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Individual quality and food availability determine yolk and egg mass and egg composition in tree swallows *Tachycineta bicolor*

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Variation in egg size and composition can have important consequences for the quality of offspring. We investigated the factors influencing the yolk mass and egg mass of tree swallows breeding in Ithaca, NY. Using a nondestructive technique to estimate yolk mass via standardized digital-candler photographs, we compared yolk size and egg size of tree swallows *Tachycineta bicolor* in response to variation in food availability and individual quality. Insect availability one to three days prior to laying, but not four to six days, predicted yolk mass, while insect availability two to three days prior to laying predicted total egg mass. This suggests that, while eggs are formed over longer periods, food availability closer to time of laying has the greatest influence on egg size. These results were supported by collected eggs, as yolk rings revealed that tree swallow eggs are formed over 5–6 days. There was an influence of female quality as well, with early laying birds, independent of food availability, laying larger eggs. Eggs laid later in the laying sequence had larger yolks and greater egg mass. Overall, variation in egg quality appears to be due to a combination of environmental conditions, reflected in food resources, individual quality, and allocation tradeoffs during the laying period.

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The decision to lay an egg is one of the most important decisions that a female bird makes during reproduction, as eggs contain all the materials needed for the development of an embryo (Burley and Vadehra 1989). Variation in the size and quality of eggs can have important long-term consequences for the survival of offspring (Williams 1994, Carey 1996). For example, larger eggs tend to have higher hatching success (Perrins 1996) and lead to larger hatchlings and faster nestling growth (Hipfner and Gaston 1999, Christians 2002). Experimental evidence suggests that even though egg size covaries with parental quality and age, egg size alone can have important effects on the quality of nestlings (Bolton 1991, Styrsky et al. 1999). However, given the possible selective benefits of larger eggs, the proximate factors influencing egg size are still ambiguous (Perrins 1996). Experimentally increasing food leads some species to increase egg size (Bolton et al. 1992, Ramsay and Houston 1997, but see Christians 2002), and anecdotal evidence suggests that higher quality territories lead to larger eggs (Potti 1993). These results suggest that food resources are critical to egg production, but few, if any, studies have investigated the timing of resource availability and its influence on egg production.

Egg formation begins with the rapid deposition of yolk, and thus investment strategies associated with egg quality must necessarily begin with consideration of yolk production. King (1973) suggested that yolk deposition occurred 3–10 days prior to egg-laying. Much of what we know about the period of rapid yolk deposition (RYD) comes from measures of diel yolk rings in the eggs of semi-precocial birds, where yolks form over periods of 6–16 days (Meijer et al. 1989, Astheimer and Grau 1990, Hatchwell and Pellatt 1990, Meathrel 1991, Ruiz et al. 2000, Durant et al. 2004). The timing of yolk deposition is still poorly understood in altricial birds, though experimental blocking of yolk precursor hormones suggests that zebra finch eggs are formed within three to four days of egglaying (Williams 2000).

In addition to the proximate role of food resources, it is also clear that parental quality, a suite of phenotypic and genetic factors that predispose certain individuals to be better suited to a given set of conditions, influences the quality of eggs (Reid and Boersma 1990, Risch and Rohwer 2000). Higher quality parents would be expected to lay not only larger eggs, but also provide better parental care. Experimental studies have found that decoupling the effects of parental quality and egg size often reveal an effect of both (Reid and Boersma 1990, Hipfner et al. 1997, Styrsky et al. 1999, Bize et al. 2002). It is likely that timing of breeding exerts a quality effect on egg size. Styrsky et al. (1999) found that young from later-laying female house wrens *Troglodytes aedon* are more strongly influenced by egg size than are young from earlier-laying individuals. In the present study, we examined how timing of breeding, a proxy for individual quality, as well as the trend of increasing fecundity between second-year and after second-year breeders, which exerts a fitness effect in tree swallows *Tachycineta bicolor* (Winkler and Allen 1996), affect the size and composition of eggs. We tested whether early-laying individuals laid eggs of higher quality, while controlling for age, as younger females tend to lay later in the season (Winkler and Allen 1996).

Tree swallows lay eggs based on current foraging intake and they are thus "income" breeders (Winkler and Allen 1996), sensu the classification of Drent and Daan (1980). In tree swallows, as in many bird species, there is strong selection for breeding early; accordingly, many individuals are producing eggs when resource availability is low. This low availability of resources for eggs combines with variation among individuals in their ability to gather scarce resources and should lead to significant interindividual variation in egg size and composition. By examining how food resources prior to egg laying influence egg size it should be possible to determine the critical period when food resources most strongly influence investment in eggs and thus better understand the effects of food and individual quality on egg composition.

