1911 \)). Adults were trapped by flushing birds off their nest into a mist-net placed adjacent to the nest site. Birds were immediately removed from the net and a blood sample of 250-500 \( \mu l \) was collected from the brachial vein to measure BL hormone concentrations. A second sample was taken following a standard capture-handle-restraint protocol (Wingfield et al. 1992). Birds were handled to take measurements after the first sample was collected, then birds were restrained by placing them securely in a cotton bag until 30 min had passed from the initial capture, at which time the second blood sample was collected. Samples were immediately placed in a microcentrifuge tube and placed in ice. Samples were centrifuged within 8 hours of capture to separate plasma from cell, and plasma samples were stored in a -80\(^\circ\) C freezer until hormone levels were assayed.

Measurements of nestling weight (± 0.1 g) were taken at the time that adults were trapped and at follow-up visits to the nest site to check the nest’s status. Measurements of adult weight (±0.1 g) and wing length (± 0.5 mm) were taken. Samples were cross-sectional with only a single sample from an adult within a single nesting attempt, although in some cases both the male and female were caught from the same nest. Only one bird was sampled more than once, during two nesting attempts that occurred more than one year apart.

For adult weight (AW) we calculated residual adult weight in grams when plotted versus wing chord length, a measure of size-independent weight (Johnson et al. 1985). When adults were relatively heavy compared to birds of a similar size, values were positive, while birds that were light for their size had negative values.

As a measure of parental effort, we calculated the residual weight for nestlings from a spline regression for nestling weight plotted versus nestling age because mean weight gain was non-linear with respect to age. This served as a measure of relative growth in weight and an indirect measure of parental effort where we assumed differences in weight gain were dependent on differences in parental feeding. We
calculated the average value of the residual weight for both nestlings in a nest and used that as an index to residual nestling weight (NW).

We also wanted to examine the effect of adult hormonal stress responses to capture on parental effort following the capture. To measure this we calculated how our measure of residual nestling weight, NW, changed from the time of adult capture to subsequent follow-up visits. We calculated the difference in NW on the date the adult was captured (time 1) and NW on the date when the nest was last visited (time 2; nestlings age 7 to 11 days) as a measure of the change in nestling weight (ΔNW). Thus, if at time 1 nestlings within a nest averaged 2 g heavier than the mean for young at that age and at time 2 nestlings within a nest averaged 3 g lighter than the average for that age, the value of ΔNW for that nest would be -5 g. This served as a measure of how investment in reproduction changed in response to the stress event.

Birds were captured under all appropriate federal and state permits and all procedures were reviewed and approved by the Iowa State University - Institutional Animal Care and Use Committee.

**Hormone assays**

Concentrations of plasma CORT and PRL were determined by double antibody radioimmunoassay (RIA). Samples were run in triplicate whenever sufficient plasma was available. Separate assays were run for each hormone in the 2 years. Intra-assay variation for CORT assays was 11.1% and 10.3% for 2005 and 2006 samples respectively and for PRL assays was 7.0% and 9.4% for the 2 years. Assays were run 1 year apart and we did not have an accurate measure of inter-assay variability because replicate samples from the first set of assays were not reliable after being stored for this long. We controlled for assay/year in all analyses; however, we were unable to distinguish annual effects from assay effects in the analyses.

CORT concentrations were measured using a commercially available immunoassay kit (ImmuChem™ Double Antibody Corticosterone $^{125}$ RIA Kit, Catalog No. 07-120103, MP Biomedicals, LLC). The kit has been previously verified for parallelism and recovery of exogenous CORT using mourning dove plasma samples
(Washburn et al. 2002). We followed the protocol outlined by Washburn et al. (2002) except we diluted plasma samples in a 1:25 ratio rather than a 1:50 ratio to maximize precision in measurements for both low (BL) and high (SI) samples.

PRL was measured using an avian prolactin double antibody RIA following the protocol for iodination and PRL assay of Vleck et al. (2000). Chicken prolactin for iodination (AFP-4444B) and reference standards (AFP-10328B) as well as rabbit anti-chicken prolactin antibodies (AFP-151040789) were obtained from Dr. A. F. Parlow and the National Hormone and Peptide Program of the National Institute of Diabetes and Digestive and Kidney Diseases. Secondary antibodies were obtained from Antibodies, Inc. (catalog # 51-155-0005). We used 20-µl samples of plasma in the assay. The assay was verified for mourning doves for parallelism by serially diluting plasma samples ranging in volume from 80 to 5 µl and testing whether slopes differed between standards and diluted samples plotted against the percent binding (p = 0.79).

BL hormone values were determined from the initial sample while SI levels were calculated as the difference between the initial sample and the sample taken 30 min after the initial capture.

Statistical Analyses

Our data sets were largely observational with the only manipulation being the capture-restraint protocol used to simulate stress. Thus observations of hormone levels were not in response to randomly assigned treatments. For each specific prediction about a relationship of BL and SI hormone levels to different combinations of explanatory variables, we developed a set of alternative multiple regression models and compared them with Akaike’s Information Criterion (AIC). Model sets included all possible combinations of main effects and interaction described below. This statistic is a measure of model parsimony that combines the negative log-likelihood of the model with a penalty for the number of parameters in the model. Model selection using this information-theoretic philosophy is an appropriate and commonly used approach for observational studies (Burnham and Anderson 1998).
After a best model was determined for each analysis, we examined each of the regression parameter estimates to assess their importance by computing confidence intervals and inferring that there was strong support for the importance of the parameter if the 95% confidence interval did not include 0. For each response variable we present the covariates included in the best model, $R^2$ values for the model, and parameter estimates along with 95% confidence intervals.

We only included samples for BL measurements that were collected within 4 min of the time of initial capture to minimize effects of handling time (Romero and Reed 2005). Even within this timeframe CORT levels can be elevated and therefore we included an effect of handling time in all analyses of baseline CORT levels. We corrected BL CORT level to a standard handling time of 1.5 minutes, the smallest handling time in our study, and below the time at which plasma CORT is expected to start significantly increasing in concentration after an initial stressor (Romero and Reed 2005). In addition to the handling time effect, for all models we also included an effect for assay/year in all analyses (see Hormone assays).

To test predictions, we examined how parents’ hormone levels varied in response to adult weight and nestling weight (AW and NW). We included covariates for nestling age, AW, and NW. We included two-way interactions between age and AW and between age and NW because the relationship between adult and nestling state may have changed as nestlings grew older and adults shifted from crop-milk feeding with endogenous resources to seed feeding with exogenous resources.

In examining how SI hormone levels related to changes in parental effort after the stress event ($\Delta$NW), we included covariates for SI hormone levels, sex, and their interaction, with $\Delta$NW as the response variable. We included only nests where one adult was captured, because we relied on measurements after the initial capture and therefore the effect of capturing the other adult was likely to have direct effect on measurements of the nestlings. However, to verify that results were independent of the sample, we also ran models with samples from nests where both adults were captured.
Our objectives in this study did not related to sex-specific hypotheses about hormonal relationships, and therefore we chose to analyze male and female data together. We made the null assumption that no difference between the males and the females occurred because both sexes play important and relatively equal roles in incubation and feeding of young. Previous studies of Columbiformes find similar patterns in hormone profiles for PRL and CORT for both sexes (Horseman and Buntin 1995, Washburn et al. 2002), and exploratory analysis with our data set found that overall mean values of both BL and SI hormone levels differed little between the sexes (Table 1). To test this assumption for patterns in individual variation as opposed to means, we compared the best model from the initial analysis to one in which all effects differed by sex to determine whether there was support for sex-specific patterns in hormone levels.

In addition to the multiple regression analysis, we used path analysis to examine relationships among BL hormone levels and adult weight and nestling weight (Olobatuyi 2006). This allowed for a more explicit estimation of relationships among parameters and a comparison of alternative models for how the parameters related to each other (Grace 2008). Hormone levels were adjusted for handling time in the case of CORT and for assay effects by adjusting to the mean between years/assays. We estimated path coefficients based on the correlation matrix for the covariates to generate standardized path coefficients. Alternative models were compared using AIC and fit of models to the overall correlation matrix was assessed using a $\chi^2$ goodness-of-fit test, which is a test for significant correlation among variables not explained by the model. Models that fit the data well were those with low AIC values and non-significant $\chi^2$ values.

**Results**

*Hormone levels, nestling weights, and adult weights*

We captured 30 male and 35 female birds during the 2 years that were used in subsequent analyses of variation in PRL and CORT among individuals during the nestling period. Ages of nestlings at the time of capture ranged from 1 to 7 days. Mean hormone levels differed little between males and females or between the late and early period (Table 1).
The best model describing BL PRL ($R^2 = 0.58$) included an effect of nestling age (-0.23; 95% CI = ±0.49), NW (1.24 ± 0.72), and their interaction (-0.26 ± 0.16). Additional parameters included in competing models with low $\Delta$AICc values all had confidence intervals that widely overlapped 0, suggesting the best model included the important parameters for this data set. BL PRL level was positively related to NW at early nestling ages while this relationship disappeared or even slightly reversed at late nestling ages (Fig. 1A). There was some evidence suggesting patterns for BL PRL differed among the sexes. When the best model was compared to a model in which parameters differed between the sexes the $\Delta$AICc value was 0.56 with three additional parameters. This model showed that the positive relationship between NW and BL PRL occurred for both sexes; however the effect was larger for females than males.

