



CHICAGO JOURNALS

Articles from 2013 and after
are now only accessible on
the Chicago Journals website at
JOURNALS.UCHICAGO.EDU

Maternal Effects Increase Within-Family Variation in Offspring Survival

Author(s): Wendy L. Reed, Mark E. Clark and Carol M. Vleck

Source: *The American Naturalist*, Vol. 174, No. 5 (November 2009), pp. 685-695

Published by: The University of Chicago Press for The American Society of Naturalists

Stable URL: <http://www.jstor.org/stable/10.1086/605962>

Accessed: 13-05-2016 19:36 UTC

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://about.jstor.org/terms>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The American Society of Naturalists, The University of Chicago Press are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*

Maternal Effects Increase Within-Family Variation in Offspring Survival

Wendy L. Reed,^{1,*} Mark E. Clark,¹ and Carol M. Vleck²

1. Department of Biological Sciences, North Dakota State University, Fargo, North Dakota 58105; 2. Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa 57001

Submitted December 3, 2008; Accepted May 7, 2009; Electronically published September 24, 2009

ABSTRACT: Maternal effects are environmental components of phenotypes that complicate relationships between natural selection and evolution because they often affect phenotypes and fitness simultaneously. We studied the effects of egg size variation on juvenile survival in a population of American coots (*Fulica americana*). We experimentally evaluated egg size variation at three levels: across the population, within natal nests, and within foster nests. Natal nests accounted for the most variation in population egg size. Within clutches, early-laid eggs were larger than later-laid eggs, with the exception of first-laid eggs, which were small. In the fostering experiment, posthatching survival was most strongly related to egg size relative to natal siblings and natal hatching order and less so to egg size within foster nests. These effects on survival were found even though young from natal nests were neither raised together nor raised by genetic parents. These results indicate that females allocate resources unequally among offspring such that offspring from larger, early-laid eggs have higher survival than offspring from smaller, later-laid eggs, regardless of their size relative to foster siblings or to mean population egg size. These results suggest that egg size variation can be maintained through selection on maternal investment strategies and not on egg size per se.

Keywords: egg size, offspring survival, maternal investment, brood reduction.

Introduction

Females influence the phenotypes of their offspring through genes and somatic investments. Our understanding of the importance of maternal investments for offspring performance and the potential for maternal effects to influence population and evolutionary dynamics has grown considerably over the past decades (Bernardo 1996a; Mousseau and Fox 1998; Wolf et al. 1998; Räsänen and Kruuk 2007). Phenotypic traits influenced by maternal environments complicate evolutionary dynamics when maternal effects influence fitness in addition to phenotypic

expression of the traits (Price et al. 1988; Stinchcombe et al. 2002). For example, it is possible for strong directional selection on a heritable trait like body size to yield no evolutionary response if body size is also influenced by maternal effects like parental provisioning and nutrition (Alatalo et al. 1990; Naguib and Gil 2005). Further complexity exists when maternal environments provided to offspring are heritable because these environments can also evolve and affect offspring phenotypes and fitness (i.e., indirect genetic effects; Wolf et al. 1998). We focus our discussion on the effects of egg size on offspring fitness, although our discussion is equally relevant for offspring size in viviparous animals, seed size in plants, and other offspring phenotypes affected by maternal environments provided to offspring.

Investment made in offspring at the egg stage consists of a large nongenetic (i.e., somatic) investment by females, with large eggs requiring greater resource investments than small eggs do. One assumption of life-history models is that offspring receiving greater investments in the form of large eggs are expected to have survival or growth advantages over offspring from small eggs (Smith and Fretwell 1974; Winkler and Wallin 1987; Stearns 1992; Bernardo 1996b). In many oviparous species, this is the case—large eggs produce larger offspring that have higher survival probability (e.g., insects, Azevedo et al. 1997; amphibians, Dziminski and Roberts 2006; reptiles, Valenzuela 2001; fish, Winemiller and Rose 1993). The influence of egg size on offspring performance in birds has been widely studied (reviewed in Williams 1994 and Christians 2002); however, the relationship between egg size and performance is unclear, which may be a function of multiple maternal investments in offspring fitness.

Classic models of female investment strategies predict a single optimal egg size for a population of females (Smith and Fretwell 1974). In some cases these models are appropriate and variation in egg size among females is small (e.g., Einum and Fleming 2002), but in many cases there is considerable variation in egg size both within populations and among females (Rollinson and Brooks 2008). In

* Corresponding author; e-mail: wendy.reed@ndsu.edu.

Am. Nat. 2009. Vol. 174, pp. 685–695. © 2009 by The University of Chicago. 0003-0147/2009/17405-5091\$15.00. All rights reserved. DOI: 10.1086/605962

birds, egg size can vary considerably within populations (Christians 2002), and the importance of egg size as a key life-history trait has been long recognized (Lack 1968). However, the evolutionary mechanisms that generate and maintain intraspecific variation in egg size in birds are unresolved. One challenge to understanding egg size evolution in birds is the high degree of parental care. Avian parents invest resources in offspring at the egg stage as well as during the incubation and posthatching periods; thus, investments during any one of these time periods can affect fitness and complicate our understanding of the mechanisms driving the evolution of egg size. Cross-fostering designs can experimentally and statistically separate maternal effects present at the egg stage (i.e., egg size) from maternal and paternal effects present after oviposition (i.e., incubation or posthatching care). Of the avian cross-fostering studies, 11 have found a positive effect of egg size on offspring performance (Amundsen and Stokland 1990; Reid and Boersma 1990; Bolton 1991; Amundsen et al. 1996; Blomqvist et al. 1997; Hipfner and Gaston 1999; Styrsky et al. 1999; Hipfner 2000; Risch and Rohwer 2000; Hipfner et al. 2001; Pelayo and Clark 2003), and seven have found no effect of egg size on offspring performance (Ricklefs and Peters 1981; Ricklefs 1984; Magrath 1992; Smith et al. 1995; Reed et al. 1999; Bize et al. 2002; Van de Pol et al. 2006). Typically, these studies swap complete clutches of eggs between females, which may result in overestimation of egg size effects if direct genetic effects covary with egg size (Krist et al. 2004). For example, if females laying large eggs also produce offspring with genes that enhance fitness, the effect of egg size as a maternal investment will be overestimated. An alternative is to directly manipulate egg size. Experimental decreases in egg size have been done in captive populations of birds and have resulted in significant decreases in offspring size (Hill 1993; Finkler et al. 1998; Wagner and Williams 2007); in the case of captive zebra finches, they have decreased the survival of nestlings (Wagner and Williams 2007). Cumulatively, these studies indicate that even though considerable variation in egg size exists within avian populations and larger eggs represent a larger per-offspring investment by females, the consequences of egg size variation are still unresolved. Without an understanding of the consequences of variation in egg size, the evolutionary mechanisms that generate and maintain variation in this central life-history trait are also unknown.