We tested the hypothesis that food resources prior to egg laying exert a strong influence over egg size. We predicted that high food availability would lead to larger yolks and eggs and that yolk size is most sensitive to conditions two to three days prior to egg laying, given the lack of laying gaps in small passerine birds and the patterns of yolk rings in tree swallows, which suggested the greatest growth of yolk rings during this period. We tested our hypothesis with standardized digital photographs (calibrated through a subsample of collected eggs) to assess yolk mass. Previously, measuring yolk mass required destruction of eggs, and the yolks in a small number of eggs per study have been measured as a result. Digital candling allows us to measure yolk mass in a large number of eggs without disturbing a breeding attempt. We can thus test hypotheses regarding the influence of environmental conditions and individual variation at a scale previously unavailable.

Methods

General field methods

We studied tree swallows breeding in nestboxes near Ithaca, Tompkins County, New York, USA (centered on 42° 29′N, 76° 27′W) in 2000. Tree swallows have been breeding since 1985 at the Ithaca site, where we have conducted long-term life history studies (Winkler 1991, Winkler and Allen 1996, McCarty and Winkler 1999, Ardia et al. 2003). We checked nestboxes daily to determine clutch initiation date. Each freshly laid egg was weighed to the nearest 0.5 g by suspension in a plastic bag with a 5 g Pesola spring scale in a clear plastic tube that kept out wind. We also recorded length and width of each egg with digital calipers to the nearest 0.05 mm. Each egg was individually marked according to laying order. On those occasions where we were not able to determine exact laying order, we classified the egg as the intermediate value. For example, two eggs discovered after a first egg was marked were both allotted a laying order of 2.5.

Daily measures of insect availability at our study site were collected in a 12-m Rothamsted aerial suction sampler used to measure insect availability during daylight hours (for details see McCarty and Winkler 1999).

Estimation of yolk mass

After measuring each egg, we took a standardized digital photograph using a modified plastic box that illuminated the egg (The "Ovolux", Fig. 1). Each photographed egg was returned to the nest and allowed to develop normally. Yolk mass was estimated by a program written in NIH-IMAGE (National Institutes of Health, Bethesda, MD). The program determined the outline of each egg and the yolk on the screen and then measured the area encompassed by the yolk. By collecting a subset of eggs to measure actual yolk mass, we developed an equation to estimate yolk mass based on the area.

Yolk mass was calculated in collected eggs by weighing freshly laid eggs in the laboratory on a Mettler balance (to the nearest 0.001 g) and then freezing the

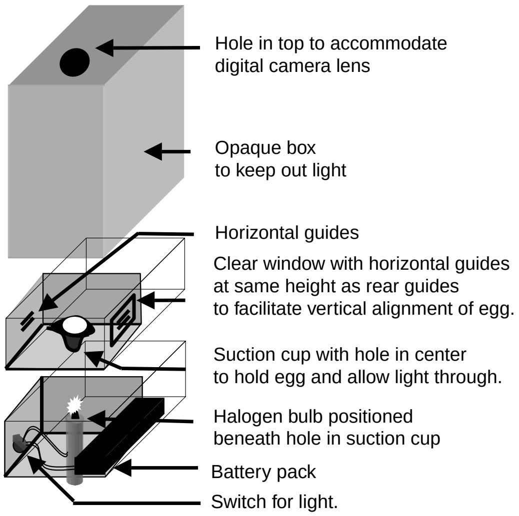

Fig. 1. Schematic of the "Ovolux" used in this study. Design has since been modified with a high-output LED rather than halogen to reduce heating.

eggs at $-20°C$ to remove albumen from yolk. The shells were then removed from the frozen egg, dried and reweighed. We carefully thawed the eggs to remove the albumen, then dried and weighed the still-frozen yolk before staining it for further analyses (see below). We regressed these direct yolk mass measurements on the areas for the yolk photographs of the same eggs when freshly collected, thus obtaining an estimation equation for yolk mass in the undisturbed, photographed eggs (yolk mass $=0.00037089 \times$estimated yolk volume$+0.125$, $R^2=0.85$, $N=17$).