The best model for SI PRL included only an intercept term, and therefore our analysis did not support a relationship between the PRL stress response and nestling or adult weight.

The best model for BL CORT ($R^2 = 0.37$) included effects for nestling age (0.25; 95% CI = ±0.24), NW (0.47 ±0.35), and their interaction (-0.08 ±0.07). The handling time effect was consistent with other studies, with CORT levels increasing 0.90 ng·ml$^{-1}$·min$^{-1}$ (±0.66). Similar to our results for BL PRL, we found that BL CORT was positively related to NW during the early nestling period, while the relationship disappeared once young reached 6 days of age (Fig. 1B). The next best model included an additional effect of AW and its interaction with age ($\Delta$AIC$_c$ = 1.2) with CORT positively related to AW and the effect declining with age. However, support for this effect was not strong with the confidence interval for both effects overlapping 0. There was little support for a difference in patterns between the sexes. The sex-specific version of the best model had a $\Delta$AIC$_c$ value of 4.56 with wide overlap of 0 for all confidence intervals of parameter interactions with sex.

The best model for SI CORT ($R^2 = 0.13$) included NW, however, the confidence interval overlapped 0 (= 0.48; 95% CI ±0.54). The model with only the assay/year effect and none of our effects of interest fit nearly as well as the best model ($\Delta$AIC$_c$ = 1.0).
Thus, we could not demonstrate conclusive support for a relationship between SI CORT and NW.

To further examine the relationship among the variables, we compared three path models for BL hormone levels and a null model that included no interactions among the parameters (Fig. 2, Table 2). Because relationships between hormone levels and NW appeared to differ between the early nestling period and the later period we fit separate models for data from nests where young were ≤ 4 days old and those where young were ≥ 5 days old (n = 35 and 30, respectively). Model 1 was our full model with all hypothesized relationships that included effects of AW on PRL and CORT as well as NW, correlation between PRL and CORT, and effects of PRL and CORT on NW. Model 2 was based on results from our regression models where the effect of AW on CORT and PRL was eliminated from the full model. Finally, Model 3 was based on results from Koch et al. (2002, 2004), which indicate that CORT elevation may occur secondarily to PRL elevation to promote hyperphagia by adults. For this model, we specified PRL to have a direct effect on NW and CORT. CORT was specified to have a direct effect on AW leading to weight gain and AW subsequently affected NW. Prior to fitting models we eliminated year/assay effects for both hormones and corrected CORT for handling time, using residual values in the analysis.

During the early period, both the null model and Model 2 had a significant lack of fit for the correlation matrix, indicating significant relationships among variables were left out of the model (Table 2). Model 3 fit the data well, while being more parsimonious than Model 1. This was reflected in the model ranks with Model 3 having the lowest AIC value. Path coefficients for the early period are shown in Figure 2. For Model 3, CORT was positively related to PRL (Fig. 3, p = 0.005) and to NW (p = 0.025), AW was positively related to CORT (p = 0.005), and NW was positively related to AW, although marginally insignificant (p = 0.054). For the late period there was little evidence for relationships among the variables. The goodness-of-fit test for lack of fit of the null model was not significant and the null model had the lowest AIC value for the late period.
Post-stressor effects

We took samples from 18 adults (11 males, 7 females) where only one adult was captured from a nest and the nest survived long enough after the capture-restraint protocol to be able to examine factors affecting \( \Delta \text{NW} \). The best model for \( \Delta \text{NW} \) \( (R^2 = 0.39) \) included an effect for SI CORT. SI CORT was negatively related to \( \Delta \text{NW} \) \((-0.29; 95\% \text{ CI} = \pm 0.20; \text{Fig. 4}) \). Nestlings of adults that showed a minimal CORT response after the stress protocol maintained similar growth rates in the following days, while nestlings of individuals that had the highest CORT response \( (\text{SI CORT} > 35) \) on average lost more than 6 g in relative weight between the stress event relative and the subsequent follow-up visit \((-10-15\% \text{ of average weight at late nestling ages}) \). Although more variation in the data occurred, results were qualitatively the same when we included samples for nests where both adults were captured \( (n = 20 \text{ males}, 14 \text{ females}) \). Again, the best model for \( \Delta \text{NW} \) \( (R^2 = 0.17) \) included a negative effect of SI \((-0.15; 95\% \text{ CI} = \pm 0.13) \). We compared results to a model where the days elapsed between the capture event and the subsequent follow-up visit were explicitly included in the structure. This approach led to a poorer fit, indicating the effect of SI CORT on parental effort neither increases nor attenuates with time; however, given the size of our data set, we did not have high power to assess differences in the form of the effect.

Discussion

Life-history theory predicts that decisions regarding reproductive investment should be optimized to maximize the combination of both current and future reproduction and those decisions will be constrained by available resources for investment \((\text{Williams 1966, Stearns 1992}) \). Parents must balance investment in their young with their own survival and future reproductive effort. In making investment decisions, mourning doves are limited by endogenous resources used for crop-milk feeding and the rate at which resources are replenished by feeding. Hormonal control has the potential to affect both the acquisition of additional resources by feeding of adults and the balance between maintaining resources for self-maintenance and the transfer of resources from adults to young through provisioning. Within this context we made predictions about how both
adult weight, a measure of current adult state, and nestling weight, a measure of parental effort by adults, would be correlated to hormone levels within individuals.

Our results are consistent with predictions for BL PRL and CORT regulating the acquisition of resources through feeding and the transfer of resources through provisioning of young. The positive relationship of BL PRL to parental effort indicates that PRL levels positively affect feeding rates of young, leading to faster growth of nestlings when adults have higher levels. Our results are not consistent with the elevation of BL CORT in response to an energy deficit in adults and instead our path analysis suggests that at early ages elevated BL CORT levels may promote adult weight gain which in turn is positively related to nestling weight gain. A positive correlation between BL CORT levels and adult weight and the positive relationship between BL CORT levels and nestling weight during the early nestling period indicate that BL CORT promoted additional energy transfer to nestlings. Past studies of ring doves indicate the mechanism by which CORT affects this process is through promotion of increased feeding by adults (Koch et al. 2002, Koch et al. 2004). CORT can function to promote feeding in birds (Astheimer, Buttemer and Wingfield 1992, Koch et al. 2002, McEwen and Wingfield 2003, Landys et al. 2004, 2006, Lõhmus et al. 2006, Angelier et al. 2007b,c). Thus BL CORT may indirectly increase parental effort, by increasing feeding rates where additional acquired resources are transferred to the young to increase growth rates.

Previous studies as well as our path analysis results indicate that PRL and CORT may act together to steer resources to greater investment in nestlings during early reproduction. Koch et al. (2002) demonstrated that in ring doves, experimental elevation of PRL levels caused increased CORT levels. They suggested that elevation in CORT may promote increased feeding necessary for provisioning young (Koch et al. 2002, 2004). We observed a similar correlation in BL PRL and CORT levels during the early nestling period when crop-milk feeding is greatest for mourning doves.

Hormonal controls of life-history decisions are likely to be characterized by pleiotropic effects because of the multiple effects associated with changes in levels of a single hormone (Sinervo and Svensson 1998). This can result in constraints on selection
on hormone systems (Ketterson and Nolan 1992, 1999, Rickelfs and Wikelski 2002). It has previously been suggested that potential negative effects on reproduction due to CORT elevation may be minimized by upregulation of other physiological actions that promote parental effort. Koch et al. (2002) suggested that increased PRL levels counteract negative effects of increasing BL CORT level during reproduction, leading to beneficial effects of CORT by increasing foraging. They hypothesized that this may explain inconsistencies in the relationship between BL CORT level and parental effort in other studies. Our study lends further support to their hypothesis by confirming that PRL and CORT are correlated and both positively related to parental effort. In contrast Anglier and Chastel (2009) review studies that indicate that CORT may have negative effects on PRL levels, however, they focus on CORT levels typical of stress-induced levels. Further studies in which individual variation in both PRL and CORT are determined along with experimental manipulation of multiple hormones will be needed to determine whether the hypothesized relationship we propose among baseline PRL, CORT, and parental effort is supported for non-Columbiformes. Other factors such as receptor actions (Landys et al. 2004), binding proteins (Love et al. 2004, Shultz and Kitaysky 2008), or alternative physiological mechanisms may act similarly to PRL to minimize negative effects of CORT on reproduction and may vary among species. The potential for changes in hormone levels to act on multiple physiological and behavioral processes makes the simultaneous study of multiple hormones important in understanding hormone/life-history relationships (Angelier et al. 2009).

Much of the focus on hormonal control in avian life-history trade-offs has focused on variation in the CORT response to unpredictable stressors (Wingfield et al. 1998, Romero 2002, McEwen and Wingfield 2003). The rapid increase in CORT level significantly above BL level that occurs in response to acute stressors has been hypothesized to help facilitate a transition into an “emergency life-history stage” where self-maintenance is prioritized with respect to other investment including investment in reproduction (Wingfield et al. 1998). The original hypothesized effects on reproduction of this transition were largely based on laboratory studies where CORT level has been
manipulated. More recently studies in which CORT level was manipulated in wild populations of birds to mimic SI level have demonstrated effects of strongly elevated CORT on reproductive parameters (Silverin 1998, Criscuolo et al. 2005, Angelier et al. 2009), however, surprisingly little attention has been given to whether natural variation in the CORT stress response is related to subsequent parental effort in wild populations.