One consequence of a maternal effect is to structure phenotypic variation within populations by decreasing variation within families and increasing variation among families. For example, the difference in size between the largest and smallest eggs in a population can be as much as 150% (Christians 2002); however, females typically account for most of this variation (Christians 2002), which

indicates that some females lay clutches of large eggs and others lay clutches of small eggs. A consequence of this phenotypic structure is that maternal effects are generally thought to generate among-family selection gradients. Traditional cross-fostering studies (switching clutches between nests) allow for evaluation of maternal effects between families but not within families (Krist et al. 2004; see above for limitations). As an alternative to cross-fostering, we fostered offspring among multiple nests in a common North American bird (American coot, *Fulica americana*), which allowed us to consider simultaneously the effects of egg size on juvenile survival at multiple levels: among all eggs in the study population, as well as among eggs associated through common prenatal and common postnatal maternal environments (both natal and foster broods). This experimental design allowed us to evaluate competing hypotheses of the mechanisms driving egg size effects on offspring survival and to avoid potential covariation between direct genetic effects and egg size effects on offspring survival. We make the following interpretations: (1) the effects of egg size on survival at the population level would suggest that females laying large eggs produce higher-quality offspring than females laying small eggs do; (2) the effects of egg size on survival at the level of natal nests would suggest that females allocate resources unequally among offspring at the egg stage and that these prenatal environments provided by females affect offspring survival; and (3) the effects of egg size at the level of foster broods would suggest that the largest chicks in a brood have a competitive advantage over smaller nestmates. With this design, we were able to evaluate whether a maternal effect (egg size) can generate selection pressure within as well as among families and to provide insight into the evolution and maintenance of egg size variation.

Material and Methods

We studied a population of American coots breeding in the prairie-parkland region south of Minnedosa, Manitoba, Canada, over two breeding seasons. American coots are locally abundant and conspicuous in the wetland bird community. Adults defend territories on ponds, which are used throughout the breeding season (May–July) during both egg-incubation and brood-rearing periods. Adult coots build nests attached to emergent vegetation, and females lay 5–16 eggs per clutch. Males and females share incubation duties, and both parents feed and brood chicks during the first few weeks after hatching. Incubation starts after the third to sixth egg is laid, which results in hatching asynchrony within broods. Movement of broods among ponds is rare, which facilitates monitoring the survival of young.

Experimental Design and Methods

During the first breeding season, we located 66 nests during the egg-laying stage or during egg incubation, marked eggs at their blunt end with a unique code, and measured length and breadth to the nearest 0.1 mm with digital calipers (651 eggs were marked and measured). Avian eggs lose approximately 15% of their mass over the course of incubation because of evaporative water loss. Accurate measures of egg mass must be taken within 24 h of oviposition to avoid underestimation of true egg mass. We measured the fresh mass of 63 eggs, each weighed to the nearest 0.01 g within 24 h of being laid, and plotted the mass against their linear dimensions to obtain the following relationship:

$$\text{Fresh egg mass} = 5.36 \times 10^{-4}(\text{length} \times \text{breadth}^2) + 0.464 \quad (1)$$

($r^2 = 0.97$). Because not all eggs were found at the start of incubation, we used this equation to predict fresh egg mass from linear dimensions (length and breadth), which remain constant over incubation (Hoyt 1979). These predicted fresh egg masses were used in all further analyses of egg size ("egg mass" and "egg size" are used interchangeably). Once a clutch was complete, we did not revisit nests until eggs were expected to initiate the hatching process (23 days after the third egg was laid).

We transported eggs that had initiated the hatching process (i.e., that had pipped) into the laboratory in warmed containers and placed them in an incubator (GQF Manufacturing, model 1202) set at 37°C and a relative humidity of 60% to complete hatching, a process that took 8–24 h. Eggs that had not pipped were left in the nest to keep the adults from abandoning them. The period of artificial incubation allowed us to identify which chick hatched from which egg. Once chicks hatched and were dry, we weighed them to the nearest 0.01 g on a digital balance and marked each chick with a uniquely colored nape tag (Gullion 1951). Of the 651 eggs measured, 59 never hatched (these were a combination of rotten or depredated eggs), 17 hatched but were not used in the study (they hatched either too early or too late to be matched with other chicks in the fostering protocol), and the fate of 16 was unknown. Chicks used in the fostering study were assigned to foster families such that each foster family received nine chicks hatched within 48 h of one another (61 foster families each received nine chicks, and one foster family received 10 chicks, for 559 chicks total). Chicks were fostered into nests in three visits, with usually two to three chicks added per visit, and adults readily accepted foster chicks. Chicks hatched within a single day were randomly assigned to foster nests. This design minimized variation in brood size

or age of chicks within a brood and allowed us to statistically separate the effects of the egg environment from those of the posthatching brood environment. For each chick, we knew the nest in which it was produced, the nest into which it was fostered, and the size of the egg from which it hatched. This information allowed us to test for egg size effects at three levels of variation: the size of an egg relative to other eggs in the study population, the size of an egg relative to eggs within its foster nest, and the size of an egg relative to eggs within its natal nest. We also recorded the order in which chicks hatched in their natal nest (hatch order) and the order in which chicks were placed in a foster nest (foster order: first, second, or third group of chicks fostered into a nest). Hatch order is a measure of laying sequence among natal siblings, whereas foster order is a measure of the synchrony in age and development among foster siblings. During the second season, we quantified the relationship between laying order and egg size in 19 complete clutches by visiting nests daily and measuring egg size as described above.

Analyses

Comparisons of egg size variation among females and among foster nests were made using an ANOVA. To compare egg size within natal clutches, within foster clutches, or across the population, we standardized the relative egg size from which each chick hatched for each level of variation (population, natal clutch, foster clutch), using the following z scores:

$$z_{\text{pop}} = \frac{m - \bar{m}_{\text{pop}}}{s_{\text{pop}}}, \quad (2)$$

$$z_{\text{nat}} = \frac{m - \bar{m}_{\text{nat}}}{s_{\text{nat}}}, \quad (3)$$

and

$$z_{\text{fos}} = \frac{m - \bar{m}_{\text{fos}}}{s_{\text{fos}}}, \quad (4)$$

where m is egg mass (in grams, calculated from eq. [1]), \bar{m}_{pop} is the mean egg mass for all the eggs in the study, and s_{pop} is the standard deviation of egg mass for all the eggs in the study; \bar{m}_{nat} is the mean egg mass for the natal clutch and s_{nat} is the standard deviation of egg mass for the natal clutch; and \bar{m}_{fos} is the mean egg mass for the foster clutch and s_{fos} is the standard deviation of egg mass for the foster clutch.

We released chicks in foster broods over a 5-week period

(June 3–July 15) and (after release) made at least weekly visits to the foster parent territory to resight chicks for analysis of survival. We observed chicks through a 20–60× spotting scope for 25–60 min to identify individual chicks by their nape tag markers. In some cases, multiple visits within a week were made to the same territory, and chick resightings that may have occurred during these visits were noted. For example, if a wetland with a foster brood was passed on the way to another wetland and marked chicks were sighted, these sightings were recorded. We quantified the number of visits each week to a territory to account for any effects of resighting effort on resighting probabilities in our analyses. Typically, fewer than three visits in a week were made to a territory.