Yolk ring deposition

For a subset of collected eggs, rather than dry the yolks to determine mass, we stained the light and dark rings of yolk to elucidate daily yolk deposition following the methods of Grau (1976). The cleaned and frozen yolks (see above) were fixed in 4% formalin for 18 hours. The yolks were then cut in half and dyed in 6% potassium dichromate for 18 hours. Dyed yolks were then placed directly on a scanner and scanned at high resolution so that images could be magnified and enhanced to facilitate identification of yolk rings.

Statistical analyses

We examined factors affecting estimated yolk mass and total egg mass with a mixed model ANOVA (PROC MIXED, Littell et al. 1996) with breeding site and nest as random effects. For each egg, we modeled yolk mass or total egg mass as a function of standardized (to a mean of 0) clutch initiation date, date of egg laying, laying sequence, female age, clutch size, and insect availability for 1–5 days prior to egg laying. For total egg mass, we also included estimated yolk mass in the analyses to control for the effects of variation in yolk mass. We ran models with all possible interaction and higher order (quadratic) terms, and we dropped from models all higher order effects and interactions, but not main effects, with P-values greater than 0.1.

Random effects were tested by subtracting the -2 Log Likelihood scores of a model containing all random effects from the -2 Log Likelihood score of the model minus the effect being tested (Littell et al. 1996). The difference in the -2 Log Likelihood scores between the full model and the model minus the variable being tested is distributed as a Chi-Square variable with one degree of freedom. In all cases, random effects were not significant, so we used linear regression to generate partial regression plots in order to illustrate the relationship between predictors and yolk or egg mass while controlling for other variables. The linear regression model predicting yolk mass included clutch initiation date, laying sequence, clutch size, female age (coded as a dummy variable of 0 or 1 for females in their first breeding year or older, respectively) and prey availability on each of the five days prior to egg laying, while the egg mass model included the same variables plus yolk mass.

To examine autocorrelation among insect availabilities over time, we ran a series of regression analyses starting with factors affecting insect availability one day prior to egg laying. In this model we included insect availability on days two to five and the maximum daily daytime temperature (recorded at a weather station on site) one to five days prior to egg laying. We then removed day one and modeled factors affecting day two (insects three to five days and temperatures two to five days prior) continuing our model simplification in sequence to insects five days prior, which were only influenced by temperatures five days prior to egg-laying.

Results

Yolk rings

Of 13 yolks examined, all showed that female tree swallows lay down between 3.5–4.5 countable ring pairs, suggesting that, including the 24 hrs required to add albumen and shell (King 1973), tree swallow eggs are formed over 5 to 6 days.

Factors affecting egg composition

We estimated yolk and measured egg mass on 585 tree swallow eggs. Estimated yolk mass ranged from 0.34 to 0.59 g (mean yolk mass 0.47 g$\pm$0.001 SE), while egg mass ranged from 1.23g to 2.30g (mean 1.84 g$\pm$0.006).

There were no random effects of research site or nest on yolk mass or egg mass (all $\chi^2 < 1.2$, Ps > 0.26). Insect availability one to three days prior to egg laying predicted estimated yolk mass while insect availability more than three days prior to egg laying did not (Table 1, Fig. 2). However, when controlling for yolk mass, only insect availability two and three days prior to egg laying predicted total egg mass, not one day prior (Table 1). Both yolk mass ($\beta = 0.0037$, $P < 0.001$, Fig. 3) and egg mass ($\beta = 0.012$, $P < 0.004$) increased with laying order.

With all other factors controlled for, earlier-laying female tree swallows laid eggs with significantly larger yolk mass than did later-laying females (Table 1, Fig. 3), but date of laying had no detectable directional effect on egg mass (Table 1). Conversely, older females laid larger eggs than did younger females, but age had no effect on yolk size (Fig. 4). Estimated yolk mass predicted total egg mass (Table 1, Fig. 5) but explained relatively little of the variation. At our study site, food availability increases as the breeding season progresses (Bowlin and Winkler 2004, Ardia 2005).

Even though our statistical analyses used Type III Sums of Squares to estimate significance, we examined temporal autocorrelation among insect availabilities (Table 2). Insect availability one day prior to egg laying was positively correlated with insect availability two and three days prior to laying but not four days. Interestingly, insect availability one and five days prior to egg-laying were negatively correlated, which suggests that environmental conditions fluctuate over periods greater than four days. This was confirmed by the lack of correlation between insect availability three and four days prior, which helps explain why the model predicting yolk mass found only insect availability one to three days before egg-laying influences egg size.