Our results are important in demonstrating that there is a strong relationship between natural variation in the SI CORT response in mourning doves and subsequent parental effort. We found a wide degree of variation in the SI CORT response among individuals ranging from increases of 14 ng mL\(^{-1}\) to 59 ng·ml\(^{-1}\) over BL CORT level. Consistent with the prediction that the magnitude of the SI CORT response would have negative effects on parental effort, we found that residual weight of nestlings for individuals that maintained CORT level near BL level did not change after the stress event. Nestling growth declined significantly when adults exhibited a strong SI CORT response with declines up to 15% in age-specific residual weight for nestlings of adults with the greatest SI CORT response. These results support the assertion that modulation of SI CORT response at levels exhibited in natural settings can have a relevant role in mediating life-history trade-offs between self-maintenance and reproduction in natural populations and are consistent with recent results for female house sparrows (Passer domesticus; Lendvai and Chastel 2008).

Because of the potential negative effects of the stress response on parental effort (Wingfield et al. 1998, Romero 2002, McEwen and Wingfield 2003), we predicted individuals would vary their response with respect to the current value of offspring and their own condition. We hypothesized that SI level of PRL and CORT would vary in response to both adult weight and nestling weight. However, we did not find a relationship of either SI CORT or SI PRL level to the condition of either adults or nestlings. Processes governing the PRL stress response and the effects of the response are not well understood in birds. At least one previous study indicates that breeding birds may modulate the decline in PRL level when facing acute stressors when compared to non-breeders (Chastel et al. 2005), indicating that the PRL stress response may have
important consequences for breeding birds. The CORT stress response is better studied in birds, but ambiguity exists in whether and when birds modulate the stress response (Shultz and Kitaysky 2008, Romero 2002, Wingfield and Sapolsky 2003). Given the dramatic effects of SI CORT level on subsequent parental effort we found in this study, it is somewhat surprising that we did not find evidence that parents modulated the response in relation to their own current conditions or that of their young. In common murre (Uria aalge), SI CORT levels are best predicted by food availability the previous month indicating that there may be a lag in the time between environmental stimuli that affect individuals and the upregulation of CORT production (Kitaysky et al. 2007). This stands in contrast to results for house sparrows (P. domesticus) where the SI CORT response was negatively related to reproductive value of offspring (Lendvai et al. 2007, Lendvai and Chastel 2008) and to differences among species where birds with greater investment in young have smaller SI responses (Bókony et al. 2009).

**Conclusions**

The importance of hormonal control of life-history decisions has been recognized in many vertebrate populations (Silver and Cooper 1983, Ketterson and Nolan 1992, Finch and Rose 1995, Horseman and Buntin 1995, Sinervo and Svensson 1998, Wingfield et al. 1998, Wang and Buntin 1999, Romero 2002, Landys et al. 2006, Bókony et al. 2009). Research in this area has concentrated on three levels of inquiry: how differences in endocrine levels among species relate to variation in life-history characteristics of the species, how levels vary among life-history stages within a population, and how levels vary among individuals of a population within a single life-history stage. Our knowledge of the effects of individual variation in hormone levels within individual life-history stages and its affect on life-history trade-offs is much more limited than the first two levels (Williams 2008) and this level was the focus of our study. Our results are consistent with individual variation being a potentially fruitful level of focus for the study of endocrinology in wild populations.

Although we demonstrate that individual variation in hormones was correlated with parental effort, we did not determine factors that lead to individual variation in
hormone levels. An important component to improving our understanding of the role that hormonal control plays in reproductive plasticity in birds will be determining whether birds vary their hormonal responses in response to their environment rather than the variation being fixed among individuals. Given that endocrine systems have characteristics allowing organisms to respond to environmental influence (e.g., CORT and the HPA axis; Sapolsky et al. 2000) and have been shown to be responsive to environmental input (e.g., Romero 2002, Lendvai et al. 2007, Bradshaw 2007, Kempenaers et al. 2008, Lendvai and Chastel 2008), we suspect that individual variation observed in this study includes both fixed and plastic components.

Given the importance of individual variation in optimizing life histories (McNamara and Houston 1996, Piersma and Drent 2003) our results are important in demonstrating that individual variation in hormone levels is correlated with parental effort by adult mourning doves. We found that individual variation in both BL CORT and BL PRL levels was positively correlated to parental effort early in the nestling period. Similarly we found that individual variation in SI CORT response was related to subsequent parental effort.

Acknowledgements
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References


Table 1. Mean (SD) corticosterone (CORT) and prolactin (PRL) levels immediately after capture (baseline), 30 minutes after capture and the change between samples (stress-induced) for adult mourning doves caring for nestlings. All values are presented in ng·mL\(^{-1}\).

<table>
<thead>
<tr>
<th></th>
<th>All Samples ((n = 65))</th>
<th>Female ((n = 35))</th>
<th>Male ((n = 30))</th>
<th>Early ((n = 35); nestlings (\leq 4) d)</th>
<th>Late ((n = 30); nestlings (\geq 5) d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baseline CORT</td>
<td>3.78 (1.66)</td>
<td>3.86 (1.79)</td>
<td>3.72 (1.57)</td>
<td>3.60 (1.61)</td>
<td>3.98 (1.71)</td>
</tr>
<tr>
<td>30 min CORT</td>
<td>29.44 (11.51)</td>
<td>31.03 (11.18)</td>
<td>28.14 (11.79)</td>
<td>28.93 (11.82)</td>
<td>29.99 (11.35)</td>
</tr>
<tr>
<td>Stress-induced CORT</td>
<td>25.66 (11.43)</td>
<td>27.17 (11.12)</td>
<td>24.42 (11.70)</td>
<td>25.33 (11.54)</td>
<td>26.01 (11.51)</td>
</tr>
<tr>
<td>Baseline PRL</td>
<td>24.55 (4.63)</td>
<td>24.14 (5.37)</td>
<td>24.88 (3.97)</td>
<td>25.46 (4.93)</td>
<td>23.57 (4.14)</td>
</tr>
<tr>
<td>30 min PRL</td>
<td>20.37 (4.85)</td>
<td>20.16 (4.88)</td>
<td>20.54 (4.90)</td>
<td>21.57 (5.57)</td>
<td>19.09 (3.61)</td>
</tr>
<tr>
<td>Stress-induced PRL</td>
<td>-4.18 (3.51)</td>
<td>-3.98 (2.95)</td>
<td>-4.34 (3.95)</td>
<td>-3.89 (3.65)</td>
<td>-4.48 (3.40)</td>
</tr>
</tbody>
</table>
Table 2. Comparison among alternative path models for the relationship among CORT, PRL, AW, and NW during the early (≤4 days) and late (≥5 days) nestling period. We used AIC to assess the relative fit of models with lower values representing a better fit. In addition we used a \( \chi^2 \) goodness-of-fit test to determine whether there was significant unexplained variation with significant p-values indicating a lack of fit for the model. During the early period the best fit was for model 3 which is consistent with CORT increasing in response to PRL elevation to promote hyperphagia. During the late period there was little evidence for a relationship among the parameters with the null model having the lowest AIC value and a strong probability that the correlation structure among variables could occur by chance.

<table>
<thead>
<tr>
<th></th>
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<th>Late</th>
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<tbody>
<tr>
<td></td>
<td>( \Delta AIC )</td>
<td>( \chi^2 )</td>
</tr>
<tr>
<td>Null</td>
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<td>24.3</td>
</tr>
<tr>
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<td>Model 1</td>
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<td>---</td>
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</tr>
<tr>
<td>Model 3</td>
<td>4.69</td>
<td>2.67</td>
</tr>
</tbody>
</table>
**Figure 1.** Estimated relationship between baseline PRL and baseline CORT and nestling weight (NW; a measure of reproductive investment) for mourning doves. Predicted values are plotted for nestlings 2, 4, and 6 days after hatch, based on regression models explaining baseline hormone levels. Predicted hormone levels were corrected for a holding time at 1.5 min for CORT and using the mean for other covariates not included in the figure. A) Baseline PRL was positively related to NW at early ages and rapidly declined as age increases. B) Baseline CORT was positively related to NW at early ages while the relationship disappeared at later nestling ages.

**Figure 2.** Estimates of standardized path coefficients for models including nestling weight (NW), adult weight (AW), and baseline prolactin (PRL) and corticosterone (CORT) level for nests ≤ 4 days after hatch. Solid lines represent effects that did not include 0 in the 95% CI, dashed lines the 90% CI, and dotted lines included 0 in the 90% CI. Results indicate the full model (model 1) was over-specified and the best fit was for model 3. These results corroborate laboratory results for ring doves (Koch et al. 2002, 2004) that indicate CORT elevation in response to PRL elevation stimulates hyperphagia to meet the energetic needs of crop milk feeding. PRL level had a direct effect on NW while CORT worked indirectly on NW by increasing AW.

**Figure 3.** Relationship between baseline CORT and PRL levels of adults with nestlings 2-4 days old. Estimates are corrected for handling time (1.5 min) and assay/year effects (average of 2 years). Levels were positively correlated (r = 0.43) during this period.