The recorded sightings of each marked chick were used to develop estimates of offspring survival and probability of resighting during the first 5 weeks after hatching with a Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965). This approach assumes that observations of offspring are affected by two components: (1) the probability of survival and (2) the probability of detection. Maximum likelihood estimates of apparent survival and probability of detection were obtained from individual encounter histories (weekly resighting data) with this approach (Lebreton et al. 1992). We developed encounter histories from the observation records and used Program MARK, version 18 (White and Burnham 1999), to generate estimates of survival and detection probability from these data.

We used an information theoretic approach to rank models for survival as well as models describing egg size variation within females. The models represent hypotheses, and information theory provides a way to quantify the relative likelihood of each of the hypotheses (models), given the data (Burnham and Anderson 2002; Johnson and Omland 2004). We compared a suite of *a priori* models that included the effects of time (day during the season), chick age, weekly resighting effort, relative (population, natal, and foster) egg mass, and combinations of these variables on weekly survival and detection probabilities. After reviewing the survival and detection probability estimates from these models, we added to the suite several *a posteriori* models that included the effects of hatch order, foster order, and natal clutch size. Linear combinations of the variables were logit transformed to constrain the survival and detection probabilities to values between 0 and 1. Models in the suite were ranked by the Akaike Information Criterion adjusted for small sample size (AIC_c ; Burnham and Anderson 2002), which provides an unbiased measure of parsimony from the difference between variation explained by a model and variation associated with the number of parameters in the model (Burnham and Anderson 2002). A smaller AIC_c value (relative to

values for other models in the suite) indicates a more parsimonious model and more support for that particular hypothesis. We also assessed model goodness of fit (because AIC_c does not indicate goodness of fit *per se*; Burnham and Anderson 2002) by using a bootstrap approach in which the observed deviance from observations for a particular model was compared with a distribution of deviances from 500 computer-replicated simulations of encounter history sets for 547 individuals (12 individuals were excluded from the analyses either because egg size was unknown [$n = 8$] or because natal nest was not recorded [$n = 4$]). We estimated overdispersion for two models in the candidate set to assess the need to adjust AIC_c ranks for excessive extrabinomial variation (Anderson et al. 1994; Burnham and Anderson 2002). Finally, we also used AIC_c to rank least squares regression models that described patterns of variation in egg size within broods.

Results

Egg masses in this population were normally distributed and ranged from 20 to 35 g. Most (75%) of the variation in egg size was due to differences among nests in the size of eggs produced (ANOVA with nest as the explanatory variable: $F_{65,545} = 22.03$, $P < .0001$), indicating that some females lay large eggs and others lay small eggs. Egg size varies systematically with laying sequence; the first- and last-laid eggs were smaller than those laid in the middle of the clutch ($n = 19$ clutches; fig. 1). Clutch sizes ranged from five to 10 eggs, with nine-egg clutches being the most

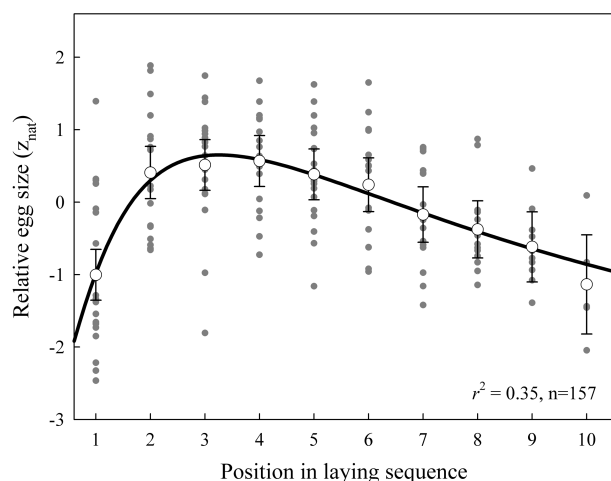


Figure 1: Relative egg size within natal nests varying with laying position. Filled circles represent observed data, open circles with bars indicate mean values and 95% confidence intervals, and the solid line indicates the best model fit to the data determined by AIC_c (Akaike Information Criterion adjusted for small sample size).

common. The relationship between laying position and egg mass is best described by a lognormal curve ($AIC_c = -78.2$, $r^2 = 0.35$ vs. $AIC_c = -59.1$, $r^2 = 0.27$ for a quadratic model; $AIC_c = -14.5$, $r^2 = 0.02$ for a linear model; and $AIC_c = -14.1$, $r^2 = 0$ for constant size). After the fostering protocol, the variation in egg size among foster nests was not different from that within foster nests (ANOVA with foster nest as the explanatory variable: $F_{61,547} = 1.31$, $P = .24$). Thus, the random assignment of chicks into foster nests resulted in all foster broods starting with the same number of chicks, a similar mean egg mass, and similar variation about the mean.

The survival analysis indicates that the most parsimonious model of survival included effects of hatchling age, relative natal egg mass, and hatch order. In the model with the lowest AIC_c value, survival varied across two age groups and with continuous effects from relative natal egg mass and hatching order (denoted as $\phi(\text{age} + z_{\text{nat}} + \text{hatch order})$; table 1) such that weekly survival, ϕ , is given by

$$\phi = \begin{cases} \frac{\exp(1.3+0.69+0.21 \cdot z_{\text{nat}} - 0.15 \cdot \text{hatch order})}{1 + \exp(1.3+0.69+0.21 \cdot z_{\text{nat}} - 0.15 \cdot \text{hatch order})} & \text{age} \leq 2 \text{ weeks} \\ \frac{\exp(1.3+0.21 \cdot z_{\text{nat}} - 0.15 \cdot \text{hatch order})}{1 + \exp(1.3+0.21 \cdot z_{\text{nat}} - 0.15 \cdot \text{hatch order})} & \text{age} > 2 \text{ weeks} \end{cases} \quad (5)$$

In this model, the weekly survival probability is higher for 1–2-week-old chicks than for 3–5-week-old chicks. Survival probability increases (equally for both age groups) as relative natal egg size increases (fig. 2a) and decreases (equally for both age groups) as hatch order increases (fig. 2b). The second-highest-ranked model indicated age and natal egg mass effects on survival but did not include the effect of hatch order (denoted as $\phi(\text{age} + z_{\text{nat}})$; table 1). The difference in AIC_c values between the first- and second-highest-ranked models (0.9; table 1) indicates

Table 1: Survival models and associated information metrics used to evaluate performance