Table 1. Factors affecting the yolk mass and total egg mass of tree swallows eggs laid in Ithaca, NY. "Prey availability lay date –x" is insect availability on x days prior to egg laying for each individual egg. Numerator degrees of freedom for all tests = 1.

Effect	Den df	F value	P value
Estimated yolk mass			
Prey availability lay date -1	466	5.87	0.02
Prey availability lay date -2	564	15.04	0.0002
Prey availability lay date -3	499	5.03	0.02
Prey availability lay date -4	547	0.05	0.82
Prey availability lay date -5	550	1.06	0.35
Clutch Initiation Date	19.2	22.62	0.0001
Date of egg laying	533	0.29	0.54
Female Age	108	2.09	0.14
Laying Order	534	8.73	0.003
Clutch Size	133	1.90	0.16
Total egg mass			
Prey availability lay date -1	495	0.24	0.62
Prey availability lay date -2	500	5.87	0.01
Prey availability lay date -3	505	4.54	0.02
Prey availability lay date -4	495	0.56	0.45
Prey availability lay date -5	484	1.58	0.20
Yolk mass	464	4.75	0.02
Clutch Initiation Date	139	0.11	0.73
Date of egg laying	533	0.12	0.72
Female Age	125	27.60	0.0001
Laying Order	522	11.03	0.001
Clutch Size	133	1.63	0.18

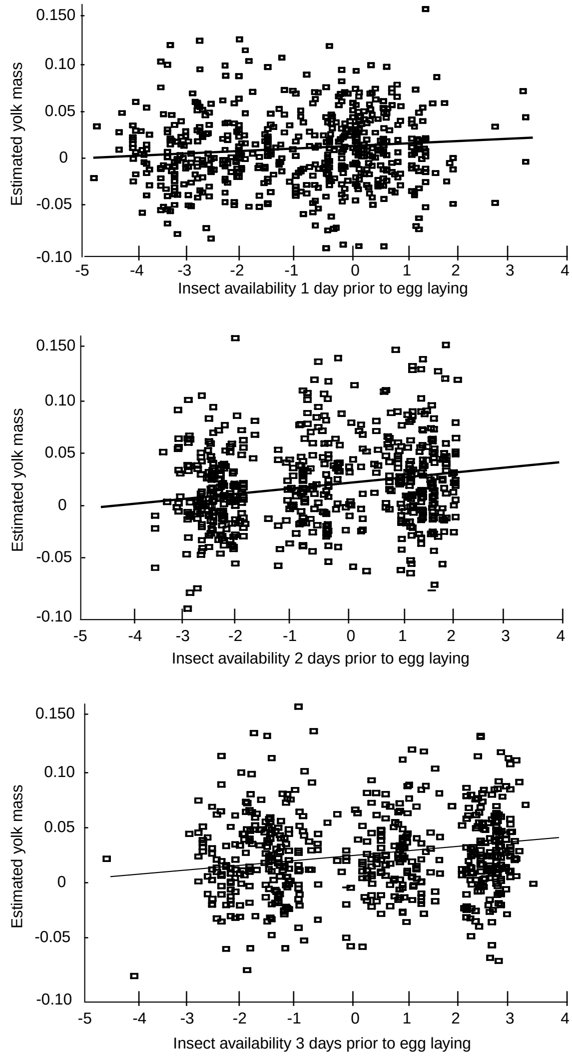

Fig. 2. Partial regression plots of the relationship between insect availability prior to egg laying and estimated yolk mass of tree swallow eggs. Values on axes are the residuals from a regression of model for estimated yolk mass on all other variables in the model minus the variable on the other axis.

Discussion

This study used a novel noninvasive method to quantify yolk size in tree swallows, thus allowing for a large enough sample size to examine in detail factors affecting variation in yolk size and egg composition. Yolk mass in tree swallows varies according to food availability, timing of breeding and laying sequence. Our results are consistent with work done on captive zebra finches that demonstrates multiple predictors and considerable

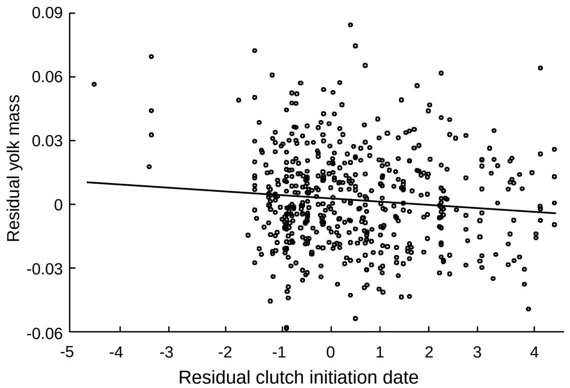

Fig. 3. Partial regression plot of the relationship between estimated yolk mass and total egg mass in tree swallows. Values are the residuals from a regression of estimated yolk mass on all other variables in the model minus clutch initiation date.

