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YOLK MASS VARIATION IN WHITE-RUMPED SWALLOWS (*TACHYCINETA LEUCORRHOA*)

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ABSTRACT.—Egg mass production is costly, but hatching from heavier eggs could be beneficial for the nestling's phenotype and fitness. Egg mass could be influenced by proximate causes, like food abundance, female condition, environmental conditions, and/or by ultimate causes, such as females depositing resources differentially within a clutch to increase the biological fitness of some eggs. Yolk mass, although poorly studied, is the source of nutrients for the embryo, so its mass should be more influential for the nestlings than total egg mass. We used a technique that allowed us to measure yolk size without destroying the eggs. We studied yolk mass in 212 eggs of White-rumped Swallows (*Tachycineta leucorrhoa*) and found that yolk mass was influenced by laying order, with last laid eggs having heavier yolks than first laid eggs, and the pattern was consistent with egg mass variation. Food abundance also affected yolk mass: when insect availability was high the yolks were heavier. We conclude that embryos in the last laid eggs have more resources from which to develop, and excluding food abundance, neither environmental conditions nor female's condition affected yolk mass. We encourage other researchers to study yolk mass given that multiple variables affected total egg mass. *Received 20 May 2013. Accepted 6 September 2013.*

Key words: egg mass, food abundance, proximate causes, *Tachycineta leucorrhoa*, yolk mass.

Egg production is expensive (Nager et al. 2000), because resources allocated to eggs are costly to the laying females (Perrins 1996) and thus, egg and clutch size are expected to be constrained (Lack 1947, Slagsvold and Lifjeld 1989, Zanette et al. 2006). Egg size is positively correlated with hatching success (Croxall et al. 1992, Perrins 1996), and many studies have determined the importance of egg size on the nestling stage (Williams 1994). In a recent review of egg size and offspring quality, Krist (2011) concluded that egg size was positively related to nearly all studied offspring traits across all stages of the life cycle. Therefore, egg size is considered an important life-history trait through which females could manipulate the phenotype of the offspring (Mousseau and Fox 1998, Gil 2003). Some studies suggest females could adaptively allocate nutrients differently to the eggs of the same clutch to produce within clutch egg-size differences (Howe 1976, Styrsky et al. 2002, Hargitai et al. 2005). Egg hormones are also responsible for within clutch egg variation as females can deposit them differentially and affect offspring phenotype (West-Eberhard 2003). It has been shown that laying order strongly influences androgen concentration in several bird species (Gil 2003), while in others, like Tree Swallows (*Tachycineta bicolor*), there is no apparent trend (Whittingham and Schwabl 2002). Other authors suggest egg size variation might be determined by proximate causes. The mechanisms invoked are related to female condition (Potti 1993, Smith et al. 1993, Ardia et al. 2006), laying date (Tsuboi and Ashizawa 2011), ambient temperature (Galbraith 1988), and the food abundance experienced by females during oogenesis (Ramsay and Houston 1997, Ardia et al. 2006, Whittingham et al. 2007).

Yolks are the principal source of nutrients for the developing embryo (Burley and Vadhera 1989, Deeming 2002), thus making it advisable to study not only total egg size but also egg content as a measure of parental investment (Astheimer and Grau 1990). Yolks are formed within the period of rapid yolk deposition (RYD), which occurs 3–10 days prior to egg laying (King 1973). In Zebra Finches (*Taeniopygia guttata*) this period lasts 3–4 days (Williams 2000), while in Tree Swallows yolks are formed 5–6 days prior to egg laying (Ardia et al. 2006). The albumin, containing 89% water and 12% proteins (Deeming 2002) is the major source of water and minerals for developing embryos; and the yolk, containing 48% water, 33% lipids, and 17% proteins is the primary source of energy and proteins (Burley and Vadhera 1989, Deeming

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2002). Egg yolks also contain androgenic hormones and steroids (Schwabl 1993), carotenoids (Bortolotti et al. 2003) and immunoglobulins, which provide the nestling's first immune response (Graczyk et al. 1994) and affect offspring survival and performance (Pilz et al. 2004).