Model	AIC_c	ΔAIC_c	QAIC _c weight	Model likelihood
$\phi(\text{age} + z_{\text{nat}} + \text{hatch order})$	2,264.17	.00	.35	1.00
$\phi(\text{age} + z_{\text{nat}})^a$	2,265.08	.90	.23	.64
$\phi(\text{age} + z_{\text{nat}} + \text{hatch order} + \text{Cs})$	2,266.11	1.94	.13	.38
$\phi(\text{age} + z_{\text{nat}} + \text{Cs})$	2,266.92	2.75	.09	.25
$\phi(\text{age} + z_{\text{nat}} + z_{\text{fos}} + z_{\text{pop}})$	2,267.50	3.32	.07	.19
$\phi(\text{age} + \text{hatch order})$	2,268.52	4.34	.04	.11
$\phi(\text{age})$	2,270.38	6.21	.02	.04
$\phi(\text{age} + z_{\text{pop}} + \text{hatch order})$	2,270.47	6.30	.02	.04
$\phi(\text{age} + \text{hatch order} + \text{Cs})$	2,270.50	6.33	.01	.04
$\phi(\text{age} + \text{foster order})$	2,271.11	6.94	.01	.03
$\phi(z_{\text{nat}})$	2,271.69	7.51	.01	.02
$\phi(\text{age} + \text{Cs})$	2,272.31	8.14	.01	.02
$\phi(\text{age} + z_{\text{pop}})$	2,272.33	8.16	.01	.02
$\phi(\text{age} + z_{\text{fos}})$	2,272.41	8.24	.01	.02
$\phi(\text{age} + z_{\text{pop}} + \text{Cs})$	2,274.27	10.09	.00	.01
$\phi(\text{hatch order})$	2,274.78	10.60	.00	.01
$\phi(\text{Cs})$	2,278.65	14.48	.00	.00
$\phi(\text{age} \times \text{time})$	2,554.74	290.56	.00	.00
$\phi(\text{age})p(\text{time})$	2,573.02	308.84	.00	.00
$\phi(\text{time})p(\text{time})$	2,638.07	373.90	.00	.00
$\phi(\text{age})p()$	2,772.11	507.94	.00	.00
$\phi()p()$	2,820.43	556.26	.00	.00

Note: Lower AIC_c (Akaike Information Criterion adjusted for small sample size) values indicate better approximation because there is lower information loss. The QAIC_c weight and model likelihoods indicate the amount of support for a particular model relative to the other models in the group (e.g., model $\phi(\text{age} + z_{\text{nat}} + \text{hatch order})$ is approximately nine times as likely, given the data, as model $\phi(\text{age} + \text{hatch order})$, according to the ratio of model likelihood). In the first 18 models listed, detection probability (p) varies between the first 4 weeks and the last 2 weeks along with weekly effort. Detection probability varies with week in the nineteenth and twentieth models listed and is constant in the twenty-first and twenty-second models listed. Cs = natal clutch size.

^a Goodness of fit for this model (and models with lower ΔAIC_c) was considered adequate because deviance for this model was between the eighteenth and nineteenth percentile of values in the cumulative distribution of deviance expected for a sample with 547 individuals. Lack of fit is indicated when observed deviance is higher than the seventieth percentile (White and Burnham 1999).

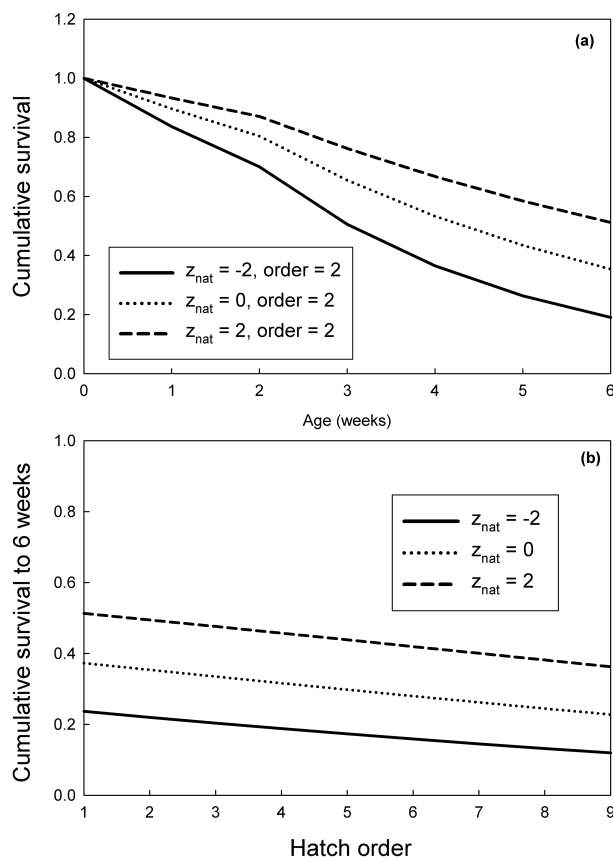


Figure 2: Cumulative survival for coot young during the first 5 weeks after hatching as a function of age (a) and hatch order (b) among natal siblings. The dashed and solid lines represent cumulative survival for chicks from a relatively large egg ($z_{\text{nat}} = 2.0$) and from a relatively small egg ($z_{\text{nat}} = -2.0$), respectively, in a natal clutch and represent the variation in survival among natal siblings reared apart in foster nests. The dotted line represents the cumulative survival for chicks from an average-size egg in a natal clutch ($z_{\text{nat}} = 0$).

nearly equal support for both models (Burnham and Anderson 2002). For example, the evidence ratio (which can be computed by either the ratio of AIC_c weights or the ratio of model likelihoods) for the first-ranked model (model $\phi(\text{age} + z_{\text{nat}} + \text{hatch order})$) to the second-ranked model (model $\phi(\text{age} + z_{\text{nat}})$) is 1.52 : 1.0 (AIC_c weight first/ AIC_c weight second = $0.35/0.23 = 1.52$; table 1). Moreover, the coefficient for the natal mass effect (0.21) has a higher absolute value than the coefficient for the hatch order effect (-0.15) does, which indicates that natal mass contributes more to early offspring survival than hatch order does (fig. 2b). Some evidence supported adding effects of natal clutch size (Cs; table 1) to the first- and second-ranked models (i.e., models $\phi(\text{age} + z_{\text{nat}} + \text{hatch order} + \text{Cs})$ and $\phi(\text{age} + z_{\text{nat}} + \text{Cs})$ in table 1). However, the absolute value of the coefficient for natal

clutch size (-0.027 in model $\phi(\text{age} + z_{\text{nat}} + \text{hatch order} + \text{Cs})$; -0.037 in model $\phi(\text{age} + z_{\text{nat}} + \text{Cs})$) indicates that clutch size effects on offspring survival were much smaller than effects due to relative natal mass (0.21 in model $\phi(\text{age} + z_{\text{nat}} + \text{hatch order} + \text{Cs})$; 0.22 in model $\phi(\text{age} + z_{\text{nat}} + \text{Cs})$) or hatch order (-0.14 in model $\phi(\text{age} + z_{\text{nat}} + \text{hatch order} + \text{Cs})$). Moreover, evidence ratios and ranks of models with these covariates isolated also indicate more support (evidence ratio of 5.75 times as likely, given the data) for natal mass effects ($\Delta AIC_c = 0.90$ for model $\phi(\text{age} + z_{\text{nat}})$) than for hatch order effects ($\Delta AIC_c = 8.14$ for model $\phi(\text{age} + \text{hatch order})$) and much more support (evidence ratio of 23.0 times as likely, given the data) than for natal clutch size effects ($\Delta AIC_c = 0.90$ for model $\phi(\text{age} + \text{Cs})$; table 1). Effects of relative natal mass were also greater than other egg mass effects. For instance, in model $\phi(\text{age} + z_{\text{nat}} + z_{\text{fos}} + z_{\text{pop}})$ the coefficient for the natal mass term (0.26) has a higher absolute value than do the coefficient for the relative population mass term (0.038) and the coefficient for the relative foster term (-0.14). Evidence ratios and model ranks also corroborate that the effects of relative natal mass explain much more of the variation in survival than do the effects of mass relative to the population or mass relative to the foster clutch (table 1), given the data. All other models in the candidate set have considerably less support than the first four models do. To illustrate, 80% of the weight of evidence (i.e., the sum of $QAIC_c$ weights; table 1) is for the four highest-ranked models, all of which assume an effect of relative natal mass (without effects of size relative to the population or foster siblings). Models that did not include effects of natal mass or hatch order have ΔAIC_c values greater than 6 and weight of evidence below 3% (table 1). Estimates of overdispersion for model $\phi(\text{age} + z_{\text{nat}})$ (1.05 based on the ratio of observed deviance to mean deviance in bootstrap estimates; Nichols 2005) and model $\phi(\text{age} \times \text{time})$ (1.42 from logistic regression module in Program MARK) were low. Estimates of overdispersion below 2 have negligible impact on model rank via AIC_c (Anderson et al. 1994); therefore, we did not adjust AIC_c values.