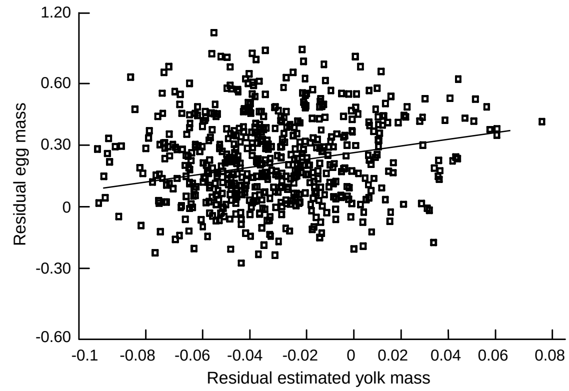

Fig. 5. Partial regression plot of the relationship between estimated yolk mass and total egg mass in tree swallows. Values are the residuals from a regression of egg mass on all other variables in the model minus yolk mass.

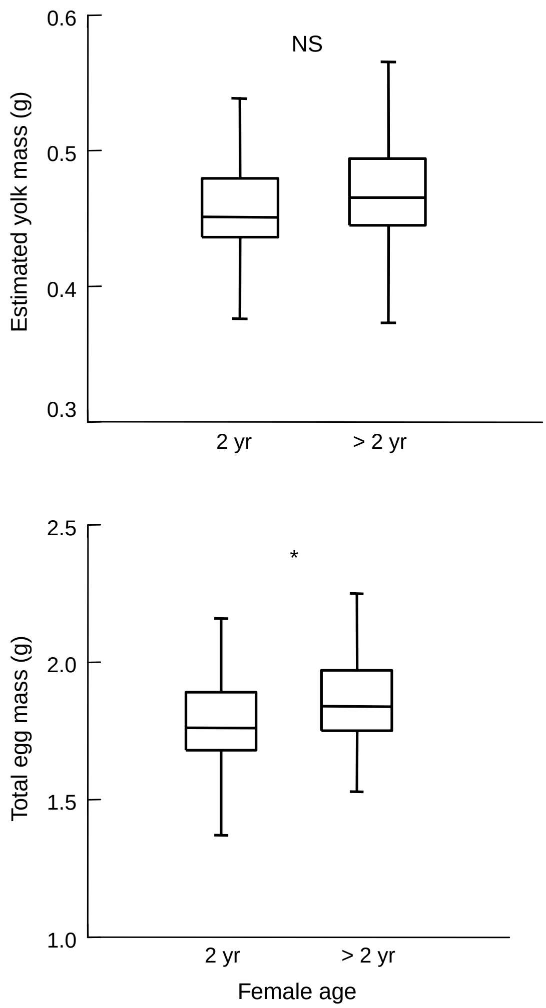

Fig. 4. Estimated yolk mass and egg mass versus female age in tree swallows. Box plot showing mean and and 2nd and 3rd quartiles. * = P < 0.05.

phenotypic variation in egg quality (Williams 2000, 2005). Resources available prior to egg-laying appear to be the strongest influence, particularly one to three days prior to egg laying. This timing is consistent with our examination of yolk rings, which indicate that the period of rapid yolk deposition (RYD) begins five to six days before laying. Given the fact that females are producing multiple eggs at the same time (up to several yolking up while one is adding albumen and shell), each yolk appears to be most sensitive to the resources available after the mid-point of RYD. Conditions during the beginning of the RYD period had no predictive effect, though in many birds the rate of yolk accumulation per day is fairly constant (Meijer et al. 1989). In general, tree swallow eggs are formed over a relatively short period compared to those of precocial and semi-altricial species (Astheimer and Grau 1990).

It is particularly interesting that yolk mass, but not total egg mass, was affected by food resources as late as the day prior to egg laying, though resources available one day prior to egg laying exerted the weakest influence. Given that the yolk is finished and only albumen and shell are being added on the day prior to egg laying, it is paradoxical that food the day before laying should be correlated with yolk mass, and this may be due to autocorrelation, either in the environment or in the birds' organismal biology. Much variation in overall egg mass tends to arise from differences in albumen and water content (Williams 1994), which presumably is less sensitive to changes in food resources. We suspect that variation in the albumen content of eggs was the principal route to larger eggs being laid by older females.

This is one of the first studies to directly measure the timing of food resources and their subsequent effect on egg composition. The correlative data reported here are not a replacement for careful experimental studies. Experimental studies supplementing the aerial insect food of swallows are very nearly impossible, but the

Table 2. Relationship between insect availability index and maximum daily temperature prior to egg-laying. Partial regression coefficients generated from a linear regression of each insect availability index vs. insect availability on days prior and temperature conditions on day of collection and all prior days. ** = $P < 0.01$. NS = non-significant P values > 0.47.

Insect availability index: days prior to egg-laying	Insect availability index: days prior to egg-laying				
	1	2	3	4	5
2	0.180**				
3	0.135**	0.119**			
4	NS	0.223**	NS		
5	−0.357**	0.175**	NS	0.264**	
Maximum temperature: days prior to egg laying					
1	NS				
2	NS	0.017**			
3	0.040**	0.037**	0.040**		
4	0.040**	0.029**	NS	0.040**	
5	−0.040**	−0.035**	0.020**	NS	0.080**

observations reported here complement experiments. Food supplementation experiments often change both laying date and egg size (see Christians 2002), thus confounding the effects of resources per se and changes in parental strategies on egg measures. In addition, it is clear that there is significant autocorrelation in insect availability; while it is possible to control for this statistically, it is difficult to determine the independent effect of insects in each time period.

Laying order exerted an effect on yolk mass in a manner similar to that reported in other studies of passerines, with increasing egg size with laying order (e.g. Ojanen 1983, Murphy 1994, Cichón 1997, but see Slagsvold et al. 1984). Later-laid eggs in the laying sequence tended to have larger yolks and overall mass than eggs laid early in the sequence. The increase in yolk size with laying order differs from the results of Ojanen (1983), who found that egg size but not yolk size increased with the laying sequence in pied flycatchers *Ficedula hypoleuca*. Given the 'competition' among eggs for resources within a female, females must be allocating resources preferentially towards late eggs, as individuals laying clutches of five eggs are beginning to produce the final egg while the first egg is yet to be laid. In the Eurasian kestrel *Falco tinnunculus*, Meijer et al. (1989) found that kestrels were depositing material in up to five eggs simultaneously.

Individuals clearly differ in their ability to gather sufficient resources to form multiple eggs simultaneously. We thus avoided using total egg volume or clutch size as a measure of quality, as this measure would be strongly linked with the variables under comparison, egg or yolk mass. We found an effect of a more independent measure of female quality. Earlier-breeders laid larger yolks and eggs, even though early-laying females produced their eggs during periods of lower food availability, as food availability generally increases at the site over the laying period; in addition early-laying females lay larger clutches, further reinforcing the link between lay date and egg production ability (Winkler and Allen 1996). Early-laying females exhibit more rapid acceleration in standardized flight tests (Bowlin and Winkler 2004), and it appears that better fliers may be more efficient at gathering the resources necessary for eggs. However, differences in eggs may not reflect constraints on the ability to gather resources. Later-laying females may reduce investment in eggs in response to lower prospects of offspring survival later in the season, which appears unlikely in tree swallows, and because of differing abilities to incubate and provision eggs and nestlings of a given size. This mix of constraint and strategy likely explains the differences found between older females and first-year breeding females (even when other factors are controlled for), as older females laid consistently larger eggs, but there was no difference between age classes in yolk mass, suggesting that there may be strong selection on maintaining yolk size but considerable latitude in varying water content (Ruiz et al. 1998). Younger females may also have more trouble gathering sufficient calcium to put a shell around larger eggs and may minimize overall egg size accordingly (Wasson 2002), though an alternative is that older females are a subset of more successful younger females.

A handful of studies have investigated the role of temperature conditions on egg quality and found that warmer temperatures lead to larger eggs (Järvinen 1996, Christians 2002, Lessells et al. 2002, Saino et al. 2004), although in some species the opposite is true, such as the "capital breeder" the snow goose (Williams and Cooch 1996). However, in most species, warmer temperatures are hypothesized to lead to either higher food availability or lower thermoregulatory demands, both of which likely translate into greater resources for egg production. In this study, we found that temperature conditions, independent of their effect on food availability, did not affect egg size, suggesting that thermoregulatory demands per se may not be a controlling influence on egg size in tree swallows at our study site.