**Figure 4.** Changes in residual nestling weight (ΔNW) were negatively related to the magnitude of the plasma stress-induced CORT response of nesting mourning doves following a capture-restraint stress event. ΔNW was measured as the change in average relative weight of nestling versus age from the date of the capture event to the final visit to the nest (nestlings age 7 to 11 days). The result is consistent with the hypothesis that the magnitude of CORT elevation following a stress event mediates trade-offs between current reproduction and self-maintenance.
Figure 1A

The graph shows the relationship between NW (g) and PRL (ng mL\(^{-1}\)).

- Solid line: 2 d
- Dotted line: 4 d
- Dashed line: 6 d
Figure 3

CORT (ng mL$^{-1}$) vs. PRL (ng mL$^{-1}$)

[Graph showing a scatter plot with data points]
Figure 4

\[ \Delta NW \text{ (g)} \]

\[ \text{SI CORT (ng mL}^{-1}\text{)} \]
Summary
Developmental plasticity can be integral in adapting of organisms to the environment experienced during growth. To evaluate the relationship between morphological plasticity and fledging age, an important life-history transition for birds, I determined the effect of brood size manipulations on growth and its relationship to flight attainment for juvenile mourning doves. Life-history characteristics of mourning doves are consistent with strong selective pressure to minimize fledging age. I predicted that in the face of nutritional stress associated with brood-size manipulations, young would prioritize growth to structures that promote early fledging to reduce the effect of slowed overall growth on fledging age. Overall structural growth of nestlings slowed with increased brood size, and relative allocation to different body parts differed among brood sizes. 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 due to slower overall growth, differential allocation to wing growth reduced this effect by an estimated 1.6 d compared to the delay if plasticity among body parts had not occurred. Results demonstrate preferential allocation to wing growth helps determine the timing of this life-history transition and that morphological plasticity during development can have adaptive near-term effects during avian development.

Keywords: brood manipulation, fledging, flight, morphology, phenotypic plasticity, sibling competition, stress.

1. INTRODUCTION
Plasticity during development is important to both ecological and evolutionary processes (West-Eberhard 1989, Schew & Ricklefs 1998, West-Eberhard 2003, Badyaev 2005, Gil...
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 will be most accurate for predicting near-term conditions (Moran 1992, DeWitt et al. 2005) and therefore plasticity may be especially important in the adaptation of organisms to their growth environment and for transitions during development.

Patterns of morphological plasticity in birds are not well understood and even less is known about whether plasticity can have adaptive consequences (Schew & Ricklefs 1998). However, recent evidence suggests that adaptive changes in morphological development may occur (Gil et al. 2008). Attainment of flight ability and leaving the nest environment (i.e., fledging) is an important life-history transition that can be directly affected by morphology. Therefore, morphological plasticity has the potential to adaptively affect the timing of this transition.

Wide variation occurs in the proportion of adult size of birds at the time of fledging (Ricklefs 1968). Theoretical and empirical data are consistent with the degree of selective pressure for early fledging driving this variation. 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). Altricial species exposed to higher nest predation rates fledge 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).

Plasticity in structural growth rates in response to developmental stress due to resource limitations can be divided into two major types of response: slowed overall growth and differential allocation among body parts (Gotthard & Nylin 1995, Schew & Ricklefs 1998). Overall growth rate of young will be slowed when constraints in resources are dictated by reduced provisioning by parents. Thus, poor conditions impose a developmental response of slowed overall growth (Smith-Gill 1983, Gotthard & Nylin 1995). Differential allocation among body parts may limit effects of developmental
stress by prioritizing growth of structures most closely tied to immediate fitness. If birds allocate relatively more resources to wing growth than other structures when conditions are poor this may reduce the delay in fledging age due to slower growth rates. Where there is strong selection to leave the nest early, this type of response is likely to be adaptive with a match between reaction norm and the developmental trajectory that maximizes fitness (Gotthard & Nylin 1995).

I manipulated brood sizes to examine the effect of nutritional stress on morphological growth and fledging age of juvenile mourning doves (Zenaida macroura). Mourning doves are characterized by high nest predation rates, rapid early growth, early fledging age, and fledge at <60% of adult size (Westmoreland et al. 1986). These traits are all 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). Therefore, 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. I then examined how morphological variation directly related to fledging age. Finally, to directly test my prediction, 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. MATERIALS AND METHODS

I studied growth in nestlings from nests in central Iowa, USA, during the summer of 2007. Eggs were candled to determine their age ± 1 d for all nests found during the incubation period (Hanson & Kossak 1957). I returned to the nest at the time of hatch to determine hatch dates of nestlings.

Mourning doves lay two eggs per nest. Previous studies have shown that increasing or decreasing clutch size has measurable effects on nestling growth within the range of capabilities for adults to successfully rear (Holcomb and Jaeger 1978, Westmoreland and Best 1987, Blockstein 1989). To systematically affect resource
allocation to nestlings, I manipulated brood sizes of nests to create 1- and 3-nestling broods in addition to naturally occurring 2-nestling broods. Adjustments were done opportunistically < 1 d 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 1-nestling and 3-nestling brood. I determined which nestling to move so that the transplant was of intermediate size between the two original nestlings to minimize size asynchrony within a nest. To monitor flight ability and growth after fledging, nestlings were removed from nests at 10-11 d of age and were brought into an aviary. Because mourning dove young are fed by parents until they are at least 21 d 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 d, 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 ~5:3 for all levels and feeding rates were 8.5, 11, and 14 g day$^{-1}$. 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 used feeding rate treatments as a blocking factor in all analyses, treating feeding rate as a fixed effect, and testing for an interaction between feeding rate and clutch 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 d (±1 d) after hatch. I took 15 structural length measurements using dial calipers and a wing rule. I measured body (base of skull to base of tail feathers), flat wing chord, 6$^{th}$ primary, and 6$^{th}$ 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, 6th primary, and 6th secondary. I calculated wing area based on a prediction equation generated for wing area for a subset of 43 birds that were photographed with wing extended on a known-size grid and from which wing area was measured. I chose to estimate wing area based on other measurements rather than taking daily photographs to avoid extra handling involved in directly measuring wing area. The equation used the linear wing measurements as explanatory variables. Among potential models using wing measures and their interactions, the equation that best predicted wing area based was: Wing Area (cm²) = -31.401 - 0.211*Wing Chord + 1.825*6th Secondary + 0.181*Ulna + 0.024*Wing Chord*Ulna (R² = 0.96). I used linear interpolation to generate values for ulna length on days when it was not measured to calculate daily estimates of wing area.

To determine the role of morphology in determining fledging ability for doves, I used birds brought into captivity. Each morning I recorded whether a bird was able to make a sustained horizontal flight of at least 3 m. Each bird was given at least 3 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 to 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 post-fledging.

Daily fledging ability was 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, structural size (see next paragraph for calculation of this parameter), wing area, and wing loading (weight/wing area), selecting among covariates based on AICc, which allowed me to compare non-nested models. For each covariate I considered models which included: 1) only the single covariate and feeding rate as a fixed block effect, 2) the covariate, brood size and feeding rate, and 3) models with main effects and interactions between treatments and covariates. The treatment effects and interaction terms allowed me to determine if different thresholds in fledging ability occurred for each treatment level, and therefore whether the covariate alone was an adequate predictor of fledging or alternatively whether treatments had an effect independent of its effect on the covariate.

I examined two components of plasticity in growth, plasticity in 1) overall size and 2) size-independent shape. 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 5 measures (0.35-0.53). Measures of structural size used for estimating fledging ability for days when all measurements were not taken were estimated by linear interpolation. Size independent shape variables were generated by regressing each of the individual measurements on structural size and using the residual as the shape measure.

All univariate responses were tested using mixed models 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 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 % quantiles of the ordered estimates from the bootstrap results.

3. RESULTS

(a) Fledging age
A total of 68 mourning doves survived the nestling period and fledged prior to or at 19 d of age. This included 19, 33, and 16 individuals from 1, 2, and 3 nestling broods, respectively. The best predictor for fledging probability was the model including a linear effect of wing area. When wing area was included as an explanatory variable, there was no support for an effect of brood size or feeding rate on fledging probability. I used a 50% probability of fledging as the threshold wing area for fledging, which was predicted to be 146.9 cm$^2$ (95% CI = 142.0-155.4; figure 1). 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$_c = 43.95$) likely because wing loading values remained relatively constant across ages with weight gain occurring at a similar rate to growth in wing area.

(b) Plasticity
I took 212 sets of measurements from the birds between 8 and 20 d 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. Results demonstrate that 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 affected size, demonstrating differential allocation among body parts. I did not find significant interactions between age and brood size for either, indicating that effects occur prior to 8 d, the age at which growth measurements began in this study.
(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 clutch 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 due 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 estimate coefficients from the ANCOVA for age as a function of brood size and overall size. This difference would be the expected difference in fledging age assuming no prioritization of wing growth with increased brood size. Based on this scenario, nestlings from 3 nestling broods would have been expected to fledge 3.81 d later than from 1 nestling broods (95% CI = 2.92-4.69 d). 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 1.61 d for 3 nestling broods versus 1 nestling broods (0.87-2.43 d), relative to the scenario where fledging was determined by overall size alone. Observed fledging ages for birds in this study were 14.6 d (13.9-15.4 d), 15.1 d (14.5-15.6 d), 15.9 d (15.1-16.8 d) for birds from one, two, and three nestling broods, respectively, which is consistent with the predicted effect on fledging age of preferential allocation to wing growth in larger broods minimizing the effect slowed overall growth on fledging age.