Discussion

Our fostering design provides a standardized competitive environment in which postnatal factors often confounded with egg size are controlled and differences in survival can be interpreted in terms of egg size variation at three levels (population, foster nest, and natal nest). An effect of egg size at any one of these levels provides information about potential mechanisms driving offspring survival as well as selection gradients that may affect egg size variation. Our results indicate that females partition prehatching re-

sources unequally among their offspring and that these resources affect offspring survival in the weeks immediately following hatching. This result is reflected in the effects of both relative natal egg size and hatching order on chick survival. Chicks hatched from a female's largest eggs (typically eggs in laying position two through five; fig. 1) had higher survival probability than did chicks hatched from a female's smallest eggs (figs. 2a, 3), even though siblings were fostered into multiple nests and were thus not raised together (and were therefore not in direct competition for posthatching parental care or resources). Likewise, hatching order, which is a proxy for laying sequence, indicates that, independent of hatching asynchrony (e.g., foster order) and relative egg size, eggs laid early in the laying sequence had higher survival probability than did eggs laid later in the sequence. Neither the size of an egg relative to all eggs in the population nor the size of an egg relative to foster siblings adequately explained the observed variation in apparent survival after hatching (table 1). Our data indicate that although the largest variation in egg size is accounted for by individual females, egg size per se is not the critical factor for survival in the first weeks after hatching; rather, the critical factor consists of other maternal effects associated with a female's largest eggs, which are laid early in the cycle. These results provide evidence of a maternal effect that generates selection potential within families and may be a general mechanism by which egg size variation is maintained.

Specific Hypotheses of Egg Size Effects

Life-history models predict that females should produce offspring of a size that maximizes lifetime fitness (Smith and Fretwell 1974), and many models predict a single optimal egg size for a given population (Smith and Fretwell 1974; Winkler and Wallin 1987). Although there is empirical evidence in fish, reptiles, and insects that supports the predictions for evolution of a single optimal egg size (e.g., Sinervo and Licht 1991; Azevedo et al. 1997; Einum and Fleming 2002), there is often considerable variation in offspring size within populations, which is contrary to expectations and has been more problematic to explain (Winemiller and Rose 1993; Einum and Fleming 2002). More recent life-history models have incorporated phenotypic variation among females as a way to explain the large among-female variation in offspring size (Hendry et al. 2001; Rollinson and Brooks 2008). Hendry et al. (2001) predict that when maternal effects influence the relationship between egg size and offspring fitness, variation between egg size and maternal phenotypes can be expected rather than a single optimum. Alternatively, variation in offspring size may occur independently of maternal effects, as in the case of models predicting more than one optimal

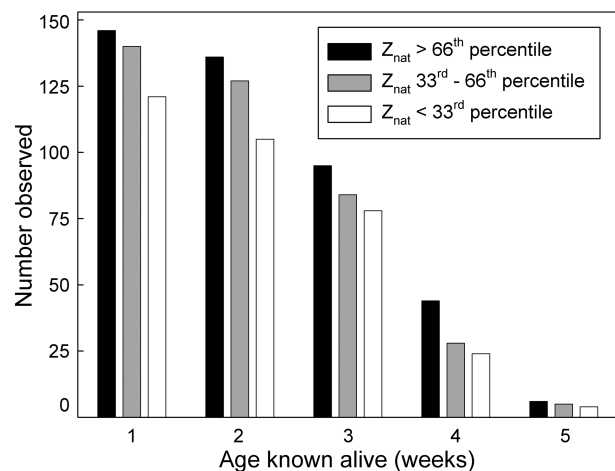


Figure 3: Number of individuals known to be alive during the first 5 weeks after hatching. Bars represent the number of individuals observed at these time periods for eggs in the largest third (black bars), middle third (gray bars), and smallest third (white bars) of their natal clutch.

offspring size when environmental quality varies (e.g., bet-hedging models; Einum and Fleming 2002; Dziminski and Roberts 2006). In birds, the adaptive significance of egg size variation has been explored in the context of female quality (high-quality females produce large eggs and chicks that survive better than those from small eggs and poorer-quality females; e.g., Styrsky et al. 1999; but see Van de Pol et al. 2006) and sibling competition (larger siblings are better competitors for parental resources than siblings from small eggs; e.g., Amat et al. 2001; but see Krist et al. 2004), but the significance of the large variation in egg size in birds remains unresolved.

In American coots, there is considerable variation in egg size (75% increase in size from the smallest to the largest egg in this study population), and individual nests account for most of that variation (75% of egg size variation is due to differences among nests). Egg size per se does not reflect the quality of offspring, as our survival models indicate very little support for an effect of population egg size on survival (table 1). Large eggs do require a larger investment of resources than small eggs do because they contain absolutely more yolk, albumen, and shell than smaller eggs (Alisauskas 1986; Arnold et al. 1991). Although large-egg females invest more resources in individual offspring, these investments do not increase juvenile survival relative to that of chicks from small eggs in the first 5 weeks after hatching, a period with high mortality rates (approximately 50%–85% mortality over 5 weeks as juveniles vs. approximately 6% mortality over 5 weeks for adults; Brisbin et al. 2002). Our fostering design decoupled any coadaptation between the size of egg a female pro-

duced and other factors that might affect the adults' ability to rear those chicks. For example, adults that produce large eggs may have also been better prepared to rear large offspring. We were unable to evaluate these types of nest effects because of limitations in the analyses and potential overparameterization of the data. A different fostering approach could be used to address these issues.