Egg size is traditionally taken as a measure of maternal investment, but variations in egg mass do not necessarily imply variations in yolk mass, as a high percentage of the egg mass variation could result from differences in the amount of albumin and water content (Williams 1994). Yolk quality, indirectly measured as the yolk size, could have a determinant influence on a hatchling's weight or performance. Despite the physiological importance of this component, few studies have investigated the potential factors that determine the yolk size or mass, mainly because measuring it requires the destruction of the egg. However, digital candling allows measuring the yolk size in a large number of eggs without disturbing the developing embryos. Yolk mass has been studied using this tool in Tree Swallows in North America (Ardia et al. 2006), providing an opportunity to compare this trait with a South American congener and look for variations with latitude.

The objectives of this study were to analyze yolk mass variation within clutches of White-rumped Swallows (*Tachycineta leucorrhoa*), to determine potential factors related to this variation, and to establish if yolk mass can be directly inferred from egg mass. We predict that females in better condition, that breed early in the season, that experienced greater food abundance, and/or higher ambient temperatures during oogenesis, produce heavier yolks.

METHODS

White-rumped Swallows are insectivorous passerines that catch their prey in flight. The breeding season lasts 4 months; females lay 1 egg/day until they complete a median clutch of 5 eggs (range: 3–6 eggs), incubate the eggs for approximately 15 days, starting after the penultimate egg was laid, and the eggs hatch with a median asynchrony of 2 days (range: 1–4 days; Massoni et al. 2007). We conducted this study in a flat farming landscape in Chascomús, Buenos Aires Province, Argentina (35° 34′ S, 58° 01′ W) during the 2007 breeding season.

We checked nestboxes daily to determine clutch initiation date. On the laying day, we marked the eggs with sequential numbers in water-proof ink at the lesser pole to indicate the laying order, weighed the eggs to the nearest 0.005 g with an electronic balance and took a digital photograph of the eggs with a CANON Powershot A570 IS using both macro and no flash functions pointing into a dark box used to trans-illuminate the eggs. The black acrylic box measured 15 cm × 15 cm on its base and 20 cm of height, and was divided into two compartments: the upper one where eggs were laid on their side on a special support with the poles forming a line parallel to the base of the box, and the lower compartment where one white LED was connected to a battery (AA). The two parts of the box were separated by an opening through which the light of the LED passed to trans-illuminate the eggs. The design of the box was taken from D. R. Ardia (pers. comm.). When the camera was positioned in the opening in the box that was sized to match the diameter of its lens, the only source of light was that of the LED.

Using Image Pro-Plus 4.5 software we estimated yolk area. First, we transformed the yolk area from pixels to mm^2 by comparing the egg width measured in the field with a digital caliper (± 0.01 mm) to the width measured on the screen (in pixels) using a subset of 15 eggs. Secondly, we transformed the yolk area (mm^2) into a mass estimation (g) using a subset of 18 collected eggs. After getting digital images of these 18 freshly laid eggs, we froze them (-20 °C), weighed the frozen yolks in a digital balance (± 0.0001 g) and regressed the yolk mass on the yolk area ($r^2 = 0.3$; $P < 0.001$), obtaining the following equation to estimate yolk mass for the undisturbed, photographed eggs:

$$Yolk\ mass(g) = -0.12 + 0.0059 * yolk\ area\ \left(mm^2\right)$$

Females were trapped on the ninth day of the incubation period as described in Massoni et al. (2007). After sex confirmation (determined by the presence of an incubation patch), we measured head + bill length using a digital caliper (± 0.01 mm) and weighed all captured individuals using a spring scale (± 0.2 g). We estimated the females' body condition index as the residuals of the linear regression of their body mass on the head + bill length. To estimate food abundance, we daily collected samples of flying insects using two passive traps that intercepted the insects in flight, and used the total number of insects caught by both traps on each day as an estimation of the amount of food available for the swallows (Barrionuevo et al. 2010). The traps consisted of 38 cm × 38 cm transparent acrylic squares resting on a plastic tray containing detergent and water, which served to retain the insects that collided with the trap. The traps caught many insects belonging to the same taxa and sizes found in the adult swallows' beaks when the birds were captured inside nest boxes during nestling feeding (Barrionuevo 2009). Traps were placed at the height of nest boxes because White-rumped Swallows spend significant amounts of time foraging at low altitude, capturing insects flying just over the pastures (VM, pers. obs.). The ambient temperature was recorded by the National Weather Center (Dolores Station, 89 km from our study site).