4. DISCUSSION

Morphological plasticity during avian development is generally treated as an artifact and its consequences for function and fitness are ignored. Differential allocation of growth to different body parts for young developing under nutritional stress has been observed in
birds (e.g., Øyan & Anker-Nilssen 1996, Schew & Rickles 1998, Lepczyk & Karasov 2000, Benowitz-Fredericks 2006, Tobón & Osorno 2006). However, little effort has gone into quantifying and comparing 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 testing predictions in response to manipulations of the developmental environment suggest that morphological development can adaptively shift in response to stressors encountered in the nesting environment (Nilsson & Gårdmark 2001, Gil et al. 2008). This study demonstrates the utility of examining patterns in preferential allocation in relation to testable adaptive hypotheses to better understand the function of morphological plasticity during development. Even in higher vertebrates such as birds with rapid growth and determinant growth, morphological plasticity may be a source of adaptation during development.

I predicted the form of an adaptive reaction norm in response to nutritional stress based on two lines of evidence and demonstrated that the actual reaction norm for the population was consistent with my predictions for phenotypic plasticity that was adaptive (Gotthard & Nylin 1995). First, variation in wing area had a direct relationship to fledging time and this relationship was independent of brood size. Second, based on the life history of mourning doves, which is characterized by high nest predation, fast growth, and relatively small fledging size compared to adult size, there was evidence that selective pressure has worked to minimize fledging age in mourning doves (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, supporting the contention that morphological plasticity in the growth trajectory was adaptive in mourning doves.

Evidence for a plastic response that has evolved under natural selection may be inferred when the response shows a high degree of integration (Gotthard & Nylin 1995).
This argument has been used to infer that complex morphological responses to predator presence are evolved adaptations (e.g., Lively 1986, Crowl & Covich 1990). Schew & Ricklefs (1998) argued that adaptive developmental responses to stress that involve preferential allocation among body parts rather than overall slowing of growth is stronger evidence of adaptation. Adaptive 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 & Nylim 1995). Work should involve 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) and if preferential allocation to wing growth under nutritional stress is greatest in species predicted to have stronger selective pressure for early fledging.

Fledging age has been observed to decrease with increased environmental stress 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 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. Raihini & Ridley (2007) found that fledging age in pied babblers (Turdoides bicolor) decreased with increased nesting density, which is strongly associated with predation rates of nestlings. Morphological plasticity is a potential mechanism by which fledging age might have been adjusted in these populations.

Developmental plasticity can have both near-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. My results are consistent with other studies of invertebrates (Crowl & Covich 1990, Gotthard 2008) and anurans (Newman 1992, Lind & Johansson 2007) where
morphological plasticity reduces time to life-history transitions when environmental cues signal that fitness will be maximized by an earlier transition.

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Table 1. Phenotypic plasticity in overall size and shape occurred in response to brood size treatments (nestlings) 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 for shape was tested using MANOVA. Feeding rate after 13-d was used as a blocking factor. 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 wing area when standardized by overall size depends on the number of nestlings in the brood.

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<tr>
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<tr>
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<tr>
<td><strong>Wing Area</strong></td>
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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 cm$^2$.

Figure 2. Relationship between size and age for mourning dove nestlings from 1 (pink), 2 (green), and 3 (blue) nestling broods. Lines connect measurements for the same individual. Young from 1 nestling broods grew faster prior to 8 d than young from 3 nestling broods, demonstrating that increased competition in the nest had a negative effect on overall growth rate that would be likely to delay fledging.

Figure 3. Relationship between wing area and size for mourning dove nestlings from 1 (pink), 2 (green), and 3 (blue) nestling broods. Lines connect measurements for the same individual. Wing area was greater for young from 3 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.
CHAPTER 6. IMMEDIATE VERSUS DELAYED EFFECTS OF DEVELOPMENTAL STRESS ON GROWTH AND FLIGHT ABILITY OF JUVENILE MOURNING DOVES.

A paper to be submitted to the Journal of Animal Ecology

David A. Miller

Summary

1. Stress during early development and adaptations to minimize the effects of stress are important components of organismal development and the relationship between development and fitness.

2. I examined the effect of developmental stress during the nestling and fledgling stages on weight gain, growth in structural size, and take-off flight speed on juvenile mourning doves (*Zenaida macroura* L.). Brood size was manipulated during the nestling stage (≤ 11 d) and feeding rates during the fledgling stage (13-25 d) using a full factorial design.

3. Effects of nutritional stress differed depending on the timing of the stress, the component for which the response was measured, and the time when it was measured. Effects were stronger for brood-size manipulations than feeding-rate manipulations, were stronger for immediate rather than delayed effects on weight and size, and treatment effects were delayed for flight ability.

4. Mourning doves were able to minimize effects of stress on flight ability at early ages when they were most vulnerable. However, by 90 d birds from larger broods were slower and take-off flight speed at 90 d was negatively correlated with weight and size at 25 d.

5. There was evidence that birds were able to catch up in size and weight after a period of lower feeding during the fledgling stage but not after brood size was increased during the nestling stage. Large differences in weight among feeding-
rate treatment levels at 25 d disappeared by 90 d and birds in the low-feed treatment grew faster with respect to structural size over this period.

6. Results support the importance of understanding effects of developmental stress and the adaptations to reduce the effects of stress in a multi-component temporal context.

Keywords: brood-size manipulation, carry-over effect, compensatory growth, developmental plasticity, nutritional stress, flight performance

Introduction

Early developmental conditions have important short and long-term consequences for life-time reproductive success (Lindstrom 1999). The effects of external stressors on near-term and long-term fitness provide a strong selective force that has shaped adaptations to mitigate negative effects during development (Schew & Ricklefs 1998, Badyaev 2005, Monaghan 2007). A conceptual framework within which to understand the relationship between developmental stress and its effect on phenotypes has begun to emerge in recent years, focusing on topics including phenotypic plasticity, compensatory growth, and carry-over effects. This framework leads to testable predictions regarding adaptive responses of individuals to stress during development (DeWitt, Sih & Sloan 1998, Piersma & Lindström 1997, Lindstrom 1999, Metcalfe & Monaghan 2001, Mangel & Munch 2005, Monaghan 2007). Responses to stress have also served as a more general model for understanding developmental plasticity and adaptation during ontogeny (Gotthard & Nylin 1995, Badyaev 2005).

Phenotypic responses to stress are central in examining the conflict between minimizing error due to developmental variation and maintaining flexibility in development that can allow organisms to adapt to individual conditions (Waddington 1942, Smith-Gill 1983, Lively 1986, DeWitt et al. 1998, Badyaev 2005). Trade-offs are likely to occur between benefits accrued by minimizing developmental variation that results from stress and the alternative potential benefit to incorporating information from stressors to adaptively adjust developmental trajectories through phenotypic plasticity.

Maintaining developmental trajectories, and as a result minimizing plasticity, may be important to limit the negative effects of poor developmental environments. This may
be especially important for structural growth in birds, which exhibits rapid, determinant growth that is generally completed in the first few months of life, even in species that do not breed until later ages. Compensatory growth, i.e., the ability to accelerate growth rates above normal or baseline after a period of slowed growth due to nutritional restriction, is an important mechanism to limit long-term effects of stress on adult size (Metcalfe & Monaghan 2001). Although compensatory growth in weight is common, the ability for compensatory growth in structural elements such as bone growth may be limited for altricial birds (Lepczyk & Karasov 2000). Thus maintenance of structural growth trajectories may be especially important to complete growth during the juvenile stage. Other factors may also favor stability of phenotypic development (DeWitt et al. 1998), including unpredictable environments (Gabriel et al. 2005), irreversibility of responses (Piersma & Lindström 1997), and maintaining integration of the resulting phenotype (Pigliucci 2003).

Plastic responses to nutritional stress during development include imposed responses due to the constraint of limited resources and induced responses that are structured by trade-offs and lead to preferential allocation of limited resources (Smith-Gill 1983, Schew & Ricklefs 1998). Nutritional restriction below optimal levels necessarily imposes constraints on growth so that energy use must be restricted. Therefore, adaptations that are induced by nutritional restriction will involve trade-offs among morphological, physiological, and behavioral components. Preferential allocation is presumably given to components that maximize fitness. Trade-offs are likely to occur both within an individual at specific times in ontogeny and across different times in ontogeny (Mangel & Munch 2005, Capellán & Nicieza 2007). Thus, allocation decisions will not only have costs in the near-term but also costs that are incurred over the long-term (Metcalfe & Monaghan 2001, Fisher, Nager & Monaghan 2006). Likewise, incurring immediate costs associated with stressors may allow individuals to reduce the long-term effects (Moe et al. 2003). Because of the sequential and multi-factored nature of ontogeny, the effects of stressors on multiple components development must be understood within a temporal context.
Plastic responses that prioritize maintenance of flight performance in the presence of different external stressors are common in birds. These include adaptations during breeding (Lee et al. 1996, Ouellet, Guillemette & Blier 2008) and molting (Williams & Swaddle 2003). Similarly evidence is emerging that prioritization of flight performance is an important and consistent response to developmental stress in many species (Nilsson & Gårdmark 2001, Bize et al. 2003, Wright, Markman & Denney 2006, Verspoor et al. 2007, Chin et al. 2009, Miller *in Review*). In mourning doves (*Zenaida macroura* L.) young reduce the effects of slowed overall growth on fledging age by prioritizing wing growth, a major determinant of fledging ability (Miller *in review*). The extent to which birds are able to continue to limit the effects of stress on flight at later ages is therefore of interest in understanding long-term costs of compensation (Metcalfe & Monaghan 2001).

