EFFECTS OF NEST SITE ENVIRONMENT AND TIMING OF BREEDING ON

REPRODUCTIVE SUCCESS IN FRANKLIN'S GULLS (*LARUS PIPIXCAN*)

A Thesis
Submitted to the Graduate Faculty
of the
North Dakota State University
of Agriculture and Applied Science

By

Emily Anne (Davenport) Berg

In Partial Fulfillment of the Requirements
for the Degree of
MASTER OF SCIENCE

Major Department:
Biological Sciences

September 2009

Fargo, North Dakota

North Dakota State University
Graduate School

Title

Effects of nest site environment and timing of breeding on reproductive

success in Franklin's gulls (*Larus pipixcan*)

By

Emily A. Davenport

The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

MASTER OF SCIENCE

ABSTRACT

Berg, Emily Anne, M.S., Department of Biological Sciences, College of Science and Mathematics, North Dakota State University, September 2009. Effects of Nest Site Environment and Timing of Breeding on Reproductive Success in Franklin's Gulls (*Larus pipixcan*). Major Professor: Dr. Mark Clark.

Offspring performance and phenotype are affected by genotype and environment, which in birds includes yolk resources (part of the embryonic environment). Female colony-nesting birds may influence offspring competitive ability in the post-hatching nest site environment by differentially allocating yolk resources to eggs based on nest site characteristics. Offspring performance may also be linked to prenatal allocation of resources, as well as post-natal parental care. Nest site characteristics, including nest size, density, and timing of breeding, influence the behavior (e.g., aggressive, social) and resource acquisition of the parents, as well as provide measureable variation in the postnatal environment. I used an experimental approach to quantify relationships among nest site characteristics, nest success, and offspring performance (growth and survival) in a nesting colony of Franklin's gull (*Larus pipixcan*). I also used a cross-foster experiment to examine the effects of parental care and provisioning on growth and survival of neonates. Timing of breeding, egg quality, chick quality, nest success and chick survival varied between the 2006 and 2007 cohorts. Nests in 2006 were initiated later than nests in 2007 and experienced lower nest survival rates but produced chicks in better condition. Chicks in 2006 also experienced higher survival than chicks in 2007; however, chicks in 2006 experienced slower growth. Timing of breeding may have influenced measures of nest and chick success examined in

this study. In Franklin's gull, a trade-off between offspring quality and offspring quantity may be a consequence of migratory delays or unusual weather patterns in this long-distance migratory species.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

viii

INTRODUCTION

An individual's phenotype is the product of its genotype and the surrounding environment, and the interactions between the two. Variability in response of genotype to environment (*i.e.*, phenotypic plasticity, Schlichting and Pigliucci, 1998) prevents separate direct measure of genetic and environmental selective pressures in free-living populations. By controlling for one of these factors (either genotype or environment) the effect of the other factor on phenotype may be evaluated. Avian populations provide a model system for examining phenotypic plasticity and selection because the embryo develops outside the female and the embryonic environment and genotype can be directly characterized.

Maternal Effects

Maternal effects are an important component of the embryonic environment and extensively influence embryonic development, subsequently affecting individual life-history and fitness of offspring. Negative effects on development may decrease fitness early in life. Enhanced early development, however, may come with later fitness consequences, such as shortened life span, fewer opportunities to breed, or chronically high levels of androgens and glucocorticoids (Metcalfe and Monaghan, 2001). Slowed prenatal development may lead to later age at maturation, and, for those species with a narrow reproductive window, a fitness disadvantage (i.e., production of fewer viable offspring; Morgan and Metcalfe, 2001; Ricklefs and Wikelski, 2002). Body mass of a neonate is a consequence of its environment during development (Godfray, 1995; Birkhead *et al.*, 1999). In birds, embryonic environments are controlled by the female during formation of

1

each egg, and are affected by the physiological and hormonal state of the female at the time of formation (Groothuis *et al.*, 2005). Differential allocation of yolk constituents allows the female to optimize potential survival and fitness of each embryo (Japanese quail (*Coturnix japonica*), Daisley *et al.*, 2005; Zebra finch (*Taeniopygia guttata*), Kilner, 1998; Rutowksa and Cichon, 2002). Yolk constituents, including glucocorticoids, are deposited by the female during egg formation (Schwabl, 1993). These constituents affect the development and physiological function of the embryo (Eising *et al.*, 2003; Hayward and Wingfield, 2004), and may continue to affect physiology in early postnatal life (Grindstaff *et al.*, 2003).

Corticosterone, a maternally invested glucocorticoid, may negatively affect offspring growth, development and survival. Steroid and glucocorticoid levels in female birds can be affected by both acute and chronic exposure to social stress and/or stimuli (Wingfield *et al.*, 1990) thereby affecting growth of their offspring. Experimental elevation of corticosterone in a laying female produced chicks with smaller body size and slowed plumage development, impairing the viability of offspring early in life (barn swallow (*Hirundo rustica*), Saino *et al.*, 1995). In Japanese quail, elevated corticosterone in the female was transferred to eggs and slowed embryonic and neonatal growth rates (Hayward and Wingfield, 2004). Chicks hatched from eggs with high corticosterone levels exhibited higher fluctuating asymmetry and reduced embryonic survival (Eriksen *et al.*, 2003). The authors suggested that eggs from females with high corticosterone levels are less likely to hatch, and those that hatch have a fitness disadvantage at both pre- and

2

postnatal stages. In isolated muscle tissue, incubation in corticosterone serum resulted in slowed protein synthesis (Klasing *et al.*, 1987).

Elevated corticosterone has also been reported to have positive effects on other aspects of development. American kestrel (*Falvo sparverius*) chicks, which hatch asynchronously, exhibited both size dimorphism and differences in baseline corticosterone across the laying sequence (Love *et al.*, 2003). The authors suggested that these hierarchies are maintained through better adrenocortical function in older chicks, providing the oldest, largest chicks with the means to acquire relatively large quantities of food.

Corticosterone also contributes to behavioral characteristics in birds. Black-legged kittiwake (*Rissa tridactyla*) chicks with corticosterone implants begged more frequently than control chicks (Kitaysky, 2001). Furthermore, parents responded by increasing feeding rates of corticosterone-implanted chicks.

Offspring performance may be especially linked to competitive ability in colony-nesting birds. Gulls in the genus *Larus* typically produce three eggs, and the third egg is often smaller than the rest (Parsons, 1970). The relatively small size of the third egg contributes to reduced egg survival (Reid, 1987). Production of a third egg is still beneficial to the parents as a replacement chick in the case of elder siblings dying prior to reproduction (the insurance-egg hypothesis, Dorward, 1962). Hario and Rüdback (1996) observed high frequency of disease in third-laid lesser black-backed gull (*Larus fuscus*) chicks, and suggested that these chicks are less successful at surviving to fledging because they are less capable of fighting disease, rather than because of a size disadvantage. Although this egg

3

size asymmetry has been interpreted as adaptive, nests that produce two or three chicks exhibited less fluctuating asymmetry than nests that produced a single chick (Kilpi, 1995).

Offspring that are large at hatch exhibit better mobility, are more successful at obtaining food, and are better able to escape predators. All of these factors contribute to early post-natal survival (Bolton, 1991), and are influenced by high levels of corticosterone and testosterone, which work antagonistically to affect growth and competitive ability. Testosterone tends to enhance growth and competitive ability in chicks, and varies between nests in different areas of the colony. Chicks hatched from nests in the center of the colony, where nest density increases, exhibit decreased plasma testosterone (Groothuis and Schwabl, 2002).

Nest Site Characteristics

Extensive effort has been directed at understanding the components used to evaluate nest site quality and determine nest site selection in birds. Here I review environmental factors likely to affect nest success including nest density, nest cover, nest size, and laying date. In waterbirds, nest site selection may be influenced by the presence of conspecifics, predators, proximity to shore, and other variables. In colonial birds, seemingly minor microhabitat differences may contribute to significant differences in breeding success.

Populations nesting in dense groups may experience enhanced predator protection with less individual vigilance (the many-eyes hypothesis: Lima, 1990). Similarly, warning calls signal the type (Griesser, 2009) and behavior (Griesser, 2008) of a predator within a colony of Siberian jays (*Perisoreus infaustus*).

4

However, disadvantages to colonial breeding also exist. For example, vigilance must constantly be exerted against conspecifics. In Franklin's gull (*Larus pipixcan*), adults are known to attack other adults and chicks and steal nest material from unattended nests (Burger and Gochfeld, 1994). In species that forage near the nest, food limitations may also present a challenge (Lack, 1968). Additionally, transmission of ectoparasites and diseases increases in colony-nesting species (Brown and Bomberger-Brown, 1986).

Nest site selection based on nest density may present a paradox. Those individuals nesting in low density areas do not reap the benefits of group vigilance, but also experience fewer interspecific interactions. Individuals that nest in high density areas expend less energy on vigilant behavior, but experience more interspecific interactions, which may often be aggressive in nature and negatively affect physiology.

Studies examining the effects of nest density on nesting success have produced diverse results, often species-specific and through various causes of mortality. For some species, nesting at either extreme is detrimental to breeding success due to the previously mentioned reasons. In Magellanic penguins (*Spheniscus magellanicus*), nests at high and low densities experienced lower success than those at intermediate density (Scolaro, 1990). These mortality rates were largely caused by egg predation during feeding trips made by parents. Breeding success was lower for pairs nesting in low density areas in the Adelie penguin (*Pygoscellis adeliae*) (Tenaza, 1971), black-headed gull (*Larus ridibundus*) (Patterson, 1965), and black-legged kittiwake (Coulson, 1968). In the

5

ring-billed gull (*Larus delawarensis*), breeding success was higher in the center of the colony (e.g., high density area) than on the periphery, but nearness of neighbors (i.e., individual colony size) did not affect nest success within the colony (Dexheimer and Southern, 1974). Furthermore, female herring gulls (*Larus argentatus*), nesting solitarily laid larger eggs (Becker and Erdelen, 1986), which yield more robust chicks, a characteristic that enhances probability of survival (Parsons, 1970). Contrarily, in the least tern (*Sterna antillarum*), nests in the center of the colony experienced higher predation rates, and therefore higher mortality, than nests on the periphery of the colony (Brunton, 1997). In the common tern (*Sterna caspia*), nests located in high density areas were less productive than nests in low density areas (Antolos *et al.*, 2006). However, nests that were initiated earlier in the season were more productive and were located in more dense areas (Antolos *et al.*, 2006).

Nest density variation has also been linked to behavioral and physiological correlates in adults and chicks. Female black-headed gulls in peripheral, low density areas of a colony produced eggs containing higher levels of androgens than females in centrally placed, high density nests (Groothuis and Schwabl, 2002).

Other nest site characteristics may also influence egg and chick survival, as well as female physiology. In black-headed gulls, nests in areas of high vegetation, which were less visible to predators and therefore were considered higher quality nest sites, produced eggs with high levels of androgens (Groothuis and Schwabl, 2002). In western gull x glaucous-winged gull (*Larus occidentalis* x *Larus*

6

glaucescens) hybrids, structures surrounding the nests, such as driftwood logs, enhanced nest success and reduced egg loss to predators (Good, 2002). Nests in high density areas, and those visually separated from conspecific nests by natural vegetation, experienced the highest success in one colony. This colony also experienced a high rate of egg loss by other gulls. In another colony, however, eggs in vegetated and rocky areas experienced similar success and low egg loss. Kelp gulls (*Larus dominicanus*) showed a strong preference for covered nesting areas, which contributed to high breeding success (Yorio *et al.*, 1995), a difference attributed to variation in heat stress and distance to cover.

Extensive research has been conducted on the effects laying date and hatching date on reproductive success. It is generally concluded that early hatching is beneficial for chick performance. Seasonal decline in chick condition has been linked to declining food resources in the European coot (*Fulica atra*) (Brinkhof and Cavé, 1997) and decline in parental quality in the herring gull (Brouwer *et al.*, 1995). Some research suggests that, in migratory birds, earlier hatching dates benefit offspring by allowing them more time to complete development and build up muscle tissue and energy reserves for the migratory period. In the great skua (*Catharacta skua*), early-hatched chicks had better body condition (weight corrected for wing length) than later-hatched chicks in 10 out of 16 years that data were recorded (Catry *et al.*, 1998). Furthermore, hatching date similarly affected post-fledging survival up to one year of age (Catry *et al.*, 1998). Contrarily, Chicon and Lindén (1995) found that hatching date had a variable effect on chick growth in the great tit (*Parus major*). Ross and McLaren (1981) found no

7

correlation between hatching date and post-fledging survival in Ipswich sparrows (*Passerculus sandwichensis princeps*).

Parental Care

Post-hatching chick survival is partially determined by yolk resources and the physical and physiological state of the offspring at hatch, but parental care (feeding, brooding, and protection from predators and conspecifics) also is critical for chick survival. Rearing conditions are dependent on both parental quality and environmental quality, again emphasizing the importance of nest site selection and the role that differences in microhabitat may play in chick survival.

The additive effects of rearing condition and egg quality determine survival and quality of offspring. Cross-foster treatments, in which offspring are switched between foster nests, are useful in separating the effects these two factors. Amundsen and Stokland (1990) conducted a cross-foster experiment on the European shag (*Phalacrocorax aristotelis*) that indicated that egg size was the more influential factor in determining chick survival. Bolton (1991) conducted a cross-foster experiment on lesser black-backed gulls and determined that adults that produced large eggs also provided better parental care than adults that produced small eggs. Both egg production and brood-rearing require significant energy investments by parents, indicating that adults that lay large eggs and are high quality parents allocate more energy to offspring.

Franklin's gulls provide a model system for studying nest characteristics, reproductive success, and chick survival because these birds nest in large, gregarious colonies, and their reproductive and behavioral habits are well-

8

documented (Burger and Gochfeld, 1974). They also use visibility of neighboring nests as an indicator of nest site quality and a criterion for nest-site selection (Burger, 1974). Although yolk glucocorticoids in Franklin's gulls have not been studied, numerous studies of such characteristics exist for other gull species (e.g., black-headed gull, Groothuis and Schwabl, 2002; lesser black-backed gull, Verboven *et al.*, 2003).

The objectives of this study were to 1) quantify variation in reproductive success associated with nest site characteristics within a colony of Franklin's gull, 2) describe natural variation in yolk glucocorticoids in Franklin's gull, and 3) identify variation in chick survival and performance as a consequence of the nest site environment.

In this study, I examined the relationships between nest success and several nest site characteristics, including nest density (i.e., nearness of neighbors), nest height, nest diameter, and vegetation height. I separated pre-hatching maternal effects from effects of post-hatching parental care on chick survival and growth by conducting a cross-foster experiment of chicks during the hatching and post-hatching stages and monitoring chick growth and survival. I also investigated a possible underlying mechanism of inter-nest differences in survival by quantifying concentrations maternally-derived corticosterone present in egg yolks.

METHODS

General Methods

I monitored wetlands at J. Clark Salyer National Wildlife Refuge in north-central North Dakota from 10 May – 14 June 2006 and 31 April – 4 June 2007, to identify active Franklin's gull nests. Nests were marked with plastic flagging placed within 1 m of the nest and checked daily to identify freshly laid eggs. Fresh eggs were identified within 24 hours of laying. Each egg was given a unique identification code using a nontoxic permanent marker, and length, breadth, and fresh mass were recorded. Second-laid eggs were collected at the time of discovery, brought in to a temporary, on-site laboratory, and dissected within 8 hours of collection. In the lab, yolks were separated into a sterilized dish and homogenized using a spatula. Yolk samples were scooped into two 1.7-mL microcentrifuge tubes and frozen at -20°C. Following clutch completion, nests were revisited at least every other day to monitor nest survival. Nests where at least one egg pipped were considered to be successful nests.

Nest density, nest height, nest diameter, and vegetation height were measured to determine nest site quality. Nest density was determined using the average distance to the five nearest conspecific nests (henceforth referred to as AD5). I used a 15-m measuring tape to determine the distance between the center of the nest bowl of the focal nest and the center of the nest bowls of the five nearest conspecific nests. Inter-nest distances greater than 15 m were assigned values of 15 m because of the low level of neighbor interaction at those distances

10

and to simplify analysis. Nests were classified as low, intermediate, or high density, based on the distribution of nearest-neighbor distances.

In 2007, several other nest site characteristics were measured during egg laying. Nest height was measured as the distance from the water surface to the highest point of the nest. Nest diameter was determined using the average of three measurements across the center of the nest, thus accounting for irregular nest shape. Vegetation immediately surrounding nests was placed in one of three classes, high (> 1 m), intermediate (1.0 m – 0.5 m), or low vegetation (< 0.5 m).

Cross-foster Treatment

Beginning at the 23rd day of incubation, nests were checked on a daily basis for pipping, which indicates the beginning of the hatching period. Upon pipping, first-laid eggs were removed from the nest and placed randomly in another nest that had pipped that day. As previously discussed, second-laid eggs had been collected at the time of laying for yolk analysis. The remaining egg (third-laid egg) was collected and taken to the lab where a blood sample was collected from the embryo via the umbilical/yolk sac vein using a 25-gauge Vacutainer blood collection set. The embryo was euthanized and tissue samples were collected for future research.

In 2006, fostering occurred in nests that had not been monitored since laying due to low nest survival immediately after laying. Late in the incubation period, nests were classified as high or low density and eggs were marked with a unique identification code. The first egg to pip was determined to be the first-laid egg, because of the consistency of hatching order observed by Burger and

11

Gochfeld (1994). Other eggs from foster nests were taken into the lab for blood sampling and to determine laying position of the remaining eggs based on development and the size of the yolk sac that had not been absorbed by the embryo.

Potential foster nests were checked daily to monitor for pipping, indicating the beginning of the hatching process. When an egg pipped, it was fostered into a randomly determined nest. The natal nest and foster nest of the chick were recorded to place the chick into a treatment group (e.g., high natal density to high foster density, high natal density to low foster density, low natal density to high foster density, or low natal density to low foster density). All nests were checked daily before foster assignments were made. Eggs were fostered into nests where an egg had pipped on the same day. An addled egg from another (non-foster) nest was placed in the foster nests to minimize parental abandonment. Within 24 hours of hatching, each chick was marked with a unique identification code on the top, left, and right sides of the head using a nontoxic, permanent marker. Mass, tarsus length, and wing chord length were also measured.

Chick searching was conducted daily to relocate chicks. Chicks were recaptured and identified when possible. Measurements of tarsus length and wing chord length were taken and chicks were remarked using a non-toxic permanent marker.

Radioimmunoassay

Corticosterone levels in yolk samples collected in 2006 and 2007 were quantified using radioimmunoassay approaches, following the protocol used by

12

Boonstra (2006). Briefly, 50-mg yolk samples were homogenized in 1-mL doubly distilled water. Yolk dilutions were extracted 5 times using 5-mL petroleum ether: diethyl ether (30:70), dried under nitrogen, and stored in 1-mL 95% ethanol. Samples were then separated using 2-mL hexane, dried under nitrogen, reconstituted in 500-µL PBSg, and separated into duplicate tubes of 200-µL. The remaining amount of sample was recorded and placed in a scintillation vial with 2.4-mL scintillation fluid. Tritium-labeled corticosterone and corticosterone antiserum (100-µL each) were added to each sample tube. Samples were refrigerated for 12-18 hours. Dextran-coated charcoal buffer (0.5-mL) was added to each tube and allowed to combine for 12 minutes. Samples were then centrifuged at 2000 rpm for 10 minutes, at 4°C. The supernatant was decanted into a scintillation vial containing 4.4-mL scintillation fluid. Samples were counted on a scintillation counter.

Statistical Analyses

Nest density categories were assigned by establishing an equal distribution of nest densities based on average distance to the five closest conspecific nests. The Mayfield method was used to determine daily nest survival (Mayfield, 1975). Model selection via Program MARK (White and Burnham, 1999) was used to determine significant parameters contributing to variation in nest success, chick growth and chick survival. Candidate models used for nest success in both years, nest success in 2006 only and chick survival, as well as notation, are listed in Tables 1, 2 and 3, respectively. I used ANOVA, t-test, regression, and correlation

13

to compare egg and chick characteristics to one another and to nest

characteristics. Statistical analyses were conducted using JMP Statistical software.

RESULTS

Females initiated nesting later in 2006 than in 2007, and nest initiation date was related to nest density. Among 231 nests for which I was able to determine the day the first egg was laid, the mean (± standard error) Julian day of clutch initiation was later in 2006 (130.0 ± 0.30 d, n = 100) than in 2007 (127.5 ± 0.25 d, n = 131; $F_{1,229}$ = 40.22, p < 0.0001, Figure 1a). I also found that the average distance to the five nearest conspecific nests (AD5) decreased for nests initiated later in the season (r^2= 0.02, $F_{1,154}$ = 4.089, n = 154, p = 0.04, Figure 1b). However there was not an effect of year ($F_{1,151}$ = 0.948, n = 154, p = 0.33) or year x initiation day interaction ($F_{1,151}$ = 1.797, n = 154, p = 0.18) on AD5. Density group changed similarly, with high density nests initiated later than low density nests (Logistic regression, χ^2 = 5.60, r^2= 0.02, p = 0.06, n=156).

Clutch sizes did not differ between years, with initiation date or with nest density. While females tended to lay fewer eggs per clutch in 2006 (mean of 2.68 ± 0.047) than in 2007 (mean of 2.77 ± 0.061), this trend was not statistically significant (Likelihood Ratio Test, χ^2 = 3.89, p = 0.28, n = 236). There was a trend for clutch size to decrease with laying day in 2006 (χ^2 = 9.47, r^2= 0.05, p = 0.013, n=74; Figure 2), but not in 2007 (χ^2 = 4.25, r^2= 0.03, p = 0.24, n=88). However in 2006, half of the observed nests (n=37) were initiated on day 132 (June 12) and affected leverage in the regression. Clutch size did not vary with (r^2 < 0.001, $F_{1,153}$ = 0.0004, n = 156, p = 0.98) or among density groups (χ^2 = 8.09, p = 0.23, n = 156).

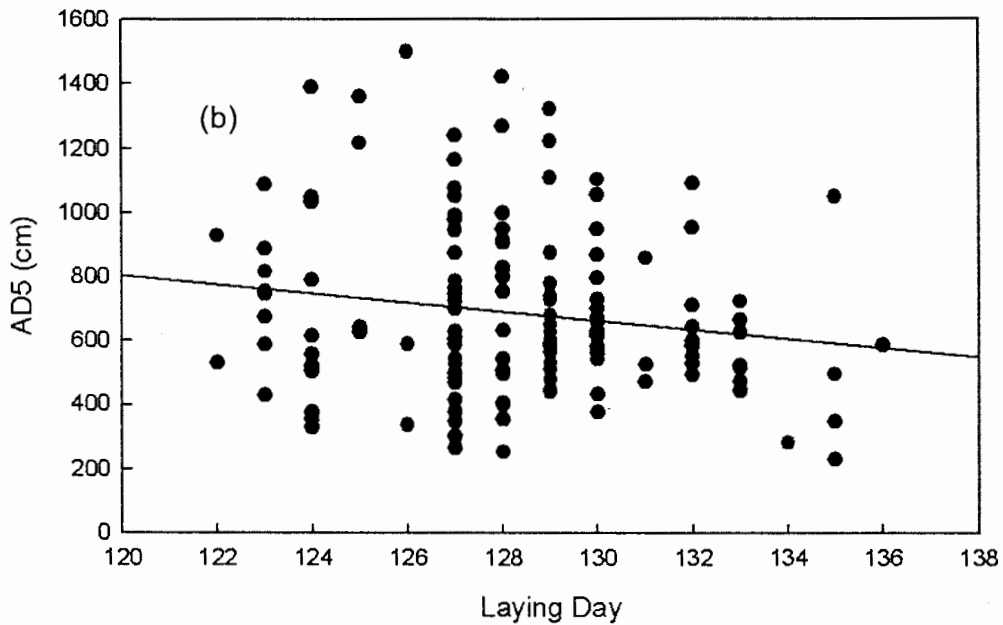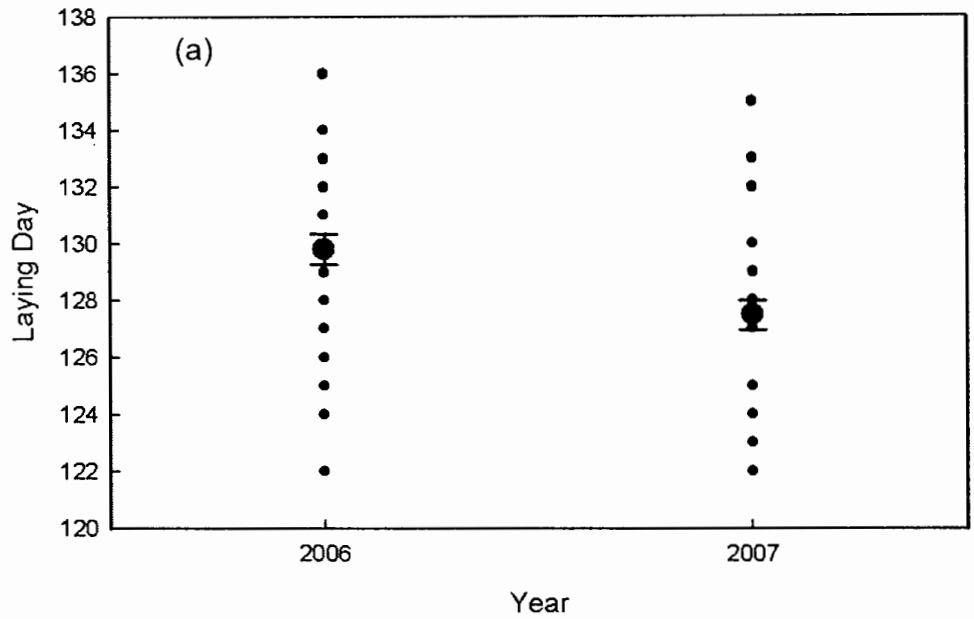Figure 1a. Relationship between year and laying day. Observed values are shown as small filled circles and mean values shown as large filled circles (error bars represent one standard errors)

Figure 1b. Relationship between laying day and average distance of the five closest nests (AD5). Observed values shown as filled circles and the line representing the linear regression AD5 = -14.072*(Laying day) + 2490.9.

16
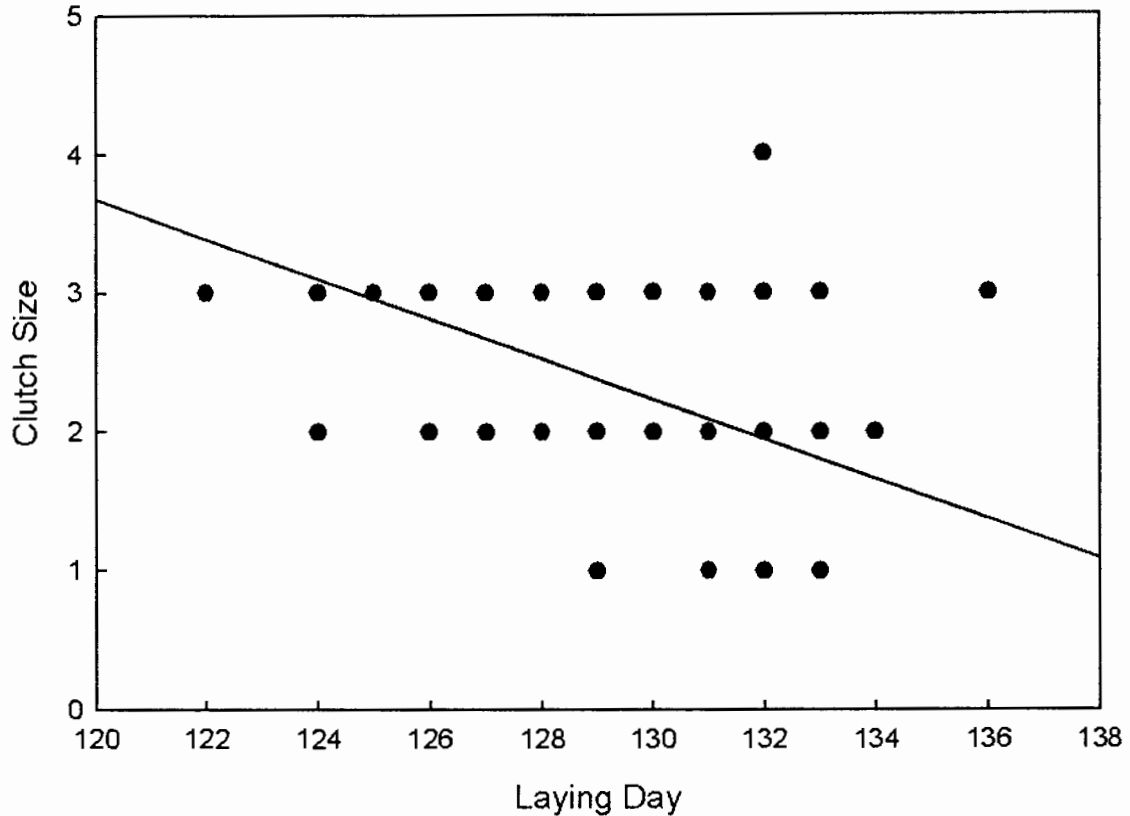
Figure 2. Relationship between laying day (as Julian day) and clutch size. Observed values are indicated by filled circles and the line represents the regression relationship Clutch Size = -0.144*Laying day + 20.955

Fresh egg mass was related to egg dimensions (length and breadth). I obtained egg mass (FM, ± 0.5 g) within 12 hours of laying (henceforth true fresh egg mass), length (L, ± 0.1 mm) and breadth (B, ± 0.1 mm) measurements for 361 eggs (60 in 2006 and 302 in 2007) to develop a regression to estimate true fresh egg mass as a power function of egg dimensions. The regression FM = $0.001434\ L^{0.89}\ B^{1.84}$ ($r^2 = 0.90$, $F_{2,359} = 1538.16$, $p < 0.0001$) explained 90% of the variation in true fresh egg mass. I then used an estimated fresh mass (henceforth

17

referred to as fresh egg mass) based on length and breadth measurements of the egg and this regression for analysis of variation in egg size.