Much less variation in egg size exists within clutches ($\leq 25\%$) than between clutches, but this variation does have consequences for juvenile survival rates. Our results suggest that differences in the quality of maternal resources provided to offspring are more important than the absolute quantity of resources and that these differences in quality ultimately affect juvenile survival. The largest eggs produced by females have a higher likelihood of survival than do their smallest eggs, regardless of whether a female produces large- or small-egg clutches. The mechanism of these egg size effects is not due to size-related competition among siblings in the nest, because we found little support for large eggs within foster broods having higher survival probability than that of small eggs. Furthermore, the differences in development and size that result from chicks hatching asynchronously (as measured by foster order) did not explain the variation in juvenile survival (table 1). For many animals, there is intense sibling rivalry within broods or litters (reviewed by Mock and Parker 1997; Forbes and Glassey 2000), in which larger offspring are at a competitive advantage over smaller siblings for resources. Females may allocate resources unequally among offspring because of the depletion of resources across the laying sequence, or the allocation may be adaptive. Evidence from a variety of species suggests two adaptive investment strategies to either mitigate or exacerbate the effects of sibling rivalry within broods when offspring hatch asynchronously. Increasing the size of later-laid eggs may compensate for the size and developmental disadvantages realized by hatching last in a brood survival strategy, whereas decreasing the size of earlier-laid eggs may exacerbate sibling rivalry and represent an optimal investment for species with brood reduction strategies (Slagsvold et al. 1984; Magrath 1992; Bonabeau et al. 1998; Maddox and Weatherhead 2008).

Brood reduction is common in American coots, and patterns of egg size variation within clutches are as predicted by brood reduction hypotheses: later-laid eggs are smaller (fig. 1). Hatchling size and egg size are correlated in coots (Reed 2000); however, the greatest difference in size among siblings at any one time is created through hatching asynchrony. In coots, chicks hatch in the approximate order in which eggs are laid, which results in marked hatching asynchrony among siblings (as much as 8–10 days between the first and last hatched young). Offspring are brooded and fed by the parents in the first 2 weeks after hatching, after which they gradually gain in-

dependence (Desrochers and Ankney 1986). The age effect on survival (table 1) indicates that survival is higher in the first 2 weeks after hatching and decreases at the time the young begin to gain independence from parents. In coot broods with natural variation in hatching asynchrony, the early-hatched young have higher survival probability than their late-hatched siblings do (Lyon 1993). These early-hatching young are from the largest eggs in the clutch, with the exception of the first-laid egg. Our results indicate that both relative egg size within natal clutches and hatch order (in natal clutches) independently contribute to higher intrinsic survival probabilities. Both of these effects suggest that what determines survival is the quality of offspring at the time of hatching and not the sibling dynamics that occur after hatching, such as those that occur because of developmental differences among siblings hatching asynchronously (i.e., foster order). These effects suggest that selection has acted on females and the patterns of resource allocation among their offspring and not on egg size per se. Relative egg size effects among natal (genetic) siblings are likely associated with multiple resources that are allocated unequally among offspring. For example, in addition to the amount of yolk, albumen, and eggshell in eggs of different size, maternally allocated testosterone levels in American coot egg yolks follow a pattern with laying sequence similar to that for egg size and are not correlated with absolute egg size (Reed and Vleck 2001).

In addition to the gross somatic investment associated with the size of an egg (i.e., the total amount of energy in the yolk, albumen, and eggshell), eggs also contain hormones, carotenoids, antibodies, and other nutrients that can affect offspring performance. For example, accumulating evidence from a wide variety of species indicates that maternally derived hormones present at the time of oviposition have long-term consequences for offspring phenotypes (reviewed in Groothuis et al. 2005; Müller et al. 2007). Elevated testosterone in egg yolks is associated with increased begging behaviors (Schwabl 1996; Eising and Groothuis 2003), increased competitiveness (Groothuis et al. 2005), and increased growth rates (Schwabl 1996; Eising et al. 2001; Groothuis et al. 2005; Navara et al. 2006) but decreased immune function (Groothuis et al. 2005; Müller et al. 2005; Navara et al. 2005) later in life. Selection on proximate mechanisms of resource allocation to eggs can result in rapid evolutionary changes and significant consequences for offspring phenotypes. For example, variation in oocyte growth dynamics in recently established populations of house finches explains differences in sex-biased levels of maternal hormones, carotenoids, and vitamins in eggs (Badyaev et al. 2006, 2008; Badyaev and Oh 2008). Maternally deposited carotenoids in yolks can affect immune function, survival, and

carotenoid-based coloration in chicks (McGraw and Ardia 2003). In coots, parents use red and orange feather coloration in chicks as a signal and bias food provisioning to more brightly ornamented chicks, which increases their survival rates (Lyon et al. 1994). The unequal allocation of resources among offspring and the survival consequences of these resources provide strong support for the hypothesis that the adaptive significance of within-clutch patterns of egg size in American coots is related to brood-reduction strategies (Slagsvold et al. 1984).

Evolutionary Consequences of Maternal Effects

Predictive models of evolution require an understanding of inheritance as well as selection pressures and fitness (Lande and Arnold 1983). Maternal effects are a unique phenomenon because there are consequences of maternal investment strategies, which balance current and future reproduction, for the female's fitness and consequences of these maternal environments for offspring fitness (Müller et al. 2007). We would expect patterns of variation in egg size and composition to reflect the influence of investment strategies on maternal fitness. Even though most of the variation in egg size occurs because of differences among females, this study suggests that the differential maternal investments made among natal siblings rather than among all offspring in the population are driving offspring quality and survival. Hence, offspring that were larger than their genetic siblings had a selective advantage, but large offspring per se in the population did not. Thus, females (both those producing small-egg clutches and those producing large-egg clutches) contribute their largest offspring to the next generation, and, when egg size is heritable, this could be a general mechanism maintaining the large egg size variation within populations.

Most studies of maternal effects of egg size or egg environments explore individual-level selection (i.e., population egg size); however, because maternal effects act to structure phenotypic variation among families, selection can act beyond the level of the individual (i.e., group or kin selection; Wade 1985, 1998; Agrawal et al. 2001). Quantitative genetic models of the evolution of maternal effects consider selection that occurs among family groups (Wade 1998) and contribute to mathematical similarities between group selection and selection due to maternal effects (Cheverud and Moore 1994; Wade 1998). Our results suggest that even though the largest fraction of variation in egg size is structured among females, the fitness consequences of egg size occur within families. Thus, the maternal effect that has consequence for offspring fitness is the unequal distribution of resources among offspring within families, not egg size per se. Our study provides evidence of a maternal effect that minimizes selection

among families and generates selection on within-clutch egg size variation in this population.

Central to an understanding of life-history evolution is an understanding of the consequences of variation in maternal investments and the mechanisms involved in maintaining and producing this variation. An evaluation of the fitness consequences of maternal investments requires careful consideration of the variance structure among and within females. In general, we expect that developmental environments created by females will show greater variation among females than within a single female (i.e., egg size varies more among females than within females). As we have shown here, fostering designs can be used to manipulate the pattern of trait variation among and within females, which allows for a mechanistic interpretation of effects of maternal traits on offspring performance.

Acknowledgments

We thank B. J. Danielson, T. E. Martin, and D. Vleck for helpful comments on earlier drafts of this manuscript. D. Evelsizer, P. Joyce, J. Pelayo, C. Seal, and A. Turner provided invaluable technical and field assistance. Funding for this project was provided by the Delta Waterfowl Foundation, National Science Foundation grant IBN-98-01503, a Sigma Xi Grant-in-Aid of Research, and the American Museum of Natural History, Frank Chapman Fund.