Prioritization of development of flight ability in response to external stressors is consistent with the strong relationship of flight performance to escape ability from predators, feeding efficiency, and migratory ability (Lima 1993, Witter, Cuthill & Bonser 1994) and indirect effects on reproductive output (Bowlin & Winkler 2004). This relationship is likely strengthened during periods of high nutritional stress when birds compensate by increasing feeding time and risk taking, resulting in increased encounters with predators (Lima & Dill 1990, Houston, McNamara & Hutchison 1993, Ydenberg et al. 2002). Take-off speed is especially important to determining escape ability from predators (Lima 1993, Kullberg, Fransson & Jakobsson 1996, Williams & Swaddle 2003). Wing shape and size (Fernández-Juricic et al. 2006, Verspoor et al. 2007), weight (Kullberg et al. 1996), and muscle size (Veasey, Houston & Metcalfe 2000, Verspoor et al. 2007) can all affect take off velocity in birds. Take-off velocity is likely to be especially important for mourning doves which feed on the ground in open areas where they are susceptible to both terrestrial and aerial predators (Lewis 1993).

Rates of growth in both structural size and weight have been shown to have both direct and indirect relationships to individual fitness (Lindstrom 1999, Metcalfe & Monaghan 2001, Sedinger, Herzog & Ward 2004). Patterns observed in growth of structural size versus weight in response to poor developmental conditions tend to differ for birds. Under food restriction, slowing of weight gain tends to occur much earlier and
more rapidly than for structural growth (Moe et al. 2004, Bize, Metcalfe & Roulin 2006). Likewise, after birds are subjected to periods of nutritional restriction, compensatory growth has been observed in weight gain, while structural growth parallels growth rates of non-restricted birds or remain slower post-treatment (Hegyi & Török 2007). Although long-term effects of food restriction can be reduced by extending growth periods (Lepczyk & Karasov 2000), effects of nutritional restriction on structural growth rates often have lasting effects on adult phenotypes (de Kogel 1997). Weight gain is a better measure of body parts such as internal organs, muscle size, and fat stores that can both increase and decrease in size throughout ontogeny. Effects of developmental stress on weight may be reversible (Piersma & Lindström 1997), allowing individuals to defer growth until later ages.

I examined the effects of early developmental stress on weight gain, structural growth, and take-off flight speed during nestling and fledgling stages for mourning doves. Birds were stressed by manipulation of brood size during the nestling stage and by restricted feeding during the fledgling stage. Effects were measured both immediately after treatments ended and more than two months later to determine whether effects differed depending on the timing of the stress, the response measured, and age. In addition, I examined how phenotypic responses covaried within and among time periods as individuals aged post-treatments.

Methods

I monitored the growth and development of juvenile mourning doves from wild populations in central Iowa during the summer of 2007. Nests were found by systematic searches of managed areas found within a row-crop agricultural matrix. When a nest was found, eggs were aged (± 1 d) by candling (Hanson & Kossack 1963), and then I returned near the predicted time of hatching to determine hatching order and date. I returned to the nest again when the oldest nestling was 4-6 d and 8-10 d of age. When the oldest nestling was 10-11 d old I removed nestlings from nests and brought them to an aviary where they were held to monitor growth post-fledging. This age coincides with the period just prior to fledging. Mourning doves typically fledge from the nest at 11-15 d of age (Hitchcock and Mirarchi 1984).
Mourning doves fledge at ~60% of their adult size (Westmoreland, Best & Blockstein 1986) and continue to be fed by the adult male for a period of up to two weeks after leaving the nest (Hitchcock & Mirarchi 1984). Therefore, I hand fed birds during their initial period in the aviary. Up to 25 d of age, birds were fed a diet consisting of a combination 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 experimentally assigned rates that were determined during a pilot study to generate typical growth trajectories of mourning doves in the wild. Birds were fed a combination of 5:3 parts dry to wet feed twice daily and were given the opportunity to feed themselves the dry feed portion starting at 17 d of age. Feeding rates from 13-25 d of age were set based on experimental treatments, and after 25-d birds were provided the dry feed mixture ad libitum. At all ages, birds were also provided cage grit and water ad libitum. Birds were held until 25 d in battery cages (0.75 x 0.6 x 0.5 m). During this period birds roost most of the time and move when the adult male returns to feed them. From 25-35 d birds were held in small flight pens (3.6 x 3.6 x 1.8 m), and after 35 d birds were moved to a large flight pen (18 x 3.6 x 1.8 m). For the first 25 d birds were allowed to make short flights daily before being fed. In addition to normal movements during the day, birds in flight pens were forced to fly ~ 5-10 min every morning and evening by an observer walking the perimeter of the pens.

Experimental design and statistical analysis

I manipulated developmental conditions during two periods, the nestling and fledgling stages, using a full factorial experimental design with two treatments. I manipulated brood sizes during the nestling period, creating one- and three-nestling broods as well as the standard two-nestling broods. Nestlings were transferred opportunistically < 1 d after all eggs in both nests were hatched. A single nestling was moved from a nest and placed in another so that the nestling added to create a three-nestling brood was intermediate in size to the two original nestlings. This minimized size asynchrony within the nest so that the effect of the larger brood size was likely to be more uniform on all individuals within a nest.
The second experimental treatment occurred in the aviary during the fledgling stage, a period when mourning dove young still benefit from parental care. At 13 d, young were assigned to low (8.5 g day$^{-1}$), medium (11 g day$^{-1}$), and high quantity (14 g day$^{-1}$) feeding-rate treatments. All birds were fed the same high quantity diet during an initial acclimation period from the time they were brought into captivity up to 13 d of age. Birds were then fed at their assigned treatment level from 13–25 d. After 25 d all birds were provided the dry food mixture ad libitum until the experiment ended. Feeding rates from 13-25 d were developed based on a trial study during the summer of 2006 (D. Miller unpublished data) to mimic the average and extremes of the range of weight gain typically seen for birds in the wild over this period (Hanson & Kossack 1963). Feeding rates were assigned sequentially so that for each of the brood-size treatments, one-third of birds were placed in each of the feeding-rate treatments.

Measuring take-off speed and growth

To assess flight performance, I determined the time it took for individuals to fly 1.5 m when startled from a perch, a measure of take-off speed. The assessment was conducted when birds were 25, 35, and 90 d old. The measure mimicked the ability to escape when a predator approached while feeding on the ground. Individuals were placed on a low perch in a long narrow flight tunnel (6.0 x 1.2 x 1.8 m) and startled using an object that swung directly underneath the perch. Flights were recorded at least twice at each age using a digital video recorder (Sony Model DCR-DVD305; 30 frames s$^{-1}$) and later processed by examining video one frame at a time using TPSDIG (version 1.40, F.J. Rohlf, State University of New York at Stony Brook). Times were calculated by determining the first frame where the bird moved off the perch until the torso crossed a radius of 1.5 m from the perch. Fractions of frames were used to determine the ending time by determining the position of birds at the video frame immediately prior to and after crossing the 1.5 m line. If more than one usable flight was recorded the fastest flight was used.

I recorded weights and structural measurements of birds immediately following flight tests. I weighed birds using a digital scale (± 0.1 g). I also took structural length measurements using dial calipers and a wing rule to measure overall structural size of
individuals. Measurements were: body (base of skull to base of tail feathers ± 0.5 mm), head (base of the bill to back of the skull, ± 0.1 mm), tarsus (± 0.1 mm), tibiotarsus (± 0.1 mm), and ulna (± 0.1 mm). I used the 1st principal component (PC1) of the log-transformed variance-covariance matrix as a metric of overall structural size that incorporated multiple components of structure (Rising & Somers 1989, Miller in Review).

**Statistical Analysis**

I analyzed data for each of the three responses (take-off flight speed, weight, and size) using an ANOVA model with a three-way factorial arrangement of fixed treatment factors (brood size, fledgling feeding rate, and age) and a random effect for individuals to account for the repeated measurement over time. Specifically, I tested for average differences in the main effects of each treatment factors and their interactions. For each response variable I also examined each age class separately, testing for main effects of the two treatment factors and their interaction using a two-way ANOVA.

Finally, to examine patterns of covariation among phenotypic measures I estimated the correlations of weight and size at 25 d with take-off speed at 25 and 90 d, and weight and size at 90 d to take-off speed at 90 d. Pearson correlation coefficients were estimated and tested for significance.

For all statistical tests, I used $\alpha = 0.05$ as the level of statistical significance.

**Results**

I monitored 49 juvenile mourning doves from hatching to 90 d age. Sample sizes for brood-size treatments were $n = 10, 25, 14$ nestlings for one-, two-, and three-nestling broods respectively. Sample sizes for feeding-rate treatments were $n = 17, 15, 17$ fledglings for the low, medium, and high feeding rates, respectively.