Fresh egg mass differed between years. Eggs were larger in 2006 (37.4 ± 0.17 g, n = 407) than in 2007 (36.9 ± 0.19 g, n = 306) ($F_{301,411}$ = 3.94, with a random effect for n = 302 females, p < 0.0001). First-laid eggs were larger in 2006 (37.7 ± 0.21 g, n = 125) than in 2007 (36.9 ± 0.21 g, n = 130; $F_{1,253}$ = 6.0338, p = 0.0147; Figure 3a). Second-laid eggs were also larger in 2006 (38.6 ± 0.3, n = 46) than in 2007 (37.4 ± 0.237, n = 91; $F_{1,135}$ = 8.6137, p = 0.0039; Figure 3b). Third-laid eggs followed a similar trend; however, the size difference was not significant
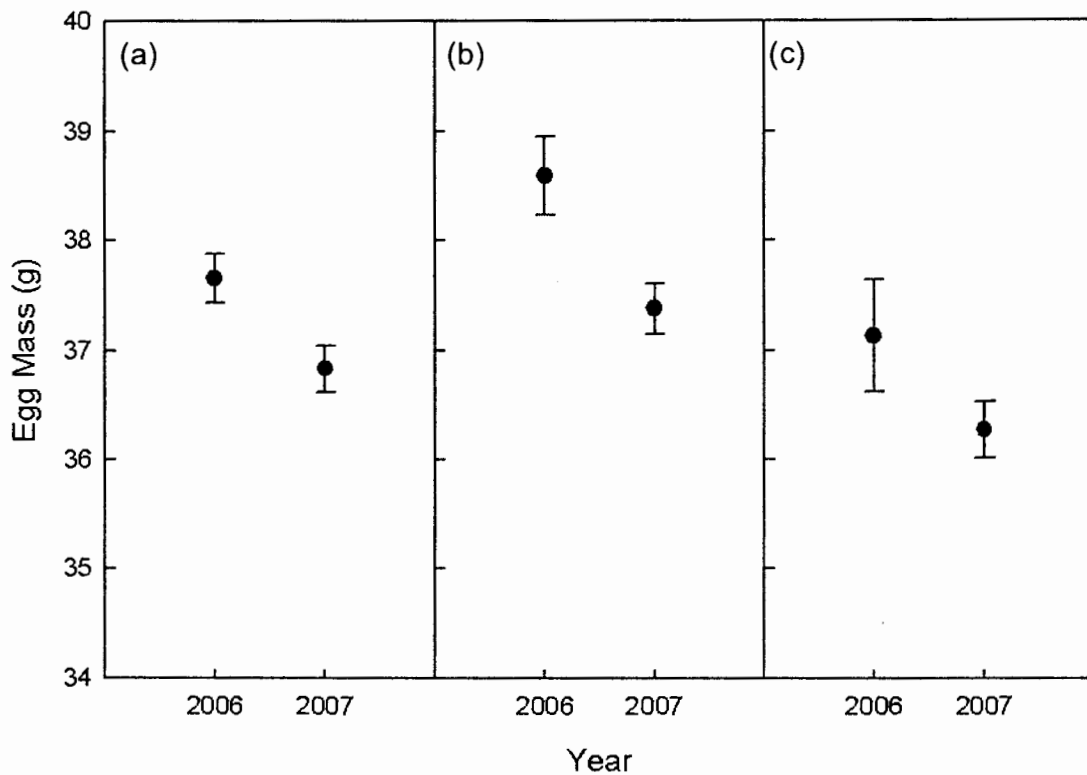

Figure 3. Mean predicted fresh egg mass by year. Predicted fresh egg mass was analyzed for (a) position 1 (i.e., first-laid) eggs, (b) position 2 (i.e., second-laid) eggs, and (c) position 3 (i.e., third-laid) eggs (c). Error bars represent two standard errors.

18

(2006: 37.1 ± 0.417, n = 38; 2007: 36.3 ± 0.295, n = 76; $F_{1,112}$ = 2.8532, p = 0.094; Figure 3c).

Fresh egg mass was related to position in the laying sequence within a clutch. I included nest (i.e., female) as a random effect to account for multiple eggs from one female within a year in a general linear model of fresh egg mass as a function of position, position*position and year. This model explained approximately 69% of the variation in fresh egg mass (r^2 = 0.69, $F_{1,250}$ = 4.43, p < 0.0001), and all terms were significant (position: $F_{1,250}$ = 25.95, p < 0.0001; position*position: $F_{1,250}$ = 32.85, p < 0.0001; year: $F_{1,250}$ = 9.49, p = 0.026). This model indicates first-laid eggs were smaller (37.3 ± 0.15 g, n = 255) than second-laid eggs (37.8 ± 0.20 g, n = 137), but were larger than third-laid eggs (36.6 ± 0.24 g, n = 114) and fourth-laid eggs (35.8 ± 2.21 g, n = 2; Figure 4). Similar trends were identified in 2006 ($F_{3,209}$ = 9.79, n = 209, p = 0.0001) and in 2007 ($F_{3,294}$ = 15.16, n= 297, p < 0.0001) when years were analyzed separately.

Additionally, for 2007, I analyzed variation in egg size within the breeding season. I restricted the analysis to the 2007 season to eliminate variation associated with between-year differences and because a disproportionately large number of nests were initiated on day 132 (June 12) in 2006. Furthermore, I restricted the analysis to first-laid eggs to eliminate variation associated with position and because this provided the largest sample size (n = 130). In 2007, first-laid eggs were heavier during the middle of the laying period (approximately Julian day 128 (8 June)) than at beginning or end of the season (Julian day 122 (2 June) – Julian day 135 (15 June)). The quadratic model Pred. Mass = 18.916314 +

19
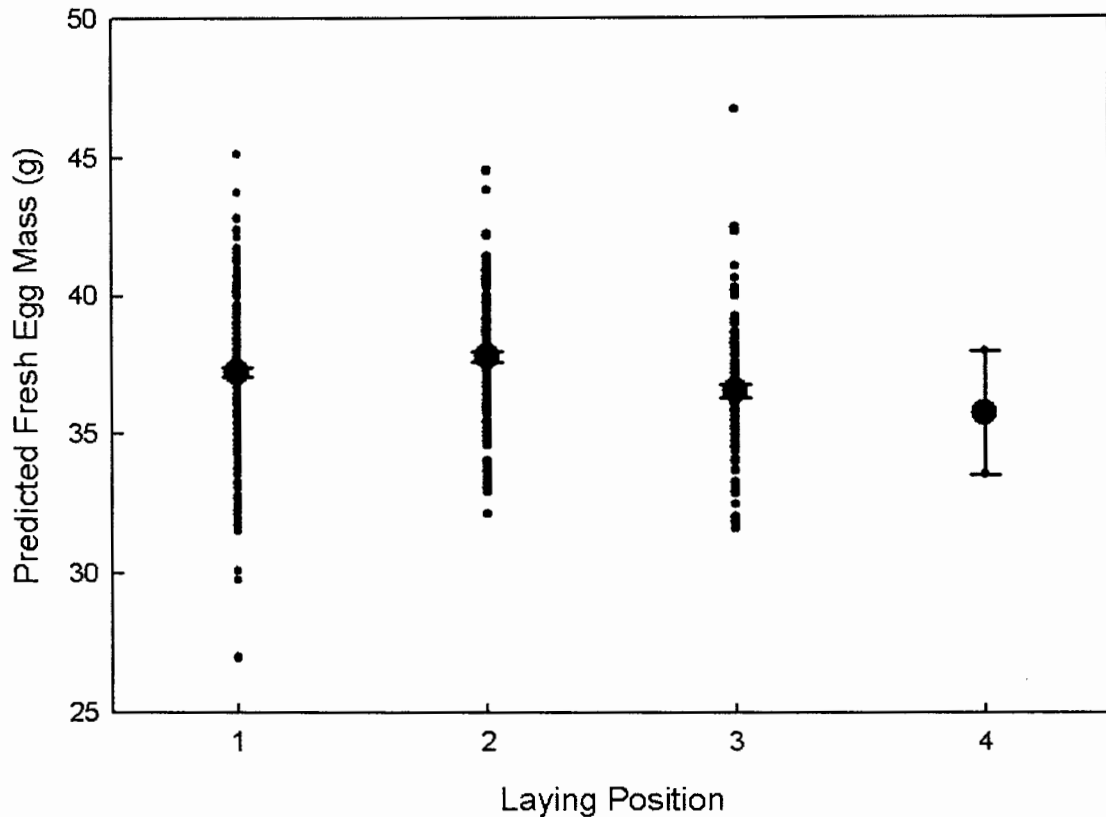
Figure 4. Relationship between position in the laying sequence and predicted fresh egg mass. Observed values are shown as small filled circles and mean values shown as large filled circles (with error bars indicating one standard error). Data for 2006 and 2007 are pooled.

$0.1431325*$Laying Day $- 0.028509*$(Laying Day $- 127.515)^2$ is nearly significant in explaining the data trend ($F_{2,127} = 2.6711$, n = 130, $p = 0.0731$); however, there was not sufficient evidence to explain variation of egg size within the 2007 season based on these data. For pooled years, eggs were larger later in the laying season ($F_{2,204} = 5.1545$, n = 207, $p = 0.0242$; Figure 5).

Chick size at hatch was related to egg mass, laying date, and year. Chick mass at hatch was positively related to egg mass ($r^2 = 0.25$, $F_{1,53} = 17.99$, n = 55,
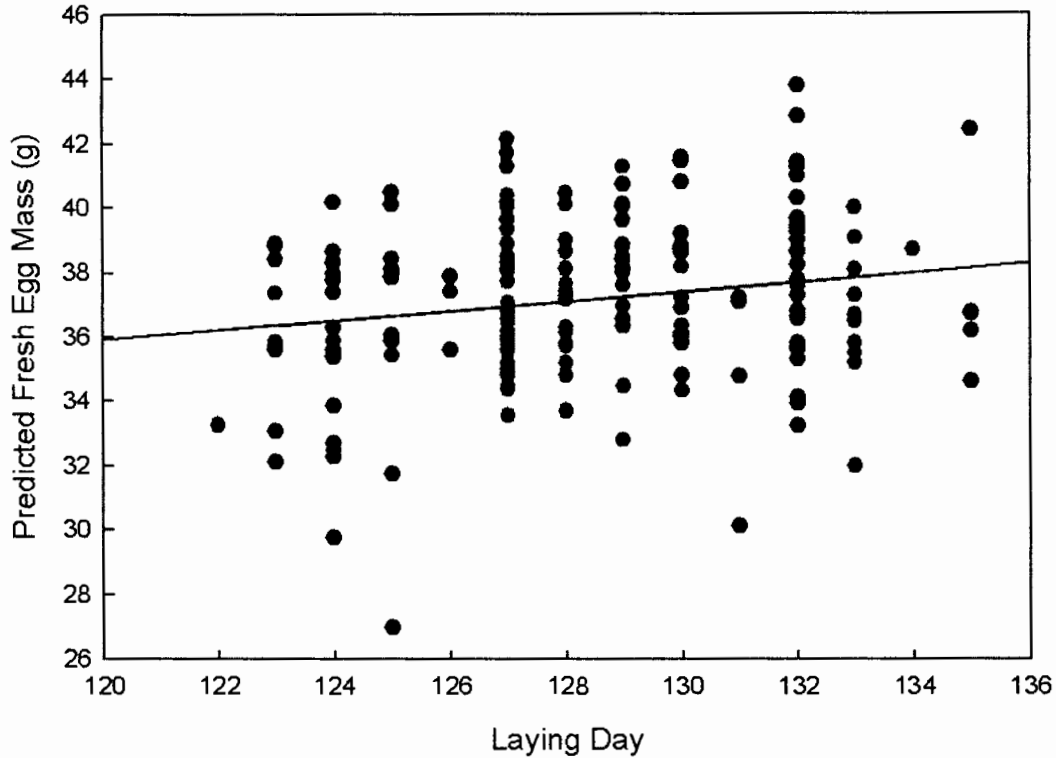
Figure 5. Relationship between laying day (as Julian day) and predicted fresh egg mass for 2006 and 2007 (years pooled). Observed values are shown as filled circles, and the line represents the regression Predicted Fresh Egg Mass = Laying Day * 0.1486+18.078.

$p < 0.0001$; Figure 6), but tarsus length at hatch was not ($F_{1,57} = 0.017$, n = 59, $p = 0.90$). In 2007, tarsus length at hatch increased with laying day ($F_{1,56} = 4.61$, n = 58, $p = 0.04$; Figure 7a), but mass at hatch did not change significantly ($F_{1,53} = 2.23$, n = 55, $p = 0.14$; Figure 7b). Chick mass at hatch did not differ between years ($F_{1,63} = 0.3490$, n = 65, $p = 0.557$), but chicks had shorter tarsi at hatching in 2006 (21.02 ± 0.163 mm, n = 52) than in 2007 (23.24 ± 0.191 mm; n = 38; $F_{1,88} = 77.98$, $p <0.0001$).
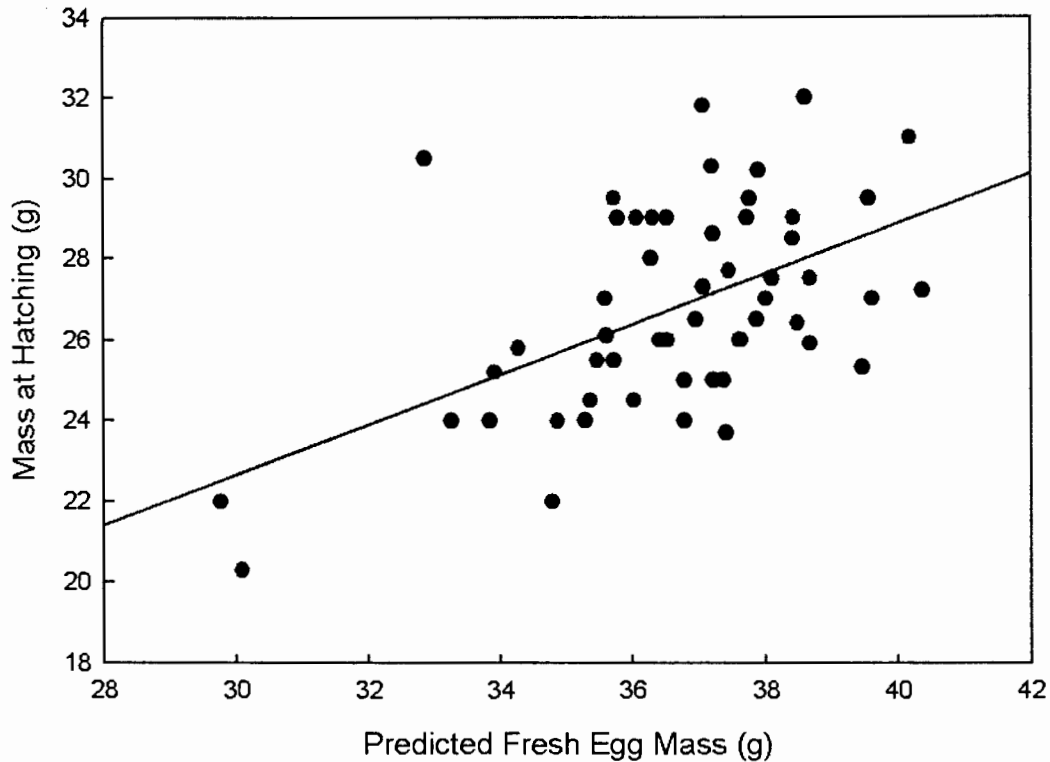
Figure 6. Relationship between predicted fresh egg mass and chick mass at hatching. Observed values are shown as filled circles and the line represents the regression Mass at Hatching = 0.6211* Predicted Fresh Egg Mass + 4.035.

Chick condition at hatch varied between years and with laying date. To quantify chick condition, I used the residual (along the mass at hatch axis) from a Type II (i.e., orthogonal) regression of mass at hatch from tarsus length at hatch (r^2 = 0.45, n = 47, years pooled). Chick condition was higher in 2006 (1.4049 ± 0.31745, n = 10) than in 2007 (-0.3797 ± 0.16504, n = 37; $F_{1,45}$ = 24.8789, p < 0.0001; Figure 8). Condition at hatch also increased with laying day (r^2 = 0.188, $F_{1,36}$ = 8.3455, p < 0.0065, n = 38, years pooled).

22
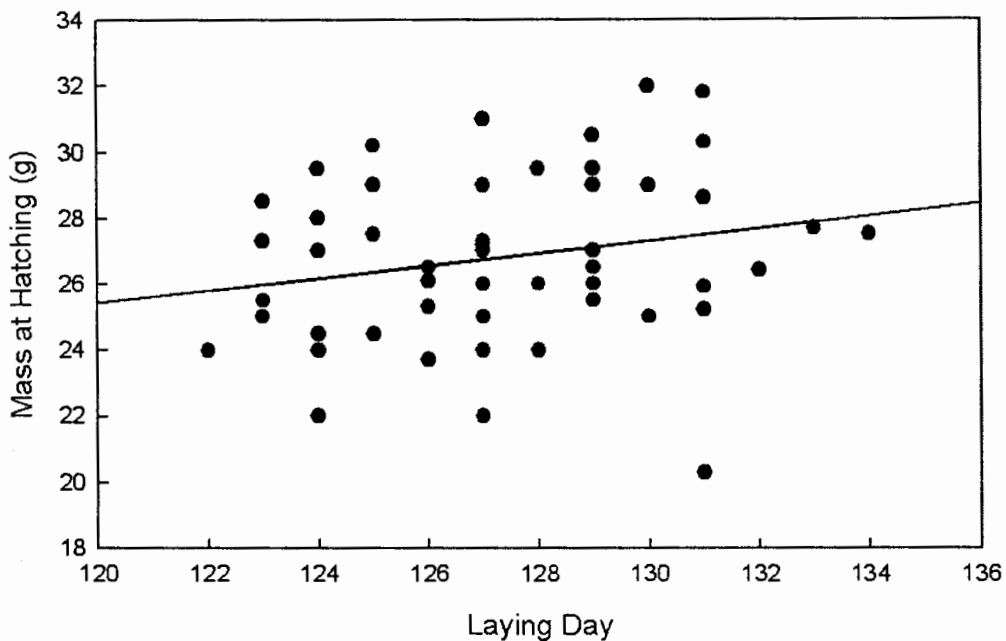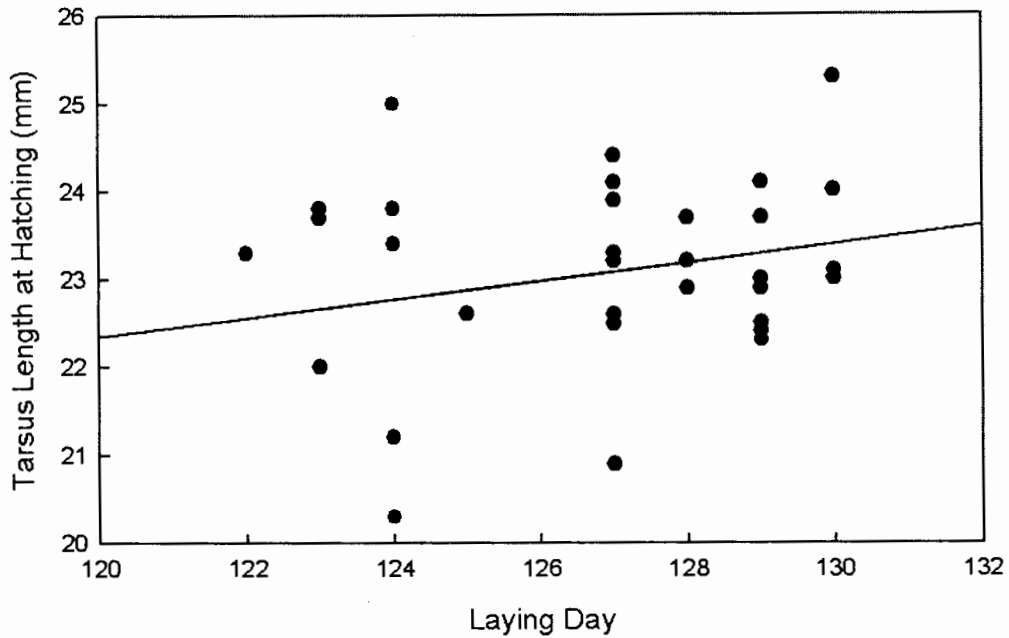
Figure 7. Relationships between laying day (as Julian day) and chick size at hatching. Relationship between tarsus length at hatching (a), with observed values shown as filled circles and the line showing the regression tarsus length at hatching = 0.1049 * laying day + 9.7606. Relationship between chick mass at hatching (b), with observed values shown as filled circles and the line showing the regression chick mass at hatching = 0.1894 * laying day + 2.6865.
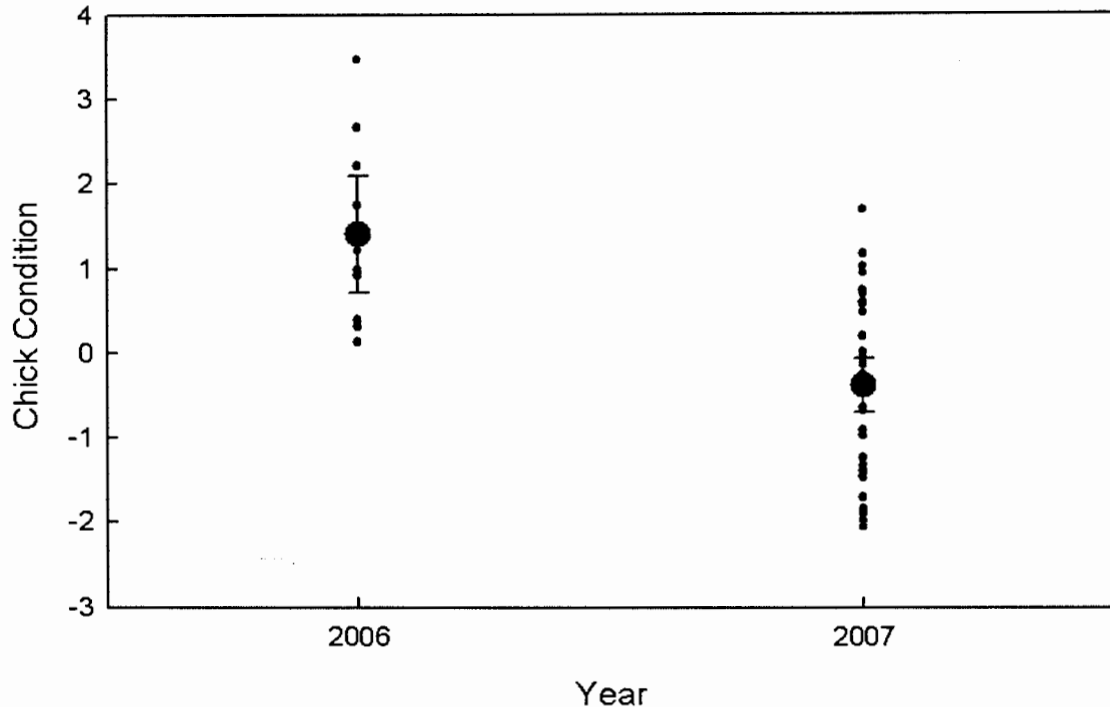
Figure 8. Relationship between chick condition and year. Observed values are shown as small circles and mean values shown as large circles (error bars indicate one standard error).

Chick growth rates varied between 2006 and 2007. Chicks exhibited slower tarsal growth in 2006 (0.87026 ± 0.15381 mm/day) than in 2007 (1.92810 ± 0.19714 mm/day; $F_{1,35}$ =17.8985, n=37, p=0.0002; Figure 9).

Corticosterone concentrations in yolks of freshly laid eggs were related to fresh egg mass, but not to nest density. Yolk samples from freshly-laid, position two eggs were only available from 2007 for analysis of corticosterone concentrations. Corticosterone concentrations in these eggs increased with egg mass, but this trend was not significant ($F_{1,31}$ = 3.50, p = 0.071, n = 33).

Corticosterone level was neither related to AD5 ($F_{1,19}$ = 0.825, p = 0.375, n = 21) nor to nest density category ($F_{1,31}$ = 0.360, p = 0.553, n = 33).

24
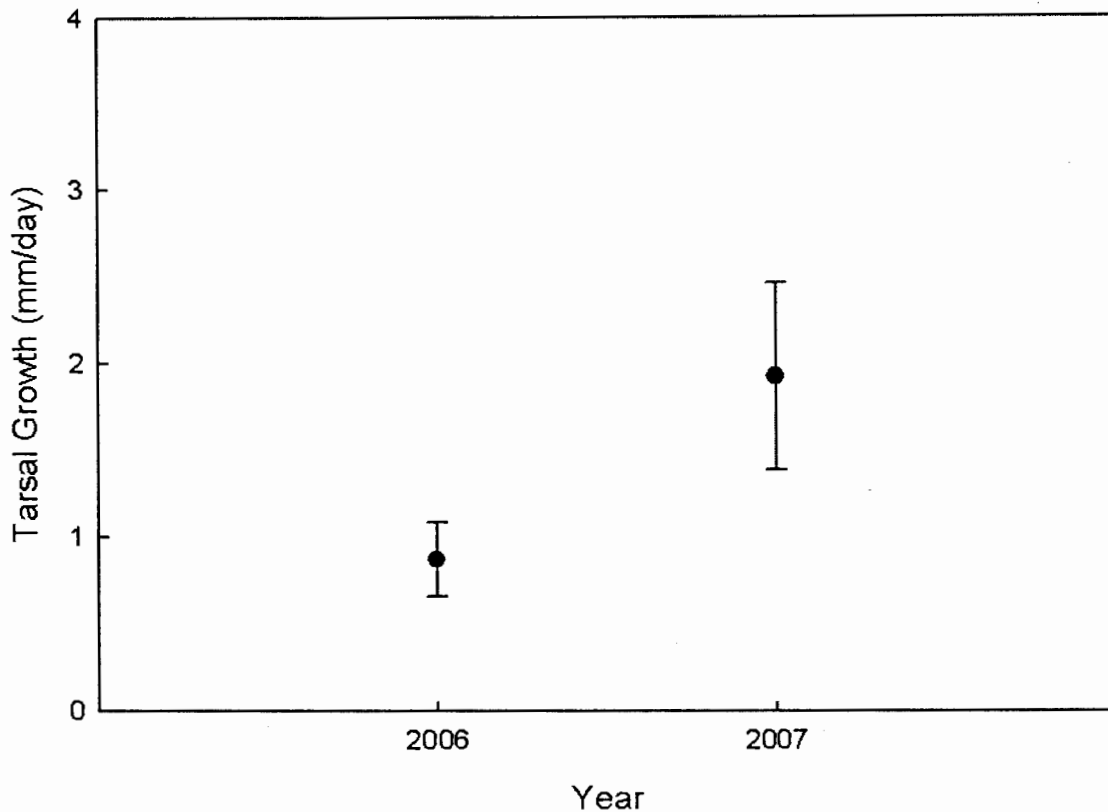
Figure 9. Relationship between year and mean tarsal growth rate. Error bars represent one standard error.

I examined nest daily survival rate as a function of year, nest density by category and average distance of the five closest nests (a continuous measure of nest density). The most competitive model assumed that year and, in 2006, nest density affected nest daily survival rate (Table 1). However, the second-ranked model assumed nest daily survival rate only varied between years (Table 1). Collectively, six of the seven highest-ranking models assume both a year and density effect on nest daily survival rate and explain more than 67% of the evidence given the data. In all of these models, differences in nest daily survival

25

rate between years were greater than differences among density groups. For instance, in the highest ranking model, nest daily survival rate was 0.91 ± 0.010 (or approximately 12% successful) for the high density group and 0.96 ± 0.009 (37% successful) for the intermediate/low density group in 2006 (n = 129), yet was 0.97 ± 0.004 (55% successful) for all density groups in 2007 (n = 121).

Table 1. Model selection results for models of nest daily survival rate for 2006 and 2007. Data are for 154 Franklin's gull nests monitored in 2006 (59 nests) and 2007 (95 nests). Nests daily survival rate (S) was modeled as a function of nest density category (H for high, I for intermediate and L for low), year (Y06 for 2006, Y07 for 2007), and average distance of the five closest nests (AD5). Model structure is indicated parenthetically. For instance, S(H IL Y06, Y07) indicates a model in which S varies between the high density group and the intermediate/low density group in 2006, but does not vary with density group in 2007. K is the number of parameters in the model, Δ AIC$_c$ is the relative Akaike Information Criteria adjusted for small sample size and w$_i$ is the model weight.

Model	K	Δ AIC$_c$	w$_i$
S(H IL Y06, Y07)	3	0.0000	0.25809
S(Y06, Y07)	2	0.4621	0.20484
S(Y06 + AD5, Y07 + AD5)	3	1.2355	0.13915
S(Y06+AD5, Y07)	3	1.7552	0.10731
S(H IL Y06, H IL Y07)	4	1.9704	0.09636
S(H Y06, I Y06, L Y06, H Y07, I Y07, LY07)	6	5.0354	0.02081
S()	1	14.2443	0.00021
S(AD5)	2	14.7015	0.00017

In 2007, I was able to examine effects of nest bowl height, nest bowl width, a categorical variable for vegetation beside the nest and average distance of the five closest nests on nest daily survival rate. The highest-ranking model assumed that nest daily survival rate varied (in a positive direction) with nest height and (in a negative direction) with nest width, but the second-ranking model assumed that

nest daily survival rate varied only with nest bowl height (Table 2). Together, these two models accounted for more than 63% of the evidence given the data (Table 2). However, two competitive models (i.e., $\Delta AIC_c < 4$, Burnham and Anderson 2002) assumed an effect of average distance of the five nearest neighbors in addition to effects of nest bowl height and width or nest bowl height (Table 2). Collectively, models assuming an effect of nest bowl height explained approximately 93% of the evidence given the data (Table 2).

Table 2. Model selection results for models of nest daily survival rate for 2007. Data are for 89 Franklin's gull nests monitored in 2007. Nest daily survival rate (S) was modeled as a function of average distance of the five closest neighboring nests (AD5), nest bowl height (Hgt, in cm), nest bowl width (Wid, cm) and a categorical variable for height of vegetation surrounding the nest (VCat1 = height < 0.5 m, VCat2 = height 0.5-1 m and VCat3 = height > 1 m). Model structure is indicated parenthetically. For instance, S(D5+Wid+Hgt) indicates a model in which S varies with average distance of the five nearest neighbors, nest bowl width and nest bowl height. K is the number of parameters in the model, ΔAIC_c is the relative Akaike Information Criteria adjusted for small sample size, and w_i is the model weight.

Model	K	ΔAIC_c	w_i
S(Wid+Hgt)	3	0.0000	0.43836
S(Hgt)	2	1.3898	0.21880
S(AD5+Wid+Hgt)	4	1.6953	0.18780
S(AD5+Hgt)	3	3.2648	0.08568
S()	1	6.0475	0.02131
S(Wid)	2	6.1662	0.02008
S(VCat1 VCat2, VCat3)	2	7.7552	0.00907

Model selection results indicate that chick daily survival was affected by year and hatch day, and that recapture probability was affected by year, hatch day, and age (i.e., whether the chick was younger or older than 2 days; Table 3). There

27

were four competitive models ($\Delta AIC_C < 10$, Burnham and Anderson, 2002) for

chick daily survival rate (Phi) and recapture probability (p). The top two models

(which collectively explain 97% of the data) indicate that daily survival was affected

only by year, and that probability of recapture was determined by year, hatch day,

and age (Table 3).

Table 3. Model selection results for models of chick daily survival rate for 2006 and 2007. Data are for 83 Franklin's gull chicks monitored in 2006 and 2007. Chick daily survival rate (S) was modeled as a function of daily survival (Phi) and recapture probability (p). Model structure is indicated parenthetically. For instance, S(Phi(Yr+Hday)p(Yr)) indicates a model in which S varies with both Phi and p, Phi varies with year and hatch day, and p varies with year. K is the number of parameters in the model, ΔAIC_c is the relative Akaike Information Criteria adjusted for small sample size, and w_i is the model weight.

Model	K	ΔAIC_c	w_i
S(Phi(Yr)p(Age2+Yr*Hday))	6	0.0000	0.58319
S(Phi(Yr)p(Age2+Yr+Hday))	6	0.8146	0.38808
S(Phi(Yr*Hday)p(Age2+Yr))	7	7.7155	0.01231
S(Phi(Yr*Hday)p(Yr))	6	8.7172	0.00746
S(Phi(Yr+Hday)p(Age2+Yr))	6	10.9330	0.00246
S(Phi(Yr)p(Age2*Yr))	6	12.4083	0.00118
S(Phi(Yr)p(Age2+Yr))	5	12.6986	0.00102

DISCUSSION

During the two years in which this study was conducted, the dynamics of breeding differed in timing, egg quality, chick quality, nest success, and chick survival. Nest initiation date can affect reproductive success in many birds (Cavé, 1968, Perrins, 1970, Verhulst and Tinbergen, 1991). In 2006, Franklin's gull nests were initiated later than in 2007 at the J. Clark Salyer colony (Figure 1), and nest success was lower in 2006 than in 2007. However, nest success alone may not be a good indicator of reproductive success (Thompson et al., 2001). Indeed, I observed that this population of Franklin's gull laid larger eggs (Figure 3) and hatched chicks in better condition (Figure 10) that had higher survival rates in 2006 compared to 2007.

Many factors influence the timing of nest initiation in migratory birds. These factors include conditions at wintering sites, during migration and at breeding sites. For instance, birds from high-quality wintering sites are known to depart on the migration flight to breeding sites earlier than birds from low-quality wintering sites (Marra and Holberton, 1998). Weather patterns can also affect the duration of spring migration in waterbirds (Beason, 1978). Finally, overwater nesting is sensitive to the timing of ice-out (Storer and Nuechterlein, 1992). Franklin's gulls are also known to forage in snow-free, plowed fields near marshes used for nesting upon spring arrival (Burger, 1974). Thus, the factors causing annual differences in the timing of breeding for Franklin's gull during this study are not clear. Although I do not have quantitative data to document this, I did consider

areas of dense emergent vegetation (where Franklin's gulls nest) to be less abundant in 2006 compared to 2007 during the time when birds initiated nesting.

Availability of emergent vegetation may affect Franklin's gull nesting dynamics in many ways. Marsh-nesting gulls use visibility of conspecifics to assess quality of nest sites, and the abundance or height of vegetation may affect visibility of conspecifics (Burger, 1974; Good, 2002). Franklin's gulls use emergent vegetation for nest material but also steal nest material from neighboring nests (Burger and Gochfeld, 1994; personal observation). Thus, vegetation characteristics may attract gulls to particular areas, but as birds concentrate in these areas unattended nests may lose material to other birds.

Indeed, I observed effects of both density and nest material on nesting success. In 2006, nest daily survival rate decreased as nest density increased in the J. Clark Salyer colony. Although nest daily survival rate was much higher in 2007, nest bowl height explained a significant amount of variation in the nest daily survival rate (Table 2). Effects of neither density nor nest characteristics on nest success have been studied previously in gulls. Nest characteristics and building are indicators of parental care (Soler et al., 1998). I did not quantify nest height in 2006, but my results suggest that an understanding of annual variation in nest characteristics would be beneficial for understanding the annual variation in nest success in gulls.

Mechanisms regulating chick survival appear equally important for understanding recruitment in Franklin's gull. Variation in chick survival was not related to nest density, and the inter-annual pattern contrasted with that of nest

30

success. Parsons (1970) found that egg size and chick condition at hatching positively affected the probability of survival in herring gull chicks. Effects of condition at hatch can be far-reaching. Robust chicks exhibit higher post-fledging survival (Van der Jeugd and Larsson, 1998, Naef-Daenzer et al., 2001), earlier recruitment to the breeding population (Smith and Moore, 2005), and social status advantages later in life (Richner, 1989) compared to chicks that hatch in poor condition.

The contrasting inter-annual patterns of nest success and chick survival I observed are unique. While nests monitored in 2006 experienced low survival rates compared to nests in 2007, nests in 2006 were initiated later than nests in 2007 (Figure 1a). Typically low reproductive success is associated with later breeding (Brinkhof et al., 1993; Verboven and Visser, 1998). In the common tern, early hatch dates led to higher survival of nestlings than late hatch dates (Arnold et al., 2004). Brinkhof et al. (1993) observed more fledglings per brood for early laid nests. Although nesting initiated later in 2006 and nest survival rates were lower in the gulls at J. Clark Salyer, chick survival was higher. The product of nest success and chick survival was $0.06 = (0.945^{23})*(0.86^{10})$ in 2006 compared to $0.0017 = (0.982^{23})*(0.55^{10})$ in 2007, suggesting that overall recruitment was higher in 2006. Although I could not test within-season differences in nest success x chick survival interactions, this does not represent evidence that within a season earlier nest initiation does not benefit reproductive success. However, it does suggest that inter-annual variation in reproductive success is greater than intra-annual variation in this Franklin's gull colony.

31

Nevertheless, density dependent effects on nest success represent a significant source of intra-annual variation. Nests in high density areas experienced 62% lower success rates than nests in low density areas of the colony in 2006, even though chick survival was not affected by nest density.

Maternal Investment and Chick Condition

Condition at hatch may have been related to factors other than nest initiation date. Egg size is positively correlated with chick condition at hatch (Williams, 1994) and female condition in lesser black-backed gull (Bolton *et al.* 1992, Bolton *et al.* 1993). Females in 2006 laid larger eggs that produced chicks in better condition at hatch than females in 2007. One hypothesis explaining this observation is that females were in better condition at the time of egg production in 2006 compared to 2007. If Franklin's gull females are capital breeders, this may indicate factors faced before or during migration were more favorable in 2006. On the other hand, if Franklin's gull females are income breeders, this may indicate resources were more favorable at J. Clark Salyer NWR in 2006.

The absence of correlations between yolk corticosterone concentration and nest site characteristics or egg mass indicates that nest site environment may not have directly affected physiology of the developing chick. Eising *et al.* (2003) indicated that maternal glucocorticoid deposition slowed chick growth; these data indicate that the nest site characteristics measured here are not straight-forward indicators of trends in chick development via maternally-deposited stress hormones.

Growth rates of chicks may not be an indication of breeding success if slow growth does not hinder chick survival and recruitment. Although slow growth may extend the fledging period (Barrett and Rikardsen, 1992), it may be independent of the overall successfulness of the nest. Although high tarsal growth rates in 2007 suggest a favorable environment for chick growth, my results indicate that the previous year, when tarsal growth was slow, was a more favorable year for chick survival. However, my analysis was restricted to tarsal growth only. Information on body mass is needed to draw a conclusion regarding total growth. At hatching, tarsus length differed between years but body mass did not; it is possible that similar patterns exist later in the chick stage.

Reproductive success in avian species is the product of multiple components. I observed significant interannual differences in components associated with each of the two major periods of reproduction, nesting and chick rearing. I hypothesize that the timing of breeding may have played a significant role in driving many of these patterns because nest initiation date varied significantly with nest density (a factor that affected nest success) and egg size (which has been shown to affect chick performance in many birds; see Williams, 1994). In long-distance migratory species, including Franklin's gull, nest initiation begins soon after arrival on the breeding ground. Migratory delays that lead to late breeding may result in females investing resources in fewer, heavier eggs that yield robust chicks; however, those females may also experience lower nest success than females that arrive and begin nesting earlier on the breeding

33

grounds. Hence, reproductive output exhibits a tradeoff between offspring quantity and offspring quality that is associated with nest initiation in Franklin's gull.

LITERATURE CITED

Amundsen, T., and J.N. Stokland. 1990. Egg size and parental quality influence nestling growth in the shag. Auk 107: 410-413.

Antolos, M., D. Roby, D. Lyons, S. Anderson, and K. Collis. 2006. Effects of nest density, location, and timing on breeding success of Caspian Terns. Waterbirds 29: 465-472.

Arnold, J.M., J.J. Hatch, and I.C.T. Nisbet. 2004. Seasonal declines in reproductive success of the common tern *Sterna hirundo*: timing or parental quality? Journal of Avian Biology 35: 33-45.

Barrett, R., and F. Rikardsen. 1992. Chick growth, fledging period, and adult mass loss of Atlantic puffins *Fratercula arctica* during years of prolonged food stress. Colonial Waterbirds 15: 24-32.

Beason, R. C. 1978. The influences of weather and topography on water bird migration in the southwestern United States. Oecologia 32: 153-169.

Becker, P.H., and M. Erdelen. 1986. Egg size in Herring Gulls (*Larus argentatus*) on Mellum Island, North Sea, West Germany: The influence of nest vegetation, nest density, and colony development. Colonial Waterbirds 9: 68-80.

Birkhead, T., F. Fletcher, and E. Pellatt. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. Proceedings of the Royal Society of London B 266: 385-390.

Bolton, M. 1991. Determinants of chick survival in lesser black-backed gull: relative contributions of egg size and parental quality. Journal of Animal Ecology 60: 949-960.

Bolton, M., D.C. Houston, and P. Monaghan. 1992. Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. Journal of Animal Ecology 61: 521-532.

Bolton, M., P. Monaghan, and D.C. Houston. 1993. Proximate determination of clutch size in lesser black-backed gulls: the roles of food supply and body condition. Canadian Journal of Zoology 71: 273-279.

Boonstra, T.A. 2006. Effects of maternal investments on egg metabolic rates, hatching synchrony, and offspring performance in Canada geese (Branta canadensis maxima). Masters Thesis, North Dakota State University,

Brinkhof, M.W.G., and A.J. Cavé. 1997. Food supply and seasonal variation in breeding success: an experiment in the European coot. Proceedings of the Royal Society of London B 264: 291-296.

Brinkhof, M.W.G., A.J. Cavé, and A.C. Perdeck. 1993.Timing of reproduction and fledgling success in the coot Fulica atra: evidence for a causal relationship. Journal of Animal Ecology 62: 577-587.

Brouwer, A., A.L. Spaans, and A.A.N. Wit. 1995. Survival of Herring Gull Larus argentatus chicks: an experimental analysis of the need for early breeding. Ibis 137: 272-278.

Brown, C., and M. Bomberger Brown. 1986. Ectoparasitism as a cost of coloniality in cliff swallows (Hirundo pyrrhonota). Ecology 67: 1206-1218.

Brunton, D.H. 1997. Impacts of predators: center nests are less successful than edge nests in a large nesting colony of Least Terns. Condor 99: 372-380.

Burger, J. 1974. Breeding adaptations of Franklin's Gull (*Larus pipixcan*) to a marsh habitat. Animal Behaviour 22: 521-567.

Burger, J., and M. Gochfeld. 1994. Franklin's Gull (*Larus pipixcan*). *In* The Birds of North America, No. 116 (A. Poole and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists Union.

Catry, P., N. Ratcliffe, and R.W. Furness. 1998. The influence of hatching date on different life-history stages of Great Skuas *Catharacta skua*. Journal of Avian Biology 29: 299-304.

Cavé, A.J. 1968. The breeding of the kestrel *Falco tinnunculus* L. in the reclaimed area Oostelijk Flevoland. Netherlands Journal of Zoology 18: 313-407.

Chicon, M., and M. Lindén. 1995. The timing of breeding and offspring size in Great Tits *Parus major*. Ibis 137: 364-370.

Coulson, J.C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217: 478-479.

Daisley, J., V. Bromundt, E. Möstl, and K. Kortschal. 2005. Enhanced yolk testosterone influences behavioral phenotype independent of sex in Japanese quail chicks *Coturnix japonica*. Hormones and Behavior 47: 185-194.

Dexheimer, M. and W. Southern. 1974. Breeding success relative to nest location and density in Ring-billed Gull colonies. Wilson Bulletin 86: 288-290.

Dorward, D. F. 1962. Comparative biology of the white booby and the brown booby *Sula* spp at Asension. Ibis 103: 174–234.

Eising, C., W. Müller, C. Dijkstra, and T. Groothuis. 2003. Maternal androgens in egg yolks: relation with sex, incubation time and embryonic growth. General and Comparative Endocrinology 132: 241-247.

Eriksen, M., A. Haug, P. Torjeson, and M. Bakken. 2003. Prenatal exposure to corticosterone impairs embryonic development and increases fluctuating asymmetry in chickens (*Gallus gallus domesticus*). British Poultry Science 44: 690-697.

Godfray, H. 1995. Evolutionary theory of parent-offspring conflict. Nature 376: 133-138.

Good, T. 2002. Breeding success in Western gull x Glaucous-winged gull complex: The influence of habitat and nest-site characteristics. Condor 104: 353-365.

Griesser, M. 2009. Mobbing calls signal predator category in a kin group-living bird species. Proceedings of the Royal Society of London B 276: 2887-2892.

Griesser, M. 2008. Referential calls signal predator behavior in a group-living bird species. Current Biology 18(1): 69-73.

Grindstaff, J., E. Brodie, and E. Ketterson. 2003. Immune function across generations: integrating mechanism and evolutionary process in maternal antibody transmission. Proceedings of the Royal Society of London B 270: 2309-2319.

Groothuis, T., and H. Schwabl. 2002. Determinants of within- and among-clutch variation in levels of maternal hormones in Black-Headed Gull eggs. Functional Ecology 16: 281-289.

Hayward, L., and J. Wingfield. 2004. Maternal corticosterone is transferred to avian yolk and may alter offspring growth and adult phenotype. General and Comparative Endocrinology 135: 365-371.

Kilpi, M. 1995. Egg size asymmetry within Herring Gull clutches predicts fledgling success. Colonial Waterbirds 18: 41-46.

Klasing, K., D. Laurin, R. Peng, and D. Fry. 1987. Immunologically mediated growth depression in chicks: Influence of feed intake, corticosterone, and Interleukin-1. Journal of Nutrition 117: 1629-1637.

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

Lima, S. 1990. The influence of models on the interpretation of vigilance. In: *Interpretation and Explanation in the Study of Animal Behavior: Vol. 2. Explanation, Evolution and Adaptation* (Ed. by M. Bekoff and D. Jamieson), pp. 246-247. Boulder, Colorado: Westview Press.

Love, O.P., D.M. Bird, and L.J. Shutt. 2003. Plasma corticosterone in American kestrel siblings: effects of age, hatching order, and hatching asynchrony. Hormones and Behavior 43: 480–488.

Marra, P.P., and R.L. Holberton. 1998. Corticosterone levels as indicators of habitat quality; effects of habitat segregation in a migratory bird during the non-breeding season. Oecologia 116: 284-292.

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456-466.

Metcalfe, N., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology and Evolution 16: 254-260.

Morgan, I., and N. Metcalfe. 2001. The influence of energetic requirements on the preferred temperature of overwintering juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Science 58: 762-768.

Naef-Danzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. Journal of Animal Ecology 70: 730-738.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). Nature 228: 1221-1222.

Patterson, I.J. 1965. Timing and spacing of broods in the black-headed gull *Larus ridibundus*. Ibis 107: 433-459.

Perrins, C.M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.

Reid, W.V. 1987. Constraints on clutch size in the Glaucous-winged Gull. Studies in Avian Biology 10: 8-25.

Richner, H. 1989. Habitat-specific growth and fitness in carrion crows (*Corvus corone corone*). Journal of Animal Ecology 58: 427-440.

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

Ross, H.A., and I.A. McLaren. 1981. Lack of differential survival among young Ipswich Sparrows. Auk 98: 495-502.

Rutkowska, J., and M. Cichon. 2002. Maternal investment during egg laying and offspring sex: an experimental study of zebra finches. Animal Behaviour 64: 817-822.

Saino, N., A.P. Møller, and A.M. Bolzern. 1995. Testosterone effects on the immune system and parasite infestations in the barn swallow (*Hirundo rustica*): an experimental test of the immunocompetence hypothesis. Behavioral Ecology 6: 397–404.

Schlichting, C., and M. Pigliucci. 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer Associates, Inc., Sunderland, Mass.

Schwabl, H. 1993. Yolk is a source of maternal testosterone for developing birds. Proceedings of the National Academy Sciences 90: 11446–11450

Scolaro, J. 1990. Effects of nest density on breeding success in a colony of Magellanic penguins (*Spheniscus magellanicus*). Colonial Waterbirds 13: 41-49.

Smith, R.J., and F.R. Moore. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology 57: 231-239.

Soler J.J., A.P. Møller, and M. Soler. 1998. Nest building, sexual selection and parental investment. Evolutionary Ecology 12: 427-441.

Storer, R.W. and G.L. Nuechterlein. 1992. Western grebe, Clark's grebe: *Aechmophorus occidentalis, Aechmophorus clarkii.in* A. Poole and F. Gill, editors. Birds of North America. American Ornithologists' Union, Washington, D.C.

Tenaza, R. 1971. Behavior and nesting success relative to nest location in Adelie penguins (*Pygoscelis adeliae*). Condor 73: 81-91.

Thompson, B.C., G.E. Knadle, D.L. Brubaker, and K.S. Brubaker. 2001. Nest success is not an adequate comparative estimate of avian reproduction. Journal of Field Ornithology 72: 527-536.

Van der Jeugd, H.P., and K. Larsson. 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. Journal of Animal Ecology 67: 953-966.

Verboven, N., and M.E. Visser 1998. Seasonal variation in local recruitment of great tits: the importance of being early. Oikos 81: 511-524.

Verboven, N., P. Monaghan, D. Evans, H. Schwabl, N. Evans, C. Whitelaw, and R. Nager. 2003. Maternal condition, yolk androgens and offspring performance: a supplemental feeding experiment in the lesser black-backed gull (*Larus fuscus*). Proceedings of the Royal Society of London B 270: 2223-2232.

Verhulst, S., and J.M. Tinbergen. 1991. Experimental evidence for a causal relationship between timing and success of reproduction in the great tit *Parus m. major*. Journal of Animal Ecology 60: 269-282.

White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: Supplement 120-138.

Williams, T.D. 1994. Intraspecific variation in egg size and egg composition in birds - effects on offspring fitness. Biological Reviews of the Cambridge Philosophical Society 69: 35-59.

Wingfield, J., R. Hegner, A. Dufty, Jr., and G. Ball. 1990. The "Challenge Hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. American Naturalist 136: 829-846.

Yorio, P., M. Bertellotti, and F. Quintana. 1995. Preference for covered nest sites and breeding success in Kelp Gulls *Larus dominicanus*. Marine Ornithology 23: 121-128.