

CLUTCH INVESTMENT IN THE CHILEAN SWALLOW (*TACHYGINETA MEYENI*) SHIFTS WITH TIME OF BREEDING AND POSITION IN THE SEQUENCE OF LAYING

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Abstract. Within a population, the sizes of eggs and clutches vary, and the combination of both determines a female's reproductive investment. We investigated females' investment in clutches of the Chilean Swallow (*Tachycineta meyeri*) at the southern limit of its range, where it breeds in an extreme climate. We analyzed variation in clutch, egg and yolk size in relation to the female's condition, date of laying, and position in the sequence of laying. As predicted by energy/nutrient constraints, clutch size and yolk size decreased over the breeding season, though egg mass increased. Females' investment strategy differed with clutch size: their investment in eggs increased with each successive egg in clutches of 4 and 5 eggs but decreased with each successive egg in clutches of 3 eggs. Eggs that were heavier for their size were more likely to hatch than eggs light for their size. Females may make a strategic decision, with high investment in eggs laid early resulting in a short sequence (small clutch) and delayed investment resulting in a long sequence (large clutch). Alternatively, the shift in clutch investment may simply be a consequence of physiology. Better estimates of female body condition are needed for these options to be distinguished.

Key words: egg size, laying order, clutch size, reproductive investment, *Tachycineta meyeri*.

La Inversión en la Puesta en *Tachycineta meyeri* Varía a lo Largo de la Estación Reproductiva y con el Orden de Puesta

Resumen. El tamaño del huevo y el tamaño de la puesta varían dentro de una población y la combinación de ambos determina la inversión reproductiva por parte de las hembras. Investigamos la inversión en la puesta por parte de las hembras de *Tachycineta meyeri* que nidifican en un sitio con condiciones climáticas adversas en el extremo más austral de su distribución. Analizamos la variación en el tamaño de la puesta, del huevo y de la yema en relación a la condición corporal de la hembra, a la fecha de puesta y a la posición en la secuencia de puesta. Acordé a lo predicho por restricciones energéticas/nutricionales, el tamaño de la puesta y de la yema disminuyeron a lo largo de la estación reproductiva, pero la masa del huevo aumentó. La estrategia de inversión de las hembras difirió según el tamaño de la puesta: la inversión en los huevos aumentó con el orden de puesta en puestas de cuatro y cinco huevos y disminuyó con el orden de puesta en puestas de tres huevos. Huevos pesados para su tamaño tuvieron una mayor probabilidad de eclosión que huevos livianos para su tamaño. Las hembras podrían estar tomando una decisión estratégica, con una mayor inversión al comienzo de la secuencia de puesta lo que resultaría en una secuencia corta (nidada pequeña) o retrasando la inversión lo que resultaría en una secuencia larga (nidada grande). Alternativamente, los cambios en la inversión en la puesta podrían ser simplemente una consecuencia fisiológica. Es necesario obtener o una mejor estimación de la condición corporal de las hembras para poder diferenciar entre estas dos alternativas.

INTRODUCTION

Egg size and clutch size can vary considerably within a population, and the combination of both determines the total reproductive investment in clutch formation by a laying female. Although Lack (1947) proposed that there should be a trade-off between clutch size and egg size, this remains unclear, with studies showing a positive, negative, or no relationship between clutch size and egg size (Christians 2002, Williams 2011).

Females have the ability to adjust some aspect(s) of egg production and to allocate reserves differentially to eggs within a clutch (and possibly between clutches) (Williams 1994). Evidence from hatching success and/or offspring fitness indicates that females can alter investment by laying larger eggs (Williams 1994, Perrins 1996), allocating more yolk to eggs, and provisioning yolk with specific nutrients (Royle et al. 1999, Pilz et al. 2003). Egg size and quality are important life-history traits because variations in these traits

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can have important consequences on the rate of the embryo's growth during incubation (Byerly 1932) and on offspring quality (Williams 1994, Mousseau and Fox 1998).

The mass of an egg consists of yolk, albumen, and shell. Yolk constitutes the major source of energy and nutrients used by the developing embryo, whereas albumen represents the primary source of water in the egg. In many avian species, intraspecific variation in the mass of the egg is attributable primarily to variation in albumen mass (Hill 1995, Flinkler et al. 1998), and as egg mass increases, the mass of the albumen increases disproportionately more than expected by isometry (Ricklefs 1984). The mass of the yolk (and the proportions of lipids and proteins it contains) may vary with egg mass (Arnold and Green 2007), and the relationship between yolk mass and egg mass may be proportional in precocial birds but unrelated in altricial birds (Ricklefs 1984, Williams 1994, Hill 1995, Wiebe 2006). Also, yolk mass may vary according to food availability, timing of breeding, and the order in which the egg is laid (Ardia et al. 2006a).

Although egg size has a high repeatability (>0.6) and heritability (>0.5) (Moss and Watson 1982, Christians 2002), females can vary their investment in egg size in relation to their own reproductive condition, environmental conditions, food availability, sequence of laying, or date of laying (Howe 1976, Parsons 1976, Birkhead and Nettleship 1982, Styrsky et al. 2002, Hargitai et al. 2005, Ardia et al. 2006a). Given that egg production is a costly process (Williams 2005), inter- and intraclutch variation in egg size could be determined by the female's energetic or nutritional constraints (Bernardo 1996). In support of this hypothesis, several studies have found that egg size among clutches increased with the female's condition (e.g. Styrsky et al. 2002, Hargitai et al. 2005). Interclutch variation in egg size could also be related to seasonal deterioration in environmental conditions. For females that lay late in the season, it should be advantageous to minimize further delays in laying by producing a small egg earlier, rather than to delay laying further to produce a larger egg (Birkhead and Nettleship 1982). Larger eggs have greater hatching success (Perrins 1996) and are often correlated with greater mass and size of offspring (Christians 2002).

Clutch size also varies within a population, and one of the most widespread patterns in avian life histories, especially in birds that lay only one clutch per breeding season, is that females that lay later in the breeding season lay smaller clutches (Drent and Daan 1980 and references therein). This seasonal decline in clutch size could be related to the effect of nonheritable variation in the female's condition (Price et al. 1988) or to a seasonal decline in environmental quality (Lack 1966, Perrins 1970).

Chilean Swallows (*Tachycineta meyeni*) breeding at Ushuaia, located at the southern tip of Argentina ($54^{\circ} 44' \text{ S}$, $61^{\circ} 12' \text{ W}$), lay between 2 and 5 eggs with a mode of 4 eggs (Liljesthröm 2011), a clutch size similar to that of other species of *Tachycineta* at low latitudes (Dyrce 1984, Allen 1996,

Townsend et al. 2008) and smaller than that of those at high-latitude locations (Ardia et al. 2006b, Massoni et al. 2006). In this study we investigated how female Chilean Swallows invest in clutches, and we analyzed clutch size, egg size, and yolk size variation in relation to the female's condition, date of laying, and order in which the eggs are laid. Since this population of the Chilean Swallow lays relatively small clutches, we looked for evidence that investment in egg production is costly. We tested the predictions related to the constraints of nutrient and energy reserves, that (1, seasonal decline) clutch size and egg size decrease through the breeding season, (2, egg sequence) within a clutch, egg size and yolk size decrease in the order in which the eggs are laid, and (3, female condition) females in better body condition lay larger clutches and larger eggs with larger yolks. We also examined the relationships between clutch size and egg and yolk size for evidence of either trade-offs or constraints. Finally, we looked for evidence of fitness consequences related to egg size by testing the prediction that larger eggs have a greater hatching success (Perrins 1996).

METHODS

STUDY AREA

We studied Chilean Swallows breeding in nest boxes at three sites near the city of Ushuaia, Tierra del Fuego, Argentina. Site A ($54^{\circ} 44' \text{ S}$, $68^{\circ} 12' \text{ W}$), was 15 km northeast of Ushuaia, site B ($54^{\circ} 44' \text{ S}$, $67^{\circ} 54' \text{ W}$) was 40 km east of Ushuaia, and site C ($54^{\circ} 53' \text{ S}$, $67^{\circ} 20' \text{ W}$) was 85 km east of Ushuaia; they had a total of 88, 68, and 62 nest boxes, respectively. For the analysis, we combined sites A and B as one inland site on the basis of their geographic similarity (they are both inland and next to peat bogs), while site C was a coastal site. The study area is part of the biogeographic region of the Andean-Patagonian woodland. During the breeding season, the monthly average ambient temperature varies from 6.2° C in October to 9.8° C in January. Daily temperatures range as low as -2.9° C and as high as 25.1° C . Monthly average precipitation varies from 33.1 mm in October to 54.1 mm in December.

DATA COLLECTION

The Chilean Swallow is an austral migrant that remains in our study area from mid October to mid March. Our study took place during the breeding seasons of 2006–07, 2007–08, 2008–09, and 2009–10. During each season, we started monitoring nest boxes in mid-October and visited nests every other day during nest construction, daily during egg laying, to determine clutch-initiation date, the sequence in which the eggs were laid, and clutch size. On the date each egg was laid, we marked each egg individually to track its order. When we could not determine the exact order (because of missing a nest box visit during laying), we assigned each egg of the pair the average between the two possible positions (e.g., if we had two eggs that we could not distinguish as second or

third, we assigned them 2.5 instead of 2 or 3). We also recorded the length and width of each egg with calipers to the nearest 0.05 mm, and we weighed each egg to the nearest 0.1 g by suspending it in a plastic bag with a 10-g Pesola spring scale in an empty plastic bottle to keep out wind. During the 2008–09 breeding season, at site A, we took a standardized digital photograph of each egg on the day after it was laid, using an ovulux, a modified plastic cylinder with a high-output light-emitting diode whose light penetrated the egg and allowed to the yolk to be distinguished clearly from the albumen (Ardia et al. 2006a).

After a clutch was complete, we checked the box every 2 days then daily near the day of predicted hatching. After hatching we noted unhatched eggs. We captured and banded females at each nest early during the chick-rearing period (within the chicks' first 6 days of age) in order to prevent the female from abandoning the nest, which is more likely during egg laying and incubation. As an index of the female's body condition we used residual body mass, calculated as the residuals of the regression of body mass against head–bill length (Ardia 2005) and included the nestlings' age at time of the female's capture as a covariate.

STATISTICAL ANALYSIS

We estimated the sizes of the yolk and egg as the cross-sectional area of each, hereafter referred to as yolk area and egg area, as extracted from the digital photographs with the program ImageJ. We used the field measurement of the width of each egg to convert the ImageJ estimates from pixels to square millimeters.

We had three variables related to egg size, egg mass, egg area, and mass–area residual, and one related to yolk size, yolk area. We did not convert these estimates to volume because cubing the terms would magnify measurement errors. While egg mass and egg area were absolute estimates of egg size, the mass–area residual was a relative estimate. To estimate egg area for eggs in years other than 2008–09, when we took the ovulux photographs, we used those photographs to model egg area as a linear function of field measurements of egg length and egg width: $R^2_{\text{adj}} = 0.95$, $F_{1,98} = 1022.4$, $P < 0.001$, egg area = -196.54 (9.39 SE) + length \times 9.898 (0.375 SE) + width \times 15.242 (0.763 SE); the model proved highly predictive. We calculated yolk area only for eggs photographed in 2008–09. We calculated mass–area residuals from the general linear mixed model of egg mass as a function of egg area, with the female's identity and the clutch's identity nested within the female's identity as random effects: egg mass = -0.24 (0.076 SE) + egg area \times 0.01 (0.0004 SE), $F_{1,357} = 785.5$, $P < 0.001$. We interpreted positive residuals as indicating eggs heavy for their size, negative residuals as indicating eggs light for their size. Mixed models allow controlling for the nonindependence of data among repeated measures, such as more than

one clutch of a female or eggs within a clutch (Pinheiro and Bates 2000, Crawley 2007).

To examine factors affecting clutch size, the three estimates of egg size (mass, area, residuals), and yolk area, we used general linear mixed models. In all models we included the date of laying and the female's condition as continuous fixed effects and year and site as categorical variables (except in the model for yolk area, which was based on date from only a single site and season). For date of laying we considered 1 October as the first day of the breeding season and report all dates with respect to that day. Year refers to each of the four breeding seasons (2006–07, 2007–08, 2008–09, 2009–10), and site refers to inland or coastal. The model with clutch size as a dependent variable included date of laying, the female's body condition, year, and place as fixed factors and the female's identity as a random effect. For models with egg-size estimates and yolk area as dependent variables we also included the order of laying as a continuous fixed effect, clutch size as a categorical variable, the interaction term clutch size \times laying order, and the female's identity and the clutch's identity nested within the female's identity as random effects.

To examine factors predicting hatching success we used logistic mixed models. Each model included one of our three estimates of egg size (egg mass, egg area, and mass–area residuals), the female's condition, order of laying, and date of laying as continuous fixed effects, clutch size, year, and site as categorical variables, and the female's identity and the clutch's identity nested within the female's identity as random effects.

We used SAS (version 9.1) to analyze data, and all statistical tests were two-tailed with α (P) set at 0.05. We present data as means \pm SE but include the median for variables that did not follow a normal distribution.

RESULTS

We recorded data from 169 clutches, mostly of 3 and 4 eggs ($n = 43$ and 105, respectively), along with 16 clutches of 5 eggs. We excluded from analyses 5 clutches of 2 eggs because the sample was small. For 23 clutches we did not have egg measurements, and for 39 clutches we did not have the eggs' exact sequence; we dropped these clutches from analyses that required egg measurements or the sequence of laying, respectively. From 146 clutches, eggs measured (length \times width) $19.1 \pm 0.9 \times 13.6 \pm 0.4$ mm (length range 16.6–24.3 mm, width range 12.2–14.7 mm, $n = 556$), egg mass was 1.9 ± 0.2 g (range 1.4–2.3, $n = 548$), and egg area was 200.6 ± 11.7 mm² (range 157.7–255.8, $n = 558$).

Yolk area increased with egg area, but at only half the rate: yolk area = -23.6 (18.8 SE) + egg area \times 0.52 (0.08 SE) + clutch size \times 5.8 (2.8 SE); egg area: $F_{1,61} = 41.4$, $P < 0.001$; clutch size: $F_{1,61} = 4.3$, $P = 0.04$; order: $P > 0.05$). Thus larger eggs had proportionally smaller yolks, though still more yolk than smaller eggs.

FACTORS AFFECTING CLUTCH SIZE, EGG SIZE, AND YOLK SIZE

Date of laying predicted clutch size and yolk area, which decreased as the season progressed (clutch size: $\beta = -0.02 \pm 0.003$; yolk area: $\beta = -0.13 \pm 0.03$; Table 1), and egg mass, which instead increased as the season progressed ($\beta = 0.002 \pm 0.0008$; Table 1). We found no significant relationship, however, between date of laying and egg area or mass–area residuals (Table 1). All estimates of egg size showed a significant interaction between laying order and clutch size, but yolk area didn't, indicating that the effect of laying order on egg size varied with clutch size (Table 1). In 3-egg clutches, egg mass and egg area decreased as the clutch was laid,

TABLE 1. Factors affecting clutch size, egg mass, egg area, mass–area residuals, and yolk area of Chilean Swallows during the breeding seasons 2006–07 to 2009–10 in Tierra del Fuego, Argentina. Numerator degrees of freedom for all tests = 1, except for clutch size and clutch size \times laying order where numerator degrees of freedom = 2 and year where numerator degrees of freedom = 3.

Effect	Denominator df	F	P
Clutch size			
Laying date	44	25.05	<0.0001
Female body condition	44	1.21	0.28
Year	44	0.68	0.57
Site	44	0.44	0.51
Egg mass			
Laying date	267	3.93	0.05
Clutch size	267	0.06	0.94
Laying order	267	0.15	0.69
Clutch size \times laying order	267	4.71	0.01
Female body condition	267	0.38	0.54
Year	267	5.84	0.001
Site	267	9.80	0.002
Egg area			
Laying date	268	2.34	0.13
Clutch size	268	1.40	0.25
Laying order	268	0.86	0.35
Clutch size \times laying order	268	4.00	0.02
Female body condition	268	1.06	0.30
Year	268	5.75	0.0008
Site	268	3.48	0.06
Mass-area residuals			
Laying date	267	0.09	0.77
Clutch size	267	5.19	0.006
Laying order	267	0.08	0.78
Clutch size \times laying order	267	6.85	0.001
Female body condition	267	1.18	0.28
Year	267	0.86	0.46
Site	267	1.38	0.24
Yolk area			
Laying date	42	15.13	0.0004
Clutch size	42	0.86	0.36
Laying order	42	0.48	0.49
Clutch size \times laying order	42	0.60	0.44
Female body condition	42	0.01	0.93

but in 4- and 5-egg clutches they increased (Fig. 1, 2). In 3- and 4-egg clutches the mass–area residual decreased, each successive egg being lighter for its size than the previous, but increased in 5-egg clutches, each successive egg being heavier for its size than the previous (Fig. 3). In 4-egg clutches, as laying progressed the increase in egg area was faster than the change in egg mass. Therefore eggs laid later in the sequence were lighter for their size (negative mass–area residual). In 5-egg clutches, in contrast, egg

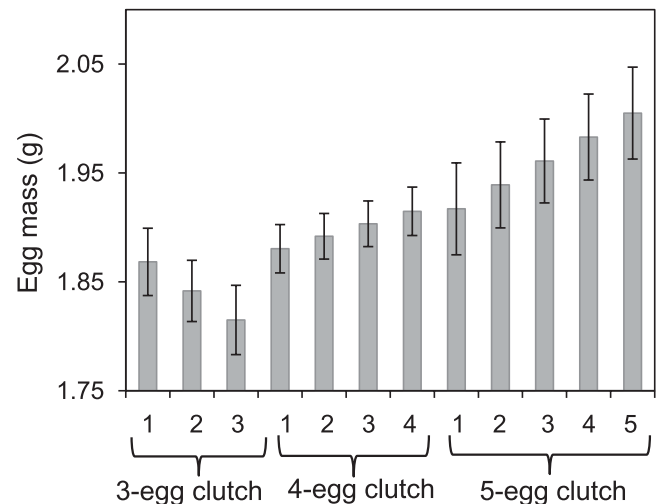


FIGURE 1. Least-square mean egg mass (with standard error bars) through the sequence of laying by clutch size from general linear mixed models with nest identity as a random effect in eggs laid by Chilean Swallows during the breeding seasons 2006–07 to 2009–10 in Tierra del Fuego, Argentina.

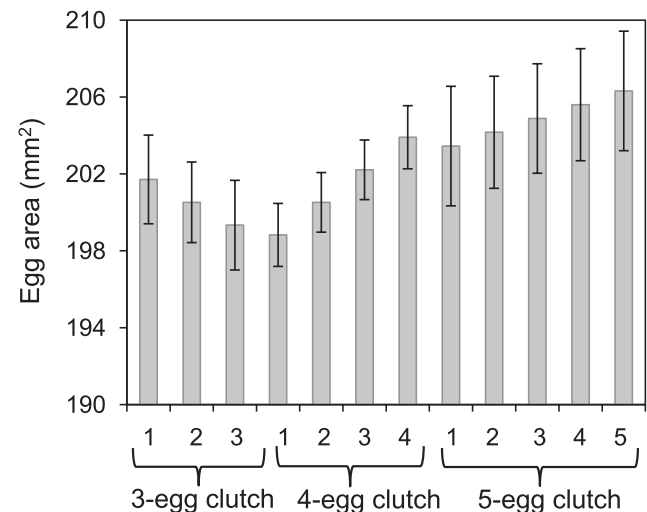


FIGURE 2. Least-square mean egg area (with standard error bars) through the sequence of laying by clutch size from general linear mixed models with nest identity as a random effect in eggs laid by Chilean Swallows during the breeding seasons 2006–07 to 2009–10 in Tierra del Fuego, Argentina.

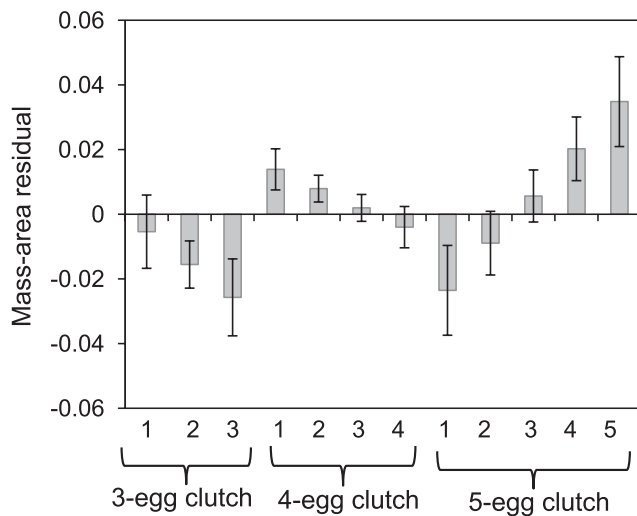


FIGURE 3. Least-square mean mass–area residual (with standard error bars) through the sequence of laying by clutch size from general linear mixed models with nest identity as a random effect in eggs laid by Chilean Swallows during the breeding seasons 2006–07 to 2009–10 in Tierra del Fuego, Argentina.

area increased through the sequence at a rate slower than did egg mass, resulting in eggs heavier for their size as laying progressed. The pattern in 3-egg clutches was the opposite, egg area decreasing through the sequence at a rate slower than did egg mass, resulting in eggs lighter for their size later in the sequence. Clutch size, egg mass, egg area, mass–area residuals, and yolk area did not vary with the female's condition (Table 1). Year and site did not predict clutch size or mass–area residuals, but egg mass and egg area did vary by year, and egg mass was greater at the coastal site than at the inland sites ($\beta = 0.002 \pm 0.0008$; Table 1).

HATCHING SUCCESS AND EGG SIZE

Of 627 eggs, 79 were in 22 clutches abandoned during incubation. Of the 548 eggs in clutches attended throughout incubation, 458 hatched, 72 failed to hatch, and another 15 either disappeared or were punctured, broken, or dented. Based on logistic mixed models, the probability of an egg hatching was not predicted by either egg mass ($F_{1,262} = 0.09$, $P = 0.76$) or egg area ($F_{1,262} = 0.47$, $P = 0.49$). The mass–area residual, however, predicted the probability of the egg hatching ($F_{1,262} = 9.14$, $P = 0.003$). Eggs that were heavy for their size were most likely to hatch, while eggs light for their size were least likely to hatch (Fig. 4).

DISCUSSION

For Chilean Swallows at the southern tip of Argentina, reproductive investment varied with date and order of laying. Our finding that clutch size decreased with date of laying supports our prediction of a seasonal decline in clutch size and is consistent with other studies of *Tachycineta*, including the Tree Swallow

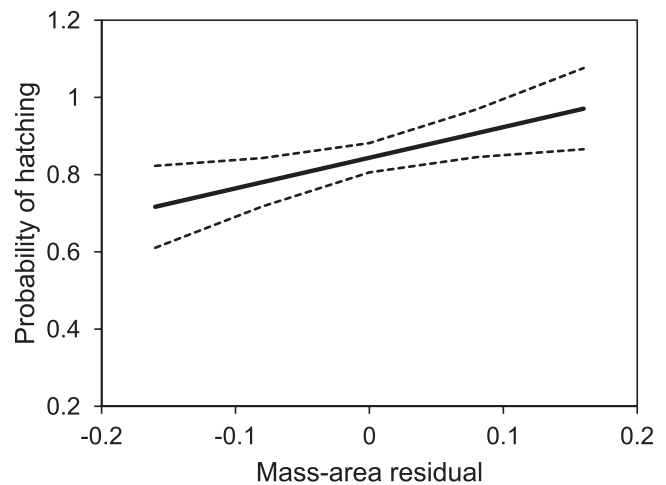


FIGURE 4. Relationship between probability of hatching and mass–area residual (solid line) with 95% confidence intervals (dashed lines) in eggs laid by Chilean Swallows during the breeding seasons 2006–07 to 2009–10 in Tierra del Fuego, Argentina.

(*T. bicolor*; Stutchbury and Robertson 1988, Winkler and Allen 1996) and White-rumped Swallow (*T. leucorrhoa*; Massoni et al. 2006) and of other birds as well (Drent and Daan 1980). Though the seasonal decline in clutch size is one of the most generalized patterns in avian life history, there is considerable disagreement on whether this correlation is caused by a seasonal decline in the quality of the environment (Lack 1966, Perrins 1970, Young 1994) or by differences in condition of birds breeding early and late (Price et al. 1988). In the Tree Swallow, Winkler and Allen (1996) found no detectable effect of condition on clutch size; instead, they suggested that the seasonal decline of clutch size was a strategic adjustment by the female to the varying prospects for her offspring's survival (if food supply decreases over the season, this limits resources available to the females) (Winkler and Allen 1996). Alternatively, it may be that no single hypothesis explains the seasonal decline in clutch size across species (Verhulst et al. 1995, Daan and Tinbergen 1997, Garamszegi et al. 2004). Our results show that clutch size was strongly related to date of laying but not to the female's condition. However, we cannot exclude the possibility that body condition measured by some better means would be a determinant of clutch size.

In the season during which we measured yolk area (2008–09), Chilean Swallows laying earlier laid eggs with larger yolks than did females laying later, which is consistent with the pattern in the Tree Swallow (Ardia et al. 2006a). However, contrary to our prediction, we found a seasonal increase in egg mass and no variation in egg area. Therefore, it is possible that variation in albumen content was the main reason for heavier eggs being laid later in the season. Much variation in overall egg mass tends to arise from differences in albumen and water content, but changes in yolk content involve

variation in lipid content and therefore in egg “quality” (Williams 1994). Provided that in the Chilean Swallow a larger yolk area correlates with a larger yolk mass, then early-laying females would be laying eggs of higher quality and with less albumen than later-laying females.

Differences in investment in yolk may be related to variation in food availability during the breeding season, may reflect constraints on the female’s ability to gather resources, and/or may be a strategy of late-laying females that reduce investment in eggs in response to nestlings’ lower chances of survival later in the season (Ardia et al. 2006a). This last explanation seems plausible for the Chilean Swallow. Though nestling survival at our site did not vary seasonally, nestlings grew slower and attained lower asymptotic mass as the breeding season advanced (unpubl. data), suggesting that in fact nestlings’ prospects may be lower later in the season. Alternatively, the female’s age may account for differences in the level of investment in yolk, with older and more experienced females laying early in the season. Though we did not know the age of our birds, this seems unlikely because older female Tree Swallows lay larger eggs (larger mass) than do younger females, but age has no effect on yolk size (Ardia et al. 2006a). Measures of food availability at our study site during laying, as well as data on females’ ages, will help elucidate these alternative explanations.

Within our Chilean Swallow population, the relationship between egg size and the order in which eggs were laid varied with clutch size. In 3-egg clutches, egg size decreased as the eggs were laid, but, as reported in other studies of passerines (Howe 1976, Ojanen 1983, Ardia et al. 2006a, Robinson et al. 2010), it increased in 4- and 5-egg clutches. Intraclutch variation in egg size is common among birds, and various adaptive explanations have been suggested. Intraclutch variation in egg size could be an adaptive response to mitigate or reinforce competition among siblings (Howe 1976, Clark and Wilson 1981, Slagsvold et al. 1984). Females may try to mitigate the initial disadvantage of the last chick to hatch by investing more in the last egg, resulting in an increase in egg size as the eggs are laid (Howe 1976, Clark and Wilson 1981, Slagsvold et al. 1984). Alternatively, females may try to maximize this disadvantage by investing less in the last egg laid (Lack 1954, Slagsvold et al. 1984), resulting in a decrease in egg size as the eggs are laid (Howe 1976). In this way, when food is scarce, the small last-hatched sibling is more likely to die, thus enabling some of the young to survive. The significant interaction term between clutch size and order of laying suggests that within our Chilean Swallow population, females appear to adjust egg-investment strategies on the basis of clutch size. Thus this population of the Chilean Swallow may have adopted both strategies, brood reduction and brood survival. Brood reduction is very low in this population (considering nests at which at least one chick fledged, nestling survival is 0.96, Liljesthröm et al. 2012), but additional studies are needed to corroborate these hypotheses, such as determining if the survival of last-hatched nestlings is affected by egg size.

On the other hand, order of laying did not have an effect on yolk area. This result is similar to that of Ojanen (1983), who reported an increase in egg size but not in yolk size with laying order, but differs from that of Ardia et al. (2006a), who reported an increase in both egg size and yolk size with laying order. The mass of the yolk (and the proportion of lipids and proteins it contains) may vary with egg mass (Arnold and Green 2007), and the yolk mass and egg mass may be proportional in precocial birds but unrelated in altricial birds (Ricklefs 1984, Williams 1994, Hill 1995, Wiebe 2006). Therefore, even though the order of laying had an effect on egg size this does not necessarily imply that it has an effect on yolk area as well. Intraspecific variation in the mass of many birds’ eggs is attributable primarily to variation in albumen mass (Hill 1995, Finkler et al. 1998). Provided that yolk area correlates with yolk mass, the effect of the order of laying on egg mass but not on yolk area suggests that in the Chilean Swallow changes in egg mass with the order of laying may be attributable mainly to changes in albumen mass.

Our finding that the female’s body condition was unrelated to variation in clutch size or egg size, which is contrary to other studies (Styrsky et al. 2002, Hargitai 2005, Ardia et al. 2006), may have been influenced by the time at which we evaluated females’ condition. Our measure was taken during the first days of the chick-rearing period, and it may not be related closely to the female’s condition during egg laying, as females’ masses can vary considerably through the breeding season (pers. obs.). In some species, the female’s mass decreases over the breeding season (Styrsky et al. 2002), and the mass of aerial insectivores such as swallows can change significantly in a short period. Unfortunately, trapping females before or during egg laying for a better estimate of their body condition at egg laying increases nest abandonment drastically and so was not possible.

Finally, are there fitness consequences related to egg size? We did not find an effect of either egg mass or egg area on the probability of an egg hatching. The mass–area residual, however, predicted the probability of egg hatching, suggesting that eggs that were heavy for their size were most likely to hatch, while eggs light for their size were least likely to hatch. This result parallels those of studies that reported higher hatching success of larger eggs (O’Connor 1979, Perrins 1996). Also, variation in egg size can have other important long-term consequences for off spring survival (Williams 1994, Christians 2002), and further studies are necessary to determine, for example, if in the Chilean Swallow larger eggs or eggs heavier for their size also lead to larger hatchlings or faster nestling growth.

There was some variation by year and site in egg mass and egg size. Resource availability can fluctuate by year and by site, and females may acquire or allocate resources differently. Unfortunately, because we did not measure food availability at our sites this question still remains unanswered. Further work is needed to examine whether other variables such as food availability (Ardia et al. 2006a) or fluctuating ambient temperature at the time of laying (Magrath 1992, Hargitai et al. 2005) may

play a role in generating intra- and interclutch variation in the sizes of eggs and clutches of the Chilean Swallow.

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LITERATURE CITED

- ALLEN, P. E. 1996. Breeding biology and natural history of the Bahama Swallow. *Wilson Bulletin* 108:380–495.
- ARDIA, D. R. 2005. Super size me: an experimental test for the factors affecting lipid content and the ability of residual body mass to predict lipid stores in nestling European Starlings. *Functional Ecology* 19:414–420.
- ARDIA, D. R., M. F. WASSON, AND D. W. WINKLER. 2006a. Individual quality and food availability determine yolk and egg mass and egg composition in Tree Swallows *Tachycineta bicolor*. *Journal of Avian Biology* 37:252–259.
- ARDIA, D. R., C. B. COOPER, AND A. A. DHONDT. 2006b. Warm temperatures lead to early onset of incubation, shorter incubation periods and greater hatching asynchrony in Tree Swallows *Tachycineta bicolor* at the extremes of their range. *Journal of Avian Biology* 37:137–142.
- ARNOLD, T. W., AND A. J. GREEN. 2007. On the allometric relationship between size and composition of avian eggs: a reassessment. *Condor* 109:705–714.
- BERNARDO, J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *American Zoologist* 36:216–236.
- BIRKHEAD, T. R., AND D. N. NETTLESHIP. 1982. The adaptive significance of egg size and laying date in Thick-billed Murres *Uria lomvia*. *Ecology* 63:300–306.
- BYERLY, T. C. 1932. Growth of the chick embryo in relation to its food supply. *Journal of Experimental Biology* 9:15–44.
- CHRISTIANS, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews* 77:1–26.
- CLARK, A. B., AND D. S. WILSON. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Quarterly Review of Biology* 56:253–277.
- CRAWLEY, M. J. 2007. *The R book*. Wiley, West Sussex, England.
- DAAN, S., AND J. N. TINBERGEN. 1997. Adaptation of life histories, p. 311–333. *In* J. R. Krebs and N. B. Davies [EDS.], *Behavioral ecology: an evolutionary approach*. Blackwell Science, Oxford, England.
- DRENT, R. H., AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252.
- DYRCZ, A. 1984. Breeding biology of the Mangrove Swallow *Tachycineta albilinea* and the Grey-breasted Martin *Progne chalybea* at Barro Colorado Island, Panama. *Ibis* 126:59–66.
- FLINKLER, 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* 168:17–24.
- GARAMSZEGI, L. Z., J. TÖRÖK, L. TÓTH, AND G. MICHL. 2004. Effect of timing and female quality on clutch size in the Collared Flycatcher *Ficedula albicollis*. *Bird Study* 51:270–277.
- HARGITAL, R., J. TÖRÖK, L. TÓTH, G. HEGYI, B. ROSIVALL, B. SZIGETI, AND E. SZÖLLOSI. 2005. Effects of environmental conditions and parental quality on inter- and intraclutch egg-size variation in the Collared Flycatcher (*Ficedula albicollis*). *Auk* 122:509–522.
- HILL, W. L. 1995. Intraspecific variation in egg composition. *Wilson Bulletin* 107:382–387.
- HOWE, H. F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle. *Ecology* 57:1195–1207.
- LACK, D. 1947. The significance of clutch size. *Ibis* 89:302–352.
- LACK, D. 1954. *The natural regulation of animal numbers*. Clarendon, Oxford, England.
- LACK, D. 1966. *Population studies of birds*. Clarendon, Oxford, England.
- LILJESTRÖM, M. 2011. Breeding biology of the Chilean Swallow (*Tachycineta meyeni*) in Ushuaia, Argentina. Ph.D. dissertation, University of Buenos Aires, Argentina.
- LILJESTRÖM, M., A. SCHIAVINI, AND J. C. REBORDA. 2012. Time of breeding and female condition affect chick-growth in the Chilean Swallow (*Tachycineta meyeni*). *Emu*, in press.
- MAGRATH, R. D. 1992. Seasonal changes in egg-mass within and among clutches of birds: general explanations and a field study of the blackbird *Turdus merula*. *Ibis* 134:171–179.
- MASSONI, V., F. BULIT, AND J. C. REBORDA. 2006. Breeding biology of the White-rumped Swallow *Tachycineta leucorrhoa* in Buenos Aires Province, Argentina. *Ibis* 149:10–17.
- MOSS, R., AND A. WATSON. 1982. Heritability of egg size, hatch weight, body weight, and viability in Red Grouse (*Lagopus lagopus scoticus*). *Auk* 99:683–686.
- MOUSSEAU, T. A., AND C. W. FOX. 1998. The adaptive significance of maternal effects. *Trends in Ecology and Evolution* 13:403–407.
- O'CONNOR, J. 1979. Egg weights and brood reduction in the European Swift (*Apus apus*). *Condor* 81:133–145.
- OJANEN, M. 1983. Effects of laying sequence and ambient temperature on the composition of eggs of the Great Tit and the Pied Flycatcher. *Annales Zoologici Fennici* 20:65–71.
- PARSONS, J. 1976. Factors determining the number and size of eggs laid by the Herring Gull. *Condor* 78:481–492.
- PERRINS, C. M. 1970. The timing of birds' breeding seasons. *Ibis* 112:242–255.
- PERRINS, C. M. 1996. Eggs, egg formation and the timing of breeding. *Ibis* 138:2–15.
- PILZ, K. M., H. G. SMITH, M. I. SANDELL, AND H. SCHWABL. 2003. Interfemale variation in egg yolk androgen allocation in the European Starling: do high-quality females invest more? *Animal Behaviour* 65:841–850.
- PINHEIRO, J. C., AND D. M. BATES. 2000. *Mixed-effects models in S and S-Plus*. Springer, Berlin.
- PRICE, T., M. KIRKPATRICK, AND S. J. ARNOLD. 1988. Directional selection and the evolution of breeding date in birds. *Science* 240:798–799.
- RICKLEFS, R. E. 1984. Variation in the size and composition of eggs of the European Starling. *Condor* 86:1–6.
- ROBINSON, T. J., L. SIEFFERMAN, AND T. S. RISCH. 2010. Seasonal tradeoffs in reproductive investment in a multibrooded passerine. *Condor* 112:390–398.

- ROYLE, N. J., P. F. SURAI, R. J. MCCARTNEY, AND B. K. SPEAKE. 1999. Parental investment and egg yolk lipid composition in gulls. *Functional Ecology* 13:298–306.
- SLAGSVOLD, T., 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.
- STUTCHBURY, B. J., AND R. J. ROBERTSON. 1988. Within-season and age-related patterns of reproductive performance in female Tree Swallows (*Tachycineta bicolor*). *Canadian Journal of Zoology* 66:827–834.
- STYRSKY, J. D., R. C. DOBBS, AND C. F. THOMPSON. 2002. Sources of egg-size variation on House Wrens (*Troglodytes aedon*): ontogenetic and environmental components. *Auk* 119:800–807.
- TOWNSEND, J. M., E. GARRIDO, AND D. A. MEJIA. 2008. Nests and nesting behavior of Golden Swallow (*Tachycineta euchrysea*) in abandoned bauxite mines in the Dominican Republic. *Wilson Journal of Ornithology* 120:867–871.
- VERHULST, S., J. H. VAN BALEN, AND J. M. TINBERGEN. 1995. Seasonal decline in reproductive success of the Great Tit: variation in time or quality? *Ecology* 76: 2392–2403.
- WIEBE, K. L. 2006. Egg composition in Northern Flickers. *Condor* 108:977–980.
- WILLIAMS, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews* 68:35–59.
- WILLIAMS, T. D. 2005. Mechanisms underlying the costs of egg production. *BioScience* 55:39–48.
- WILLIAMS, T. D. 2011. Experimental manipulation of female reproduction reveals an intraspecific egg size-clutch size trade-off. *Proceedings of the Royal Society B* 268:423–428.
- WINKLER, D. W., AND P. E. ALLEN. 1996. The seasonal decline in Tree Swallow clutch size: physiological constraint or strategic adjustment? *Ecology* 77:922–932.
- YOUNG, B. E. 1994. Geographic and seasonal patterns of clutch-size variation in House Wrens. *Auk* 111:545–555.