Statistical Analysis.—We analyzed yolk mass variations in 212 eggs, belonging to 47 nests with a linear mixed model with a Gaussian family distribution and an identity-link function. We only used first clutches and did not evaluate replacement second clutches because of the small sample size. We used nest identity as a random factor to account for the lack of independence of the eggs belonging to the same nest and clutch; the significance of random effects was tested with a likelihood ratio test. We considered as fixed predictors, the body condition of the female, clutch size, the laying date, and the laying order. As we were also interested in the potential effects of environmental conditions (temperature and food) on the yolk mass during egg formation, we added to the model as fixed variables the average of the daily mean temperature from the 5 days prior to the laying day of each egg, and the average of the daily total amount of insects collected 5 days prior to the laying day. We also included the following interactions: (1) laying order and insect availability, (2) female body condition and insect availability, (3) temperature and insect availability, and (4) laying date and female body condition. We employed a background selection procedure removing the terms one by one in decreasing order of complexity (interactions first) and *P*-value (Crawley 2007). After identifying the significant factors, we compared the model with and without the corresponding factor using likelihood ratio tests to estimate a unique *P*-value including all the levels of the factor. In the case of fixed variables, we conducted the same procedure to report concordant *P*-values. We used the ''nlme'' from the R software package, version 2.12.1 (R Development Core Team 2010) and report values as means ± SE, considering differences significant at $P < 0.05$.

RESULTS

Yolk mass was correlated positively and significantly with egg mass (Spearman rank order, $r^2 = 0.25$, $P < 0.001$, $n = 231$) and the yolk represented 30% of total egg mass ($n = 231$ eggs). Yolk mass ranged from 0.28–0.99 g (mean = 0.65 g ± 0.01 g), and egg mass ranged from 1.64–2.94 g (mean = 2.15 g ± 0.016 g). Insect abundance did not increase or decrease significantly across the broad time scale encompassing the laying period (mid-Sep to mid-Dec, $P = 0.95$), but we did detect important short-term oscillations (Fig. 1).

Random effects resulted in significant patterns ($\chi^2 = 56.87$, $P < 0.001$). Females that had access to greater food abundance during the egg formation period produced heavier yolks (L-ratio tests, $P < 0.001$), and laying order also affected yolk mass (L-ratio tests, $P < 0.001$). Within broods, we found no significant differences in yolk mass among the first three eggs (*t*-test; first vs. second and first vs. third: see Table 1; second vs. third: $t = -1.08$, $P = 0.28$) but their yolks were lighter than those from the last two eggs (contrast between the third and fourth yolk: $P < 0.002$), fourth and fifth yolks were also similar (*t*-test; fourth vs. fifth: $t = -0.11$, $P = 0.91$) (Fig. 2).

Neither of the other variables nor the interactions analyzed presented significant effects (L-ratio tests): female condition and laying date ($F = 0.67$, $P = 0.41$), female condition and insect availability ($F = 1.10$, $P = 0.29$), laying order and insect availability ($F = 8.95$, $P = 0.11$, Fig. 3), temperature and insect availability ($F = 0.48$, $P = 0.49$), clutch size ($F = 3.06$, $P = 0.38$), female body condition ($F = 2.22$, $P = 0.14$), temperature ($F = 0.089$, $P = 0.77$) and laying date ($F = 1.06$, $P = 0.30$).