What are the consequences to offspring of the differences in yolks and eggs reported here? Egg mass effects tend to occur during the early nestling period, and differences in growth or nestling body mass are often minimized by the time of fledging (Williams 1994, Christians 2002, Krist et al. 2004). But these early differences may be critical to other measures of quality, such as lysozymes, antibodies and carotenoids (Saino et al. 2004), especially given the likelihood of higher yolk stores in hatchlings from eggs with high yolk mass.

Overall, yolk mass appears to be influenced by the interaction of environmental conditions and individual quality. Early-laying individuals produce larger yolks and eggs; lower food availability appears to cause variation among individuals in their abilities to gather resources sufficient to produce large eggs. Our results are suggestive of an influence of both strategy and constraint. Later-laying individuals may be both less able to gather sufficient resources to allocate towards yolk production, as well as under selection to minimize investment in late offspring. The same mix may explain differences in egg quality between older and younger females. In addition, the availability of calcium to produce egg shells may also exert an influence on egg size and composition. Further work is needed to examine whether and how some individuals lay smaller eggs in order to maximize reproductive investment based on their own sets of tradeoffs.

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References

Ardia, D.R. 2005. Individual quality mediates tradeoffs between reproductive effort and immune function in tree swallows. – J. Anim. Ecol. 74: 517–524.

Ardia, D. R., Schat, K. A. and Winkler, D. W. 2003. Reproductive effort decreases long-term immunity in breeding tree swallows. – Proc. R. Soc. B 270: 1679–1683.

Astheimer, L. B. and Grau, C. R. 1990. A comparison of yolk growth rates in seabird eggs. – Ibis 132: 380–394.

Bize, P., Roulin, A. and Richner, H. 2002. Covariation between egg size and rearing condition determines offspring quality: an experiment with the alpine swift. – Oecologia 132: 231–234.

Bolton, M. 1991. Determinants of chick survival in the lesser black-backed gull: relative contributions of egg size and parental quality. – J. Anim. Ecol. 60: 949–960.

Bolton, M., Houston, D. C. and Monaghan, P. 1992. Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. – J. Anim. Ecol. 61: 521–532.

Bowlin, M. S. and Winkler, D. W. 2004. Natural variation in flight performance is related to timing of breeding in tree swallows (*Tachycineta bicolor*) in New York. – Auk 121: 345–353.

Burley, R.W. and Vadehra, D.V. 1989. The avian egg: chemistry and biology. – Wiley, New York.

Carey, C. 1996. Female reproductive energetics. – In: Carey, C. (ed.). Avian energetics and nutritional ecology. Chapman and Hall, New York, pp. 324–374.

Christians, J.K. 2002. Avian egg size: variation within species and inflexibility within individuals. – Biol. Rev. 77: 1–26.

Cichón, M. 1997. Egg weight variation in collared flycatchers *Ficedula albicollis*. – Ornis Fennica 74: 141–147.

Drent, R. H. and Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. – Ardea 68: 225–252.

Durant, J. M., Massemin, S. and Handrich, Y. 2004. More eggs the better: egg formation in captive barn owls (*Tyto alba*). – Auk 121: 103–109.

Hipfner, J. M. and Gaston, A. J. 1999. The relationship between egg size and post-hatching development in the thick-billed murre. – Ecology 80: 1289–1297.

Hipfner, J. M., Gaston, A. J. and de Forest, L. N. 1997. The role of female age in determining egg size and laying date of thick-billed murres. – J. Avian Biol. 28: 271–278.

Grau, C. R. 1976. Ring structure of the avian egg. – Poultry Sci. 55: 1418–1422.

King, J. R. 1973. Energetics of reproduction in birds. – In: Farner, D. S. (ed.). Breeding biology of birds. National Academy of Sciences, Washington, DC, pp. 78–117.

Krist, M., Remeš, V., Uvírová, L., Nádvorník, P. and Bureš, S. 2004. Egg size and offspring performance in the collared flycatcher (*Ficedula albicollis*): a within-clutch approach. – Oecologia 140: 52–60.

Hatchwell, B. J. and Pellatt, J. 1990. Intraspecific variation in egg composition and yolk formation in the common guillemot (*Uria alge*). – J. Zool. Lond. 220: 279–286.

