Fitness-related consequences of egg mass in nestling house wrens

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The fitness-related consequences of egg mass, independent of confounding influences associated with parental quality, remain poorly understood for wild birds in general and for passerines in particular. We performed cross-fostering experiments to test the hypothesis that egg mass, independent of parental quality, is the primary determinant of fitness-related traits in nestling house wrens (*Troglodytes aedon*), an insectivorous passerine. Nestling mass was significantly correlated with the mass of the eggs from which nestlings hatched early but not late in the nestling period in early-season broods. In contrast, in late-season broods, nestling mass was correlated with egg mass until nestlings achieved asymptotic mass. Neither nestling growth nor survival to nest leaving was related to egg mass in either early- or late-season broods; however, nestlings in late-season broods grew more slowly than did nestlings in early-season broods. We propose that nestling mass and egg mass remained correlated throughout the nestling period in late-season broods because decreased arthropod food resources late in the breeding season constrain parents' ability to provision nestlings. We conclude that female house wrens in this population trade-off clutch size for greater egg mass to maximize reproductive success in late-season broods.

Keywords: egg mass; nestling growth; nestling survival; maternal effects; cross-fostering; *Troglodytes aedon*

1. INTRODUCTION

The size and number of independent offspring produced during each breeding attempt represent a compromise in reproductive investment adjusted by natural selection to optimize parental fitness (Clutton-Brock 1991; Roff 1992). Although increased size potentially benefits each offspring, additional energy allocated to larger offspring necessarily reduces the number of offspring in which parents can invest (Daan & Tinbergen 1997). Investigations of this trade-off in birds have focused primarily on variation in clutch size, with the significance of variation in egg mass having received comparatively little attention (Magrath 1992; Williams 1994). Intraspecific variation in egg mass is common in birds (Boag & Van Noordwijk 1987) and reflects variation in the amount of energy and resources invested in eggs (reviewed in Williams 1994; Ward 1995). Such variation in reproductive investment may lead to differential growth and survival of nestlings (Williams 1994).

Nestling growth and survival are positively correlated with egg volume or egg mass in several avian taxa (reviewed in Williams 1994). However, any correlation between fitness-related traits of nestlings and egg size (mass or volume) may be confounded by covariation between egg size and maternal ability to incubate eggs or to raise a brood (Amundsen & Stokland 1990; Mueller 1990; Reid & Boersma 1990; Bolton 1991; Magrath 1992; Williams 1994; Bernardo 1996a). For example, egg

volume is positively correlated with territory quality in pied flycatchers (*Ficedula hypoleuca*) (Potti 1993) and with female age and experience in western gulls (*Larus occidentalis*) (Sydeman & Emslie 1992), and egg mass is positively correlated with subsequent female provisioning rate in house wrens (*Troglodytes aedon*) (J. D. Styrsky, unpublished data). Swapping partial or complete clutches of small and large eggs between nests decouples prehatching attributes of egg mass (e.g. maternal effects which could include nutritional, hormonal or genetic factors) (Mather & Jinks 1971; Magrath 1992; Bernardo 1996a,b) from parental quality expressed during incubation, brooding and provisioning of nestlings. Thus, cross-fostering experiments permit an evaluation of the association between fitness-related traits of nestlings and egg mass, independent of parental quality as reflected in the mass of eggs produced by the foster mother (Nisbet 1978; Amundsen & Stokland 1990; Reid & Boersma 1990; Bolton 1991; Magrath 1992; Smith *et al.* 1995; Amundsen *et al.* 1996; Blomqvist *et al.* 1997).