DISCUSSION

The ratio between yolk and egg mass in White-rumped Swallows was slightly larger than that observed in Tree Swallows (0.30 vs. 0.26, respectively, Ardia et al. 2006); the yolk mass range was broader (0.28–0.99 g vs. 0.34–0.59 g, respectively) and the average mass heavier (0.65 g

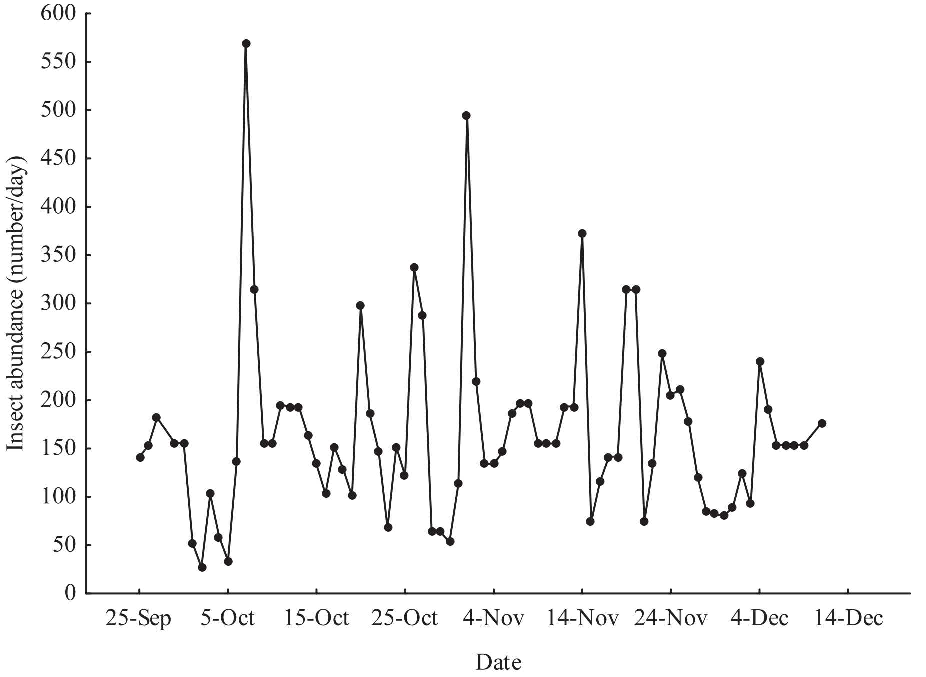

FIG. 1. Insect abundance (number of insects per day) during the laying season.

± 0.012 g vs. 0.47 g ± 0.001 g, respectively) in the South American species than in the northern one (this work, Ardia et al. 2006). Geographically, relatively larger eggs are generally found in the tropics and southern hemisphere relative to those in northern temperate zones (Martin et al. 2006), but the yolk to egg mass ratio comparison awaits further analysis across this genus.

The relationship between yolk mass and egg mass was statistically significant but weak. Moreover, in a previous study, we found significant variables affecting egg mass that are different from the variables affecting yolk mass (female body condition and ambient temperature did affect egg mass; Barrionuevo et al. 2010). These results indicate the relevance of considering egg and yolk mass to describe females' investment in egg production, as diverse ecological and/or individual factors may affect the deposition of different egg components.

TABLE 1. Results of the linear mixed model on yolk mass including insect availability, clutch size, laying order, laying date, temperature, female body condition, clutch size, and some double interactions. Only significant results are shown (n = 212 eggs, 47 first clutches).

	Estimate	t-value	P-value
Intercept	0.36	4.82	<0.001
Insect availability	0.0014	3.32	0.001
Laying order 2	−0.0027	−0.11	0.92
3	0.044	1.71	0.089
4	0.13	4.97	<0.001
5	0.13	4.57	<0.001

Insect availability during egg production in swallows is expected to be an important factor influencing egg mass (Nilsson and Svensson 1993) because they are ''income'' breeders, using the current food intake to produce the eggs (Winkler and Allen 1996, Nooker et al. 2005). We found that insect availability during the 5-day period before egg laying affected yolk mass, when food was scant yolks were lighter, irrespective of female body condition or laying order. This suggests that the resources acquired during yolk formation were directly invested into the yolk. Our results are in accordance with those of Ardia et al. (2006) who found a positive effect of insect availability in the days prior to the laying day in Tree Swallows' yolks, demonstrating its importance to the genus despite differences in latitude. Insect availability could affect egg size by constraining the females (Perrins 1970, Slagsvold

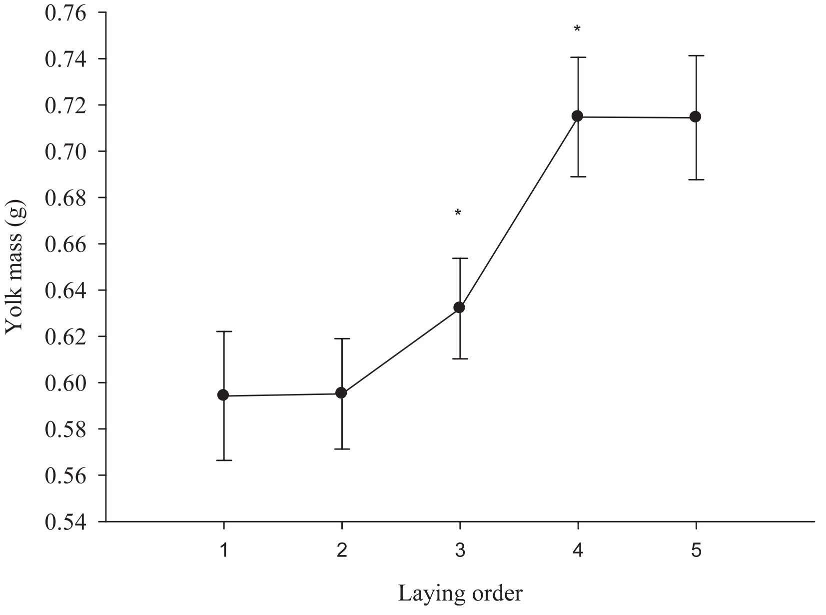

FIG. 2. Yolk mass according to laying order, error bars are ±SE and significant differences are shown with asterisks.

and Lifjeld 1989, Lifjeld et al. 2005) or because females use food availability as cues to establish their investment into eggs (Lack 1954, Arnold 1994, Hau et al. 2000).

We also found that yolk mass increased with laying order, contrary to Liljesthröm et al. (2012) who found no relation of yolk mass and laying order in the congeneric Chilean Swallow (*Tachycineta*

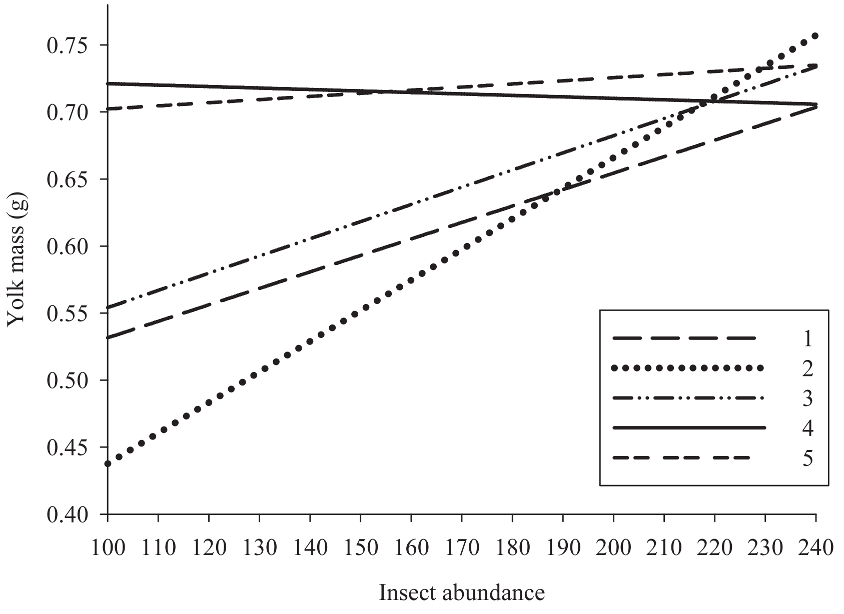

FIG. 3. Average insect abundance during the 5 days prior to the laying day vs. yolk mass for each egg of the clutches (1 = first laid egg, $r^2 = 0.042$, $F = 1.64$, $P = 0.20$; 2 = second laid egg, $r^2 = 0.044$, $F = 4.32$, $P = 0.84$; 3 = third laid egg, $r^2 = 0.055$, $F = 2.12$, $P = 0.15$; 4 = fourth laid egg, $r^2 = 0.0001$, $F = 0.006$, $P = 0.94$; and 5 = fifth laid egg, $r^2 = 0.001$, $F = 0.044$, $P = 0.84$).

leucopyga). In most avian orders, eggs hatch asynchronously because incubation begins before the clutch is complete (Stoleson and Beissinger 1995, Stenning 1996), resulting in a size hierarchy within the brood (Howe 1976, Aparicio 1999, Viñuela 2000). The last hatched eggs of White-rumped Swallows showed a median hatching asynchrony of 2 days compared to first hatched eggs (Massoni et al. 2007). Thus, if egg size is related with the size of the hatchlings, variations in egg size relative to the laying order may influence the degree of sibling competition. In Tree Swallows, Whittingham et al. (2007) found an effect of egg mass on nestling's quality, and Rosivall et al. (2005) found, in the Collared Flycatcher (*Ficedula albicollis*), that despite the last offspring having a lower body mass growth rate, the larger the last egg was, the smaller the growth rate lag of the offspring was. Howe (1976) suggested that an increase in egg size with laying order is an adaptation to counteract the effect of hatching asynchrony; the last eggs to hatch are bigger and compete better with already grown siblings. However, variation in size associated with laying order could be a consequence of proximate constraints, like daily changes in food abundance (Perrins 1970) or in temperatures (Ojanen et al. 1981, Järvinen and Ylimaunu 1986, Magrath 1992). None of these variables interacting with laying order were significant in our study. However, when plotting yolk mass and insect availability for each egg, a pattern was apparent, with differences between the first three eggs and the last two eggs. We believe these results did not reach statistical significance owing to sample size and further research is needed to ascertain their robustness.

The pattern observed in this study has been found in the Tree Swallow (Ardia et al. 2006), suggesting it may entail fitness benefits across the genus. As the yolk is the principal reservoir of nutrients (Deeming 2002) and where hormones and precursors of immune response are laid (Graczyk et al. 1994), the last chicks to hatch could have relatively more resources during initial development and would benefit from a better immune response and physiological quality.

Female condition was not related to yolk mass. Female condition is the integrated result of environmental conditions during migration and arrival at the breeding site, and during the pre-laying period; while yolk formation lasts only 5 to 6 days in the similarly sized Tree Swallow (Ardia et al. 2006). Female body condition was positively related to total egg mass (Barrionuevo et al. 2010); therefore total egg mass, which includes egg shell and albumin in addition to the yolk, is probably the product of energetically demanding processes lasting longer than the yolk formation process. Alternatively, the lack of an effect of female condition on yolk mass could be a consequence of delayed capture, since we measured female body condition 4 days after clutch completion. We believe that, though slightly imprecise because of the inclusion of days in which females incurred incubation costs, the index of their body condition still reflected variation among the females. As we found an effect of female body condition on egg mass on the same data set (Barrionuevo et al. 2010), we reject this alternative.

In a variety of species, ambient temperature has been shown to affect the thermoregulatory capacity of females (Ojanen 1983). This relationship between the ambient temperature and the energy expenditure assigned into thermoregulation could limit the energy females are able to invest into yolk or egg production. However, we did not find any relationship between yolk size and ambient temperature. During the 2007 breeding season, temperatures at Chascomús were not low enough to compromise the thermoregulatory ability of females, averaging 18 °C from September 2007 to January 2008. Finally, temperature could have an indirect effect on yolk mass through its influence on the amount or activity of flying insects, which are critical for insectivorous birds (Taylor 1963, Eeva et al. 2000). Nonetheless, the interaction between temperature and insect availability did not affect yolk mass in White-rumped Swallows.

We encourage using this non-destructive technique in studies of egg investment because the yolk is the major source of nutrients for the embryo and yolk quality could be more influential on hatchling condition than total egg size. We conclude that yolk mass was related to food abundance and varied with the laying order following a pattern compatible with the brood survival hypothesis, which proposes that females invest more in last-laid eggs to mitigate the disadvantage of these last-hatched chicks, when competing for food with the earlier-hatched chicks (Slagsvold et al. 1984, Budden and Beissinger 2005).

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