Järvinen, A. 1996. Correlation between egg size and clutch size in the pied flycatcher Ficedula hypoleuca in cold and warm summers. – Ibis 138: 620–623.

Lessells, C. M., Dingemanse, N. J. and Both, C. 2002. Egg weights, egg component weights, and laying gaps in great tits (*Parus major*) in relation to ambient temperature. – Auk 119: 1091–1103.

Littell, R.C., Milliken, G.A., Stroup, W.W. and Wolfinger, R.D. 1996. SAS system for mixed models. – SAS Inst, Cary, NC.

McCarty, J.P. and Winkler, D.W. 1999. Foraging ecology and diet selectivity of tree swallows feeding nestlings. – Condor 101: 246–254.

Meathrel, C.E. 1991. Variation in the eggs and the period of rapid yolk deposition of the silver gull *Larus novaehollandiae* during a protracted laying season. – J. Zool., Lond. 223: 501–508.

Meijer, T., Masman, T. and Daan, S. 1989. Energetics of reproduction in female kestrels. – Auk 106: 549–559.

Murphy, M.T. 1994. Breeding patterns of eastern phoebes in Kansas: adaptive strategies or physiological constraints? – Auk 111: 617–633.

Ojanen, M. 1983. Effects of laying sequence and ambient temperature on the composition of eggs of the great tit and the pied flycatcher. – Ann. Zool. Fennici 20: 65–71.

Perrins, C. M. 1996. Eggs, egg formation and the timing of breeding. – Ibis 138 (supplement): 2–15.

Potti, J. 1993. Environmental, ontogenic, and genetic-variation in egg size of pied flycatchers. – Can. J. Zool. 71: 1534–1542.

Ramsay, S.L. and Houston, D.C. 1997. Nutritional constraints on egg production in the blue tit: a supplementary feeding study. – J. Anim. Ecol. 66: 649–657.

Reid, W. V. and Boersma, P. D. 1990. Parental quality and selection on egg size in the Magellanic Penguin. – Evolution 44: 1780–1786.

Risch, T.S. and Rohwer, F.C. 2000. Effects of parental quality and egg size on growth and survival of herring gull chicks. – Can. J. Zool. 78: 967–973.

Ruiz, X., Jover, L. and Pedrocchi, V. 1998. Audouin's gull intraspecific variability in yolk and albumen egg contents: why is yolk size so constant? – Biol. Cons. Fauna 102: 327–334.
Ruiz, X., Jover, L., Pedrocchi, V., Oro, D. and González-Solís, J. 2000. How costly is clutch formation in the Audouin's gull *Larus audouinii*? – J. Avian Biol. 31: 467–575.
Saino, N., Romano, M., Ambrosini, R., Ferrari, R. P. and Møller, A. P. 2004. Timing of reproduction and egg quality covary with temperature in the insectivorous barn swallow, *Hirundo rustica*. – Funct Ecol. 18: 50–57.
Slagsvold, T., Sandvik, J., Rofstad, G., Lorentsen, O. and Husby, M. 1984. On the adaptive value of intraclutch egg-size variation in birds. – Auk 101: 685–697.
Styrsky, J. D., Eckerle, K. P. and Thompson, C.F. 1999. Fitness-related consequences of egg mass in nestling house wrens. – Proc. R. Soc. B 266: 1253–1258.
Wasson, M.F. 2002. Causes and consequences of Calcium limitation in breeding passerine birds. – Unpubl. Ph.D. Dissertation, Cornell University, Ithaca, NY.
Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. – Biol. Rev. 68: 35–59.
Williams, T.D. 2000. Experimental (tamoxifen-induced) manipulation of female reproduction in zebra finches (*Taeniopygia guttata*). – Physiol. Biochem. Zool. 73: 566–573.
Williams, T.D. 2005. Mechanisms underlying costs of egg production. – Bioscience 55: 39–48.
Williams, T.D. and Cooch, E.G. 1996. Egg size, temperature and laying sequence: why do snow geese lay big eggs when it is cold? – Funct. Ecol. 10: 112–118.
Winkler, D. W. 1991. Parental investment decision rules in tree swallows: parental defense, abandonment and the so-called Concorde Fallacy. – Behav. Ecol. 2: 133–142.
Winkler, D.W. and Allen, P.E. 1996. The seasonal decline in avian clutch size: strategy or physiological constraints? – Ecology 77: 922–932.

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