Literature Cited

- Agrawal, A. F., E. D. Brodie III, and M. J. Wade. 2001. On indirect genetic effects in structured populations. *American Naturalist* 158: 308–323.
- Alatalo, R. V., L. Gustafson, and A. Lundberg. 1990. Phenotypic selection on heritable size traits: environmental variance and genetic response. *American Naturalist* 135:464–471.
- Alisauskas, R. T. 1986. Variation in the composition of the eggs and chicks of American coots. *Condor* 88:84–90.
- Amat, J. A., R. M. Fraga, and G. R. Arroyo. 2001. Intracatch egg-size variation and offspring survival in the Kentish plover *Charadrius alexandrinus*. *Ibis* 143:17–23.
- Amundsen, T., and J. N. Stokland. 1990. Egg size and parental quality influence nestling growth in the shag. *Auk* 107:410–413.
- Amundsen, T., S. H. Lorentsen, and T. Tveraa. 1996. Effects of egg size and parental quality on early nestling growth: an experiment with the Antarctic petrel. *Journal of Animal Ecology* 65:545–555.
- Anderson, D. R., K. P. Burnham, and G. C. White. 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75: 1780–1793.
- Arnold, T. W., R. T. Alisauskas, and C. D. Ankney. 1991. Egg composition of American coots in relation to habitat, year, laying date, clutch size, and supplemental feeding. *Auk* 108:532–547.
- Azevedo, R. B. R., V. French, and L. Partridge. 1997. Life-history consequences of egg size in *Drosophila melanogaster*. *American Naturalist* 150:250–282.
- Badyaev, A. V., and K. P. Oh. 2008. Environmental induction and phenotypic retention of adaptive maternal effects. *BMC Evolutionary*

- Biology 8: 3, doi:10.1186/1471-2148-8-3. <http://www.biomedcentral.com/1471-2148/8/3>.
- Badyaev, A. V., D. Acevedo Seaman, K. J. Navara, G. E. Hill, and M. T. Mendonça. 2006. Evolution of sex-biased maternal effects in birds. III. Adjustment of ovulation order enables sex-specific allocation of hormones, carotenoids, and vitamins. *Journal of Evolutionary Biology* 19:1044–1057.
- Badyaev, A. V., R. L. Young, G. E. Hill, and R. A. Duckworth. 2008. Evolution of sex-biased maternal effects in birds. IV. Intra-ovarian growth dynamics can link sex-determination and sex-specific acquisition of resources. *Journal of Evolutionary Biology* 21:449–460.
- Bernardo, J. 1996a. Maternal effects in animal ecology. *American Zoologist* 36:83–105.
- . 1996b. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *American Zoologist* 36:216–236.
- Bize, P., A. Roulin, and H. Richner. 2002. Covariation between egg size and rearing conditions determines offspring quality: an experiment with the alpine swift. *Oecologia* (Berlin) 132:231–234.
- Blomqvist, D., O. C. Johansson, and F. Gotmark. 1997. Parental quality and egg size affect chick survival in a precocial bird, the lapwing *Vanellus vanellus*. *Oecologia* (Berlin) 110:18–24.
- Bolton, M. 1991. Determinants of chick survival in the lesser black-backed gull: relative contributions of egg size and parental quality. *Journal of Animal Ecology* 60:949–960.
- Bonabeau, E., J.-L. Deneubourg, and G. Theraulaz. 1998. Within-brood competition and the optimal partitioning of parental investment. *American Naturalist* 152:419–427.
- Brisbin, I. L., H. D. Pratt, and T. B. Mowbray. 2002. American coot (*Fulica americana*) and Hawaiian coot (*Fulica alai*). *The Birds of North America*, ed. A. Poole and F. Gill. No. 697. Academy of Natural Sciences, Philadelphia; and American Ornithologists' Union, Washington, DC.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Springer, New York.
- Cheverud, J. M., and A. J. Moore. 1994. Quantitative genetics and the role of the environment provided by relatives in behavioral evolution. Pages 67–100 in C. R. B. Boake, ed. *Quantitative genetic studies of behavioral evolution*. University of Chicago Press, Chicago.
- Christians, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews of the Cambridge Philosophical Society* 77:1–26.
- Cormack, R. M. 1964. Estimates of survival from the sightings of marked animals. *Biometrika* 51:429–438.
- Desrochers, B. A., and C. D. Ankney. 1986. Effects of brood size and age on the feeding behavior of adult and juvenile American coots (*Fulica americana*). *Canadian Journal of Zoology* 64:1400–1406.
- Dziminski, M. A., and J. D. Roberts. 2006. Fitness consequences of variable maternal provisioning in quacking frogs (*Crinia georgiana*). *Journal of Evolutionary Biology* 19:144–155.
- Einum, S., and I. A. Fleming. 2002. Does within-population variation in fish egg size reflect maternal influences on optimal values? *American Naturalist* 160:756–765.
- Eising, C. M., and T. G. G. Groothuis. 2003. Yolk androgens and begging behavior in black-headed gull chicks: an experimental field study. *Animal Behaviour* 66:1027–1034.
- Eising, C. M., C. Eikenaar, H. Schwabl, and T. G. G. Groothuis. 2001. Maternal androgens in black-headed gull (*Larus ridibundus*) eggs: consequences for chick development. *Proceedings of the Royal Society B: Biological Sciences* 268:839–846.
- Finkler, M. S., J. B. Van Orman, and P. R. Sotherland. 1998. Experimental manipulation of egg quality in chickens: influence of albumen and yolk on the size and body composition of near-term embryos in a precocial bird. *Journal of Comparative Physiology B* 168:17–24.
- Forbes, S., and B. Glassey. 2000. Asymmetric sibling rivalry and nestling growth in red-winged blackbirds (*Agelaius agelaius*). *Behavioral Ecology and Sociobiology* 48:413–417.
- Groothuis, T. G. G., W. Muller, N. von Engelhardt, C. Carere, and C. Eising. 2005. Maternal hormones as a tool to adjust offspring phenotype in avian species. *Neuroscience and Biobehavioral Reviews* 29:329–352.
- Gullion, G. W. 1951. A marker for waterfowl. *Journal of Wildlife Management* 15:222–223.
- Hendry, A. P., T. Day, and A. B. Cooper. 2001. Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. *American Naturalist* 157:387–407.
- Hill, W. L. 1993. Importance of prenatal nutrition to the development of a precocial chick. *Developmental Psychobiology* 26:237–249.
- Hipfner, J. M. 2000. The effect of egg size on post-hatching development in the razorbill: an experimental study. *Journal of Avian Biology* 31:112–118.
- Hipfner, J. M., and A. J. Gaston. 1999. The relationship between egg size and posthatching development in the thick-billed murre. *Ecology* 80:1289–1297.
- Hipfner, J. M., A. J. Gaston, and A. E. Storey. 2001. Food supply and the consequences of egg size in the thick-billed murre. *Condor* 103:240–247.
- Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96:73–77.
- Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology & Evolution* 19:101–108.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225–247.
- Krist, M., V. Remes, L. Uvirova, P. Nadvornik, and S. Bures. 2004. Egg size and offspring performance in the collared flycatcher (*Ficedula albicollis*): a within-clutch approach. *Oecologia* (Berlin) 140: 52–60.
- Lack, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lyon, B. E. 1993. Conspecific brood parasitism as a flexible female reproductive tactic in American coots. *Animal Behaviour* 46:911–928.
- Lyon, B. E., J. M. Eadie, and L. D. Hamilton. 1994. Parental choice selects for ornamental plumage in American coot chicks. *Nature* 371:240–243.
- Maddox, J. D., and P. J. Weatherhead. 2008. Egg size variation in birds with asynchronous hatching: is bigger really better? *American Naturalist* 171:358–365.
- Magrath, R. D. 1992. Roles of egg mass and incubation pattern in