Although there is experimental evidence in semi-precocial and precocial species of birds of a positive relationship between nestling growth and egg mass (Reid & Boersma 1990; Amundsen & Stokland 1990; Amundsen *et al.* 1996) and between nestling survival and egg mass (Bolton 1991; Blomqvist *et al.* 1997), the relationship between fitness-related traits and egg mass in nestlings of altricial passerines is largely unknown (Ricklefs 1984; Williams 1994). Ricklefs & Peters (1981) and Ricklefs (1984) performed partial cross-fostering experiments with European starlings (*Sturnus vulgaris*) and found

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a significant effect of the foster-nest environment (without specific regard to parental quality as reflected in egg mass) on several aspects of nestling growth, but no effect of egg mass *per se*. Ricklefs (1984) suggested that factors associated with parental care, such as brooding or provisioning, exert a greater influence on nestling growth and development than do attributes of eggs, such as mass or composition (see also Price 1991; Smith 1993; Smith & Wettermark 1995). Magrath (1992) and Smith *et al.* (1995) later demonstrated in European blackbirds (*Turdus merula*) and European starlings, respectively, that the mass of cross-fostered nestlings was correlated positively with egg mass early but not late in post-hatching development. In contrast, neither growth (Smith *et al.* 1995) nor survival of nestlings (Magrath 1992; Smith *et al.* 1995) was related to egg mass.

In this paper, we present results from complete cross-fostering experiments designed to test the hypothesis that egg mass, independent of parental quality (expressed as mean mass of eggs produced by the foster mother), is the primary determinant of nestling growth and survival in an altricial passerine, the house wren. The egg-size hypothesis predicts that mass, growth rate and survival to nest leaving of cross-fostered nestlings should be positively correlated with the mass of the eggs from which the nestlings hatched, independent of parental quality.

2. METHODS

(a) Study area and species

This study was conducted in 1997 using house wrens that bred in nest-boxes on the forested 108 ha Mackinaw study area in McLean County, Illinois, USA (40° 40' N, 88° 53' W). Nest-boxes were mounted on 1.5 m greased steel poles to deter predators and were distributed 30 m apart along N-S lines separated by 60 m (see Drilling & Thompson 1988). House wrens in this population are typically double brooded, producing a modal clutch size of seven eggs in early-season broods (initiated in early May) and six eggs in late-season broods (initiated in early July) (Finke *et al.* 1987).

(b) General field procedures

Nest-boxes were inspected at least every other day throughout the breeding season (May–August) to determine when clutches were initiated in each nest. We weighed eggs to the nearest 0.005 g on a portable reloading scale (Ohaus 7401-02) before noon on the day they were laid, and numbered each egg with a permanent marker. In ten nests, we weighed some eggs 1–2 days after they were laid, but before incubation began. Mass loss of unincubated eggs during the egg-laying period is negligible (*ca.* 0.005 g d⁻¹) (J. D. Styrsky, unpublished data).

As the end of the incubation period approached, we visited nests daily to determine when the first egg of the clutch hatched (brood day 0). We weighed each nestling to the nearest 0.1 g on a portable electronic balance (Acculab PocketPro 250) on brood days 0, 1, 2, 4, 6, 8, 10 and 12. Nests were visited usually once each day, so we occasionally missed first-hatched nestlings on the day they hatched. We determined brood day 0 for those nests using the criteria of Harper *et al.* (1992). On brood day 12, we gave each nestling a numbered, aluminium US Fish and Wildlife Service leg ring. We visited nests daily, taking care to prevent premature nest leaving, from brood day 14 until all surviving nestlings had left the nest (typically brood days 15–17).

Table 1. Mean egg mass per clutch for each of the four treatments in both early- and late-season cross-fostering experiments, 1997

(Treatments: matched–small, small-egg producers given foster clutches of small eggs; reversed–small, large-egg producers given foster clutches of small eggs; matched–large, large-egg producers given foster clutches of large eggs; reversed–large, small-egg producers given foster clutches of large eggs.)

brood	treatment	<i>n</i> clutches	egg mass, g (mean ± s.d.)
early season	matched–small	14	1.35 ± 0.06
	reversed–small	16	1.34 ± 0.05
	matched–large	10	1.48 ± 0.04
	reversed–large	16	1.51 ± 0.06
late season	matched–small	8	1.41 ± 0.04
	reversed–small	10	1.42 ± 0.05
	matched–large	8	1.56 ± 0.07
	reversed–large	10	1.58 ± 0.09