Treatment effects differed depending on the age of the nestlings and the phenotypic response (Table 1, 2, Figure 1). There was a significant interaction between the effect of brood size and age as it related to flight performance (Table 1). Take-off speed was slowest for birds from one-nestling broods at 25 d, with no significant difference among treatments at 35 d, and an inverse relationship between speed and brood size by 90 d (Table 2). At 25 d birds from one-nestling broods took 20% longer on
average than birds from three-nestling broods to fly 1.5 m, while at 90 d birds from one-nestling broods took 9% less time. Take-off speed was not affected by feeding-rate treatments at either 25 or 35 d. There was a significant difference among feeding-rate treatment levels at 90 d, with birds in the low treatment were slowest, in the medium treatment were fastest, and in the high treatment were intermediate in speed (Table 2, Figure 1). There was no significant difference in the treatment effect among ages (Table 1).

There were significant differences in structural body sizes among brood-size treatments (Table 1). At all ages, size was inversely related to brood size (Figure 1). There was evidence that the effect of feeding-rate treatments on structural size changed through time (Table 1), with birds in the low feeding-rate treatment growing faster than medium and high treatment individuals between 25 and 90 d (Figure 1). However, the range of mean treatment differences for feeding rate were much smaller than those for brood size (Figure 1) and differences in structural size among feeding-rate treatment levels were not significant at any age (Table 2).

At all ages significant differences in weight occurred among brood-size treatments, with no change in the effect across ages (Table 1, 2). After controlling for feeding-rate treatment, average weight for birds from one- and two-nestling broods was 10% heavier at 25-d than for birds from three-nestling broods, and was 30% heavier for birds from the high-feed treatment than the low feed treatment. At 90-d birds from one- and two-nestling broods were still 10% heavier while the mean difference in weight among all feeding-rate treatments was < 2% (Figure 1). This result was consistent with the significant change in treatment effects for feeding treatments across ages as opposed to no change in brood-size effects (Table 1).

Correlation between take-off speed and size and weight at 25 d were positive, but differences were not statistically significant (Figure 2A, 2B). Take-off speed at 90 d was significantly negatively correlated with size and weight at 25 d (Figure 2C, 2D). In both cases individuals that were smaller at early ages were slower at late ages. At 90 d, there was no significant relationship of current weight and size to take-off speed (Figure 2E, 2F).
Discussion

Understanding phenotypic responses to nutritional stress early in development requires examining the process across multiple factors including: the timing of the stressor, timing of the phenotypic response, and the type of phenotypic response. Responses exhibited by mourning doves varied across all three. For example, effects of nutritional stress were greater for brood-size treatments, which were manipulated at earlier ages, than effects for feeding-rate treatments. Effects differed across ages for all three responses. And, effects of feeding-rate manipulations on weight relaxed as young aged while the effects of brood-size manipulations on flight performance increased with age. These results are consistent with other studies that demonstrate that developmental stress leads to hierarchical responses that differ across measured components (e.g., Ricklefs, Shea & Choi 1994, Soler et al. 2003, Moe et al. 2004, Fisher et al. 2006).

Timing of stress

The effects of experimental treatments on phenotypic measures differed depending on the timing at which the manipulations occurred. Feeding-rate treatments during the fledgling stage had a substantial effect on individuals, with high feeding rate birds being 29% heavier at 25 d than low feeding rate birds. However, in contrast to brood-size manipulations, there were no effects of feeding treatments on structural growth, effects on weight were transient and disappeared by 90 d, and the effect on flight performance was non-linear with medium feeding rate birds performing best in flight trials. The balance between the potential to adapt to variation in conditions versus maintenance of growth is likely to depend directly on the amount of variation experienced in the developmental environment (Schew & Ricklefs 1998). Development of mourning doves and other altricial species transitions through periods of decreasing nutritional stability, beginning in the highly controlled egg stage, through the nestling stage in which brooding of young and feeding by both parents occurs, to the fledgling stage when a single parent feeds young and dependence on parental care is gradually reduced. Variability during the early nestling stage may be further reduced in mourning doves specifically because crop-milk feeding of young using endogenous resources reduces fluctuations in provisioning of young (Horseman & Buntin 1995). In this study
the effect sizes were smaller for manipulations during the fledgling stage versus the nestling stage, consistent with increased ability to deal with variability in food availability in later periods during which variability is likely to be greater. In addition, effects of feeding rate on size and weight were transient, indicating greater potential to catch up after the period of restriction ends for nutritional stress at later ages. These results are consistent with results for other studies that have demonstrated that effects of nutritional stress decrease with age (Lepczyk & Karasov 2000, Bize et al 2006).

**Delayed Effects on Flight Performance.**

My results are consistent with recent evidence that suggests that maintenance of flight ability may be prioritized in the face of developmental stress (Nilsson & Gårdmark 2001, Bize et al 2003, Wright et al. 2006, Verspoor et al. 2007, Chin et al. 2009, Miller *in Review*). European starlings exposed to higher levels of corticosterone in the egg, a signal that conditions outside of the egg are more likely to be poor, have improved flight performance when they leave the nest, consistent with a prioritization of flight ability in poor environments (Chin et al. 2009). Similarly, female starlings raised under poor conditions maintain flight performance equivalent to those raised under good conditions (Verspoor et al. 2007). Mourning doves from broods manipulated to be larger prioritize wing growth, thus compensating for overall slower growth and reducing the effect on fledging age (Miller *In review*). In this study, despite significantly greater structural growth and weight gain associated with reduced brood size, individuals from one-nestling broods had the slowest take-off speed at 25 d and there was no difference at 35 d among brood sizes.

Young are likely to be more vulnerable to predation immediately fledgling making it important for young to limit effects of poor developmental conditions on flight performance. Young at 25 d on average took 36 % longer than at 90 d to complete the flight trial, thus young birds feeding in mixed aged groups are likely to be especially vulnerable because slower individuals will be most susceptible to capture by predators. In addition, variance in flight performance is much higher at this age and thus differences among individuals within the age group are greater. At 25 d young likely spend more time foraging compared to later ages as they learn foraging techniques and are still
actively growing. Predation is a major source of mortality for mourning doves and overall mortality rates are also likely to be higher at younger ages (Otis, Schulz & Scott 2008), and therefore survival selection related to performance parameters is likely to be stronger at younger ages.

**Effects on Growth**

My results are consistent with other recent studies that suggest altricial birds have a limited potential for compensatory growth in structural components after periods of nutritional restriction, where growth rates are accelerated above baseline levels after a period of slowed growth (Lepczyk & Karasov 2000). Likewise, they are consistent with the finding that there is a hierarchical order in which weight and structural components respond to food restriction and periods of realimentation (Bize et al. 2006, Hegyi & Török 2007, Müller, Jenni-Eiermann & Jenni 2009).

In birds, structural growth is rapid and determinant with completion early in development (O’Connor 1984). Thus growth rates may be near maximum levels, especially at early ages when growth is most rapid, and increasing growth rate further may not be possible. Instead my results suggest that mourning doves from larger broods grew at rates parallel to those from smaller broods after the nestling period. However, during the fledgling stage when overall growth rates are lower than the nestling stage, there was some evidence for faster growth in low-feed treatments compared to the other treatments between 25 and 90 d. Differences were small however, and did not result in significant differences in size among treatment levels within any age.

Results differed when examining patterns of weight gain post-treatment. Similar to structural size, weight gain with respect to brood size was parallel among groups and differences in weight did not change over time. Weight gain with respect to feeding-rate treatments differed in showing clear patterns of compensatory growth, with individuals from the low and medium feeding-rate levels nearly catching from weight deficits by 35 d and completely catching up to high-feed birds by 90 d. Plasticity in size of organs and muscle groups in response to external stimulus is common in animals (Piersma & Lindström 1997) and likely underlies the high degree of flexibility in weight gain seen in this study. Thus results for growth are consistent with predictions that plasticity should
be greater in reversible traits (Piersma & Lindström 1997) and that the need to minimize variation in structural growth especially early in development, may limit potential for plastic responses under stress.

**Covariation and Trade-offs.**

Patterns of covariation among phenotypic measures in this study were strongest between time periods rather than within. The strongest correlations were negative relationships between size or weight at 25 d and take-off speed at 90 d. Correlations within ages were weak, and although not statistically significant, correlations between take-off speed and size or weight trended positive at 25 d. In response to experimental manipulations, doves minimized the negative effects of developmental conditions on flight performance at early ages in opposition to negative effects on both size and weight. However, at 90 d flight performance was negatively affected by manipulations. Thus doves are able to prioritize performance in the short-term, however, the pattern of covariation between take-off speed and size and weight of individuals indicates that there may be a direct relationship between early effects on growth and later flight performance. This correlation is dampened by 90 d with no significant relationship between size and weight at 90 d and flight ability at this age. Catch-up growth that was observed in both weight gain and to a lesser degree structural growth after the feeding-rate treatment negated the relationship between weight and take-off speed at 90 d and greatly weakens the correlation between size and take-off speed at 90 d.

**Importance of examining multiple phenotypic components across time**

Understanding how organisms adapt to poor developmental conditions requires examining variation among multiple phenotypic measures across multiple time periods. The ability to which organisms can limit the effects of poor conditions on fitness and prioritize growth among components in a way that leads to the greatest benefit can only be understood within this multi-component temporal context. Based on our understanding of how plasticity, compensation, and carry-over effects occur and affect adaptations of individuals to poor developmental conditions, the effect of early stress will be expressed at different times and among different components of an individual’s
ontogeny such as seen in this study. This framework appears to have structured potential adaptation to poor conditions during mourning dove development.

In mourning doves, developmental responses to stress were expressed in a hierarchical order so that immediate effects at 25 d are stronger for weight than for structural growth, while flight ability is maintained. Similarly, the response of take-off speed, weight, and size to development stress differed among components and varied with age. Effects of stress on flight ability were compensated for at early ages and the costs of stress to flight ability were realized at later ages as decreased flight performance with greater early stress. For weight gain, immediate effects are large; however, for manipulations during the fledgling stage, compensatory growth eliminates the effects by 90 d of age. For size, the effects of experimental manipulations are most consistent across all ages. Results demonstrate the utility of examining multiple components of development across multiple time points during ontogeny.

Acknowledgements
D. Otis provided helpful advice on experimental design and comments on this manuscript. Funding for this research came from a U.S. Fish and Wildlife Service – Migratory Game Bird Research Grant. All procedures following animal care guidelines and were overseen by the Iowa State University IACUC and proper state and federal permitting agencies. A. Bronikowski and C. Vleck provided comments on an earlier draft.

References


Table 1. Results from repeated measure ANOVA for effects of age, brood size (BS), and feeding rate (FR) on take-off speed, size, and weight of juvenile mourning doves at 25, 35, and 90 d of age. A random effect was included for individuals and denominator degrees of freedom were calculated based on Kenward-Roger method. P-values for effects significant at the level of $\alpha < 0.05$ are shown in bold.

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<td>2, 39.7</td>
<td>3.23</td>
<td><strong>0.050</strong></td>
</tr>
<tr>
<td>Feeding Rate</td>
<td>2, 39.7</td>
<td>0.61</td>
<td>0.549</td>
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<tr>
<td>Brood Size * Age</td>
<td>4, 76.0</td>
<td>0.66</td>
<td>0.620</td>
</tr>
<tr>
<td>Feeding Rate * Age</td>
<td>4, 76.0</td>
<td>3.88</td>
<td><strong>0.006</strong></td>
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<tr>
<td>Brood Size * Feeding Rate</td>
<td>4, 39.7</td>
<td>0.16</td>
<td>0.957</td>
</tr>
<tr>
<td>Brood Size * Feeding Rate * Age</td>
<td>8, 75.9</td>
<td>0.88</td>
<td>0.538</td>
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<tr>
<td><strong>Weight</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Age</td>
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<td>162.92</td>
<td>$&lt;0.001$</td>
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<tr>
<td>Brood Size</td>
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<tr>
<td>Feeding Rate</td>
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<td>0.517</td>
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<tr>
<td>Feeding Rate * Age</td>
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<td>Brood Size * Feeding Rate</td>
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<tr>
<td>Brood Size * Feeding Rate * Age</td>
<td>8, 77.5</td>
<td>1.23</td>
<td>0.292</td>
</tr>
</tbody>
</table>
Table 2. Results of analysis of variance for treatments effects on mourning dove young on phenotypic measures at 25, 35 and 90 d after hatching. I manipulated brood size in the nest and feeding rates of fledglings. P-values for effects significant at the level of $\alpha < 0.05$ are shown in bold.

<table>
<thead>
<tr>
<th>Response</th>
<th>Age (d)</th>
<th>Brood Size</th>
<th>Feeding Rate</th>
<th>Brood Size x Feeding Rate</th>
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<tr>
<td>Take-off speed</td>
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<td>p = 0.009</td>
<td>0.935</td>
<td>0.456</td>
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<td></td>
<td>35</td>
<td>0.348</td>
<td>0.305</td>
<td>0.855</td>
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<tr>
<td></td>
<td>90</td>
<td><strong>0.049</strong></td>
<td><strong>0.013</strong></td>
<td>0.713</td>
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<tr>
<td>Size</td>
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<td>0.011</td>
<td>0.195</td>
<td>0.737</td>
</tr>
<tr>
<td></td>
<td>35</td>
<td>0.151</td>
<td>0.810</td>
<td>0.978</td>
</tr>
<tr>
<td></td>
<td>90</td>
<td>0.100</td>
<td>0.831</td>
<td>0.753</td>
</tr>
<tr>
<td>Weight</td>
<td>25</td>
<td><strong>0.021</strong></td>
<td>&lt; <strong>0.001</strong></td>
<td>0.925</td>
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<tr>
<td></td>
<td>35</td>
<td><strong>0.005</strong></td>
<td>0.061</td>
<td>0.717</td>
</tr>
<tr>
<td></td>
<td>90</td>
<td><strong>0.006</strong></td>
<td>0.928</td>
<td>0.613</td>
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</table>
Figure 1. Effects of brood-size treatments (A, C, E) and feeding-rate treatments (B, D, F) on fledgling mourning doves at 25, 35, and 90 d. I determined the effect of treatments on flight time (the time it took an individual to fly 1.5 m when startled from a perch; A, B), size (first principal component of 5 structural measures; C, D), and weight (E, F). Presented values are least-square means for each treatment category ± SE.

Figure 2. Covariance between phenotypic measures of juvenile mourning doves were evaluated to determine potential trade-offs that occurred in response to experimental treatments on brood size of nestlings and feeding rate of fledglings. I examined how flight time (the time it took an individual to fly 1.5 m when startled from a perch) at 25 d (A, B) and 90 d (C-F) was related to size (first principal component of 5 structural measures) and weight at 25 d (A-D) and 90 d (E, F).
Figure 1

(A) Flight Time (s) vs. Age (d) for different groups: One, Two, Three.

(B) Flight Time (s) vs. Age (d) for different diets: Low, Medium, High.

(C) Size (PC1) vs. Age (d) for different groups: One, Two, Three.

(D) Size (PC1) vs. Age (d) for different diets: Low, Medium, High.

(E) Weight (g) vs. Age (d) for different groups: One, Two, Three.

(F) Weight (g) vs. Age (d) for different diets: Low, Medium, High.
Figure 2
CHAPTER 7. CONCLUSIONS

Several threads of inference connect the chapters of my dissertation. My results provided new insights into mechanisms that allow mourning doves to adapt to the broad range of environments to which they are exposed. In addition, my work has provided a foundation for further use of mourning doves as a model system to examine large-scale population dynamics and phenotypic plasticity during breeding in the future.

Populations of mourning doves are found breeding across a wide gradient of habitats and environments. In addition, individuals are exposed to a high degree of environmental variability across protracted breeding seasons. Results from my work help elucidate some of the processes that allow for their success in such a wide range of environments. Life-history strategies vary significantly across their range, with reproductive output greatest east of the Mississippi River and in the Pacific Northwest, with lower annual recruitment in the Southwest and Great Plains. These differences likely represent adaptations to unique environments and have important consequences for population demography on sensitivities to survival and reproduction. Differences in life-histories throughout the range are likely to have consequences for how life-history trade-offs are structured and therefore influence decisions individuals make during breeding related to parental effort. In addition, there is some evidence that the relationship of annual weather variation to reproduction varies across the climatic gradient within their range, representing another source of environmental variation within which this generalist species must adapt. Methodology presented in this dissertation form a strong statistical basis for continuing to study broad-scale reproductive ecology of mourning doves based on harvest wing collections.

I also demonstrated mechanisms by which mourning doves may use adaptive plasticity to deal with environmental variability. Hormonal systems are an important mediator of plasticity in response to environmental inputs, by facilitating response to external stimuli and initiating broad physiological responses, e.g., actions of the hypothalamic-pituitary-adrenal axis. The relationship of prolactin and corticosterone in
adult mourning doves to growth rates of young suggests that these hormones may be important pathways for parents to adjust reproductive effort in response to environmental variability. Plasticity during development is another source of adaptation that can allow individuals to mediate the negative effects of stress during development. Consistent with results for other species of birds, mourning doves were able to mediate the effects of stress on flight ability at early ages, apparently by modifying patterns in growth in order to prioritize development of the wings, thereby reducing negative effects of stress on fledging age. The ability to minimize effects of stress on flight ability continued during the early post-fledging stage. Effects on take-off speed were not realized until 90 d of age, after the period of highest vulnerability of young. Potential to reduce the negative effects of developmental stress may be an important mechanism that allows for mourning doves to adapt reproductive strategies to the broad set of breeding conditions.

My results demonstrated the utility of mourning doves as a model system for future work. Monitoring programs and statistical methodology for estimating mourning dove reproduction developed in this dissertation, coupled with programs for monitoring survival and abundance, present a unique opportunity to examine population dynamics for a species across a broad range of spatially replicated sites. These data sets will provide further insights into life-history variation across the species’ range, the role of annual variability in structuring local population dynamics, and the relationship of climatic and short-term weather variation to population dynamics. In addition, mourning doves are an ideal system to continue work on parental effects and developmental plasticity. Their ubiquity, ease of finding nests, and adaptability to captive environments are conducive to data collection and experimental manipulation. In addition, the species benefits from a long history of research on their natural history and behavior. By coupling this work with information about geographic variation in life-history strategies emerging from monitoring work in the future, predictions about how differences in life-history trade-offs among populations influence these processes can also be tested.