- establishment of hatching hierarchies in the blackbird (*Turdus merula*). *Auk* 109:474–487.
- McGraw, K. J., and D. R. Ardia. 2003. Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. *American Naturalist* 162:704–712.
- Mock, D. W., and G. A. Parker. 1997. The evolution of sibling rivalry. Oxford University Press, London.
- Mousseau, T. A., and C. W. Fox, eds. 1998. Maternal effects as adaptations. Oxford University Press, London.
- Müller, W., T. G. G. Groothuis, A. Kasprzik, C. Dijkstra, R. V. Alatalo, and H. Siitari. 2005. Prenatal androgen exposure modulates cellular and humoral immune function of black-headed gull chicks. *Proceedings of the Royal Society B: Biological Sciences* 272:1971–1977.
- Müller, W., C. M. Lessels, P. Korsten, and N. von Engelhardt. 2007. Manipulative signals in family conflict? on the function of maternal yolk hormones in birds. *American Naturalist* 169:E84–E96.
- Naguib, M., and D. Gil. 2005. Transgenerational effects on body size caused by early developmental stress in zebra finches. *Biology Letters* 1:95–97.
- Navara, K. J., G. E. Hill, and M. T. Mendonça. 2005. Variable effects of yolk androgens on growth survival and immunity in eastern bluebird nestlings. *Physiological and Biochemical Zoology* 78:570–578.
- . 2006. Yolk testosterone stimulates growth and immunity in house finch chicks. *Physiological and Biochemical Zoology* 79:550–555.
- Nichols, J. D. 2005. Modern open-population capture-recapture models. Pages 58–87 in S. C. Amstrup, T. L. McDonald, and B. F. J. Manly, eds. *Handbook of capture-recapture analysis*. Princeton University Press, Princeton, NJ.
- Pelayo, J., and R. Clark. 2003. Consequences of egg size for offspring survival: a cross fostering experiment in ruddy ducks (*Oxyura jamaicensis*). *Auk* 120:384–393.
- Price, T., M. Kirkpatrick, and S. J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. *Science* 240:798–799.
- Räsänen, K., and L. E. B. Kruuk. 2007. Maternal effects and evolution at ecological time-scales. *Functional Ecology* 21:408–421.
- Reed, W. L. 2000. Maternal effects in the American coot: consequences for offspring growth and survival. PhD diss. Iowa State University, Ames.
- Reed, W. L., and C. M. Vleck. 2001. Functional significance of variation in egg-yolk androgens in the American coot. *Oecologia* (Berlin) 128:164–171.
- Reed, W. L., A. M. Turner, and P. R. Sotherland. 1999. Consequences of egg-size variation in the red-winged blackbird. *Auk* 116:549–552.
- Reid, W. V., and P. D. Boersma. 1990. Parental quality and selection on egg size in the Magellanic penguin. *Evolution* 44:1780–1786.
- Ricklefs, R. E. 1984. Components of variance in measurements of nestling European starlings (*Sturnus vulgaris*) in southeastern Pennsylvania. *Auk* 101:319–333.
- Ricklefs, R. E., and S. Peters. 1981. Parental components of variance in growth-rate and body size of nestling European starlings (*Sturnus vulgaris*) in eastern Pennsylvania. *Auk* 98:39–48.
- Risch, T. S., and F. C. Rohwer. 2000. Effects of parental quality and egg size on growth and survival of herring gull chicks. *Canadian Journal of Zoology* 78:967–973.
- Rollinson, N., and R. J. Brooks. 2008. Sources and significance of among-individual reproductive variation in a northern population of painted turtles (*Chrysemys picta*). *Copeia* 2008:533–541.
- Schwabl, H. 1996. Environment modifies the testosterone levels of a female bird and its eggs. *Journal of Experimental Zoology* 276:157–163.
- Seber, G. A. 1965. A note on the multiple recapture census. *Biometrika* 52:249–259.
- Sinervo, B., and P. Licht. 1991. Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. *Science* 252:1300–1302.
- Slagsvold, T. J., J. Sandvik, G. Rofstad, Ö Lorentsen, and M. Husby. 1984. On the adaptive value of intraclutch egg-size variation in birds. *Auk* 101:685–697.
- Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108:499–506.
- Smith, H. G., T. Ohlsson, and K. J. Wettermark. 1995. Adaptive significance of egg size in the European starling: experimental tests. *Ecology* 76:1–7.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.
- Stinchcombe, J. R., M. T. Rutter, D. S. Burdick, P. Tiffin, M. D. Rausher, and R. Mauricio. 2002. Testing for environmentally induced bias in phenotypic estimates of natural selection: theory and practice. *American Naturalist* 160:511–523.
- Styrsky, J. D., K. P. Eckerle, and C. F. Thompson. 1999. Fitness-related consequences of egg mass in nestling house wrens. *Proceedings of the Royal Society B: Biological Sciences* 266:1253–1258.
- Valenzuela, N. 2001. Maternal effects on life history traits in the Amazonian giant river turtle *Podocnemis expansa*. *Journal of Herpetology* 35:368–378.
- Van de Pol, M., T. Bakker, D. Saaltink, and S. Verhulst. 2006. Rearing conditions determine offspring survival independent of egg quality: a cross-foster experiment with oystercatchers *Haematopus ostralegus*. *Ibis* 148:203–210.
- Wade, M. J. 1985. Soft selection, hard selection, kin selection, and group selection. *American Naturalist* 125:61–73.
- . 1998. The evolutionary genetics of maternal effects. Pages 5–21 in T. A. Mousseau and C. W. Fox, eds. *Maternal effects as adaptations*. Oxford University Press, New York.
- Wagner, E. C., and T. D. Williams. 2007. Experimental (antiestrogen-mediated) reduction in egg size negatively affects offspring growth and survival. *Physiological and Biochemical Zoology* 80:293–305.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews* 68:35–59.
- Winemiller, K. O., and K. A. Rose. 1993. Why do most fish produce so many tiny offspring? *American Naturalist* 142:585–603.
- Winkler, D. W., and K. Wallin. 1987. Offspring size and number: a life history model linking effort per offspring and total effort. *American Naturalist* 129:708–720.
- Wolf, J. B., E. D. Brodie III, J. M. Cheverud, A. J. Moore, and M. J. Wade. 1998. Evolutionary consequences of indirect genetic effects. *Trends in Ecology & Evolution* 13:64–69.

Associate Editor: Edmund D. Brodie III
 Editor: Michael C. Whitlock