(c) Cross-fostering experiments

The cross-fostering experiments consisted of swapping whole clutches between nests at the onset of incubation. We established four treatments in which females that produced small eggs and females that produced large eggs were given foster clutches of small or large eggs (table 1). Mean egg mass was 1.43 g (*n* clutches = 80, s.e. = 0.01) in early-season clutches and 1.48 g (*n* clutches = 43, s.e. = 0.02) in late-season clutches (two-sample equal variance *t*-test; *t*₁₂₁ = 2.60, *p* = 0.01). Mean clutch size was 6.6 eggs (*n* clutches = 80, s.e. = 0.14) in early-season clutches and 5.8 eggs (*n* clutches = 43, s.e. = 0.12) in late-season clutches (two-sample equal variance *t*-test; *t*₁₂₁ = 3.77, *p* = 0.0002). Because of the significant differences in mean egg mass and mean clutch size between broods, data from early- and late-season clutches were analysed separately. For both early- and late-season nests, we categorized clutches as small-egg clutches if their mean egg mass was equal to or less than their respective season's mean and as large-egg clutches if their mean egg mass was greater than the mean. This procedure resulted in experimental dyads that varied in the magnitude of the difference between original-egg mass and foster-mother-egg mass, but this was controlled for statistically, as described below. Clutches were paired randomly to control for territory quality but were matched by clutch size. We exchanged clutches within two days of clutch completion to control for any difference in incubation ability based on the mass of eggs that females produced.

(d) Statistical analyses

With the likely exception of nestling mass at hatching, any association between egg mass *per se* and fitness-related traits of altricial nestlings cannot be established as strictly causal, even using a cross-fostering experimental design (see Magrath 1992). We therefore used correlation analyses (CORR procedure; SAS Institute 1990) to test for relationships of egg mass (original-egg mass) and parental quality (foster-mother-egg mass) with nestling mass, growth and survival (Reid & Boersma 1990; Amundsen & Stokland 1990; Smith *et al.* 1995). We used mean values for each brood to avoid pseudoreplication. We applied partial correlation procedures to control for parental quality (foster-mother-egg mass) in comparisons of fitness-related traits with original-egg mass, and to control for original-egg mass in

comparisons of fitness-related traits with foster-mother egg mass. In addition, we partialled out the hour at which nestlings were weighed in the analyses of nestling mass and egg mass because nestling mass increases with the time of day (C. F. Thompson, unpublished data). We also partialled out brood size because brood size varied, individual nestlings that died during the course of the experiments were not replaced and mean nestling mass was inversely related to brood size throughout the nestling period (J. D. Styrsky, unpublished data).

We used nonlinear least-squares estimation (NLIN procedure; SAS Institute 1990) to fit mean nestling mass on successive two-day intervals to the generalized logistical growth equation

$$W_t = W_\infty W_0 e^{gt} / (W_\infty - W_0 + W_0 e^{gt}), \quad (1)$$

where W_t is body mass at age t , W_∞ is asymptotic body mass, W_0 is initial body mass, and g is an exponential rate constant of growth (*sensu* Peters 1983). Mean nestling growth for each brood is estimated by g , which describes the rate (day^{-1}) at which asymptotic mass is achieved. We included only broods in which nestlings were weighed at least five times during the nestling period. We calculated nestling survival for each brood as the proportion of nestlings surviving to leave the nest.

Predation during the incubation period accounted for the loss of five early-season clutches and one late-season clutch. Data from six nests that were depredated during the nestling period were excluded from analyses of nestling growth (g) and survival, but were used in analyses of nestling mass.

As both clutch size and egg mass differ between early- and late-season clutches, we tested for seasonal differences in nestling growth (g), nestling mass on brood day 12 and total number of nestlings that survived to leave the nest using two-sample t -tests. Statistical tests for predicted positive correlations of nestling mass, growth and survival with original-egg mass are one-tailed. Tests for correlations of nestling mass, growth and survival with parental quality (foster-mother-egg mass) are two-tailed because we did not predict the direction of the relationships. As a consequence of the experimental design, a single nest represents the original nest to one brood and the foster nest to the other brood in each experimental dyad. This results in two partial correlation analyses based on the same set of data on each brood day; therefore, we considered p -values $\leq$ the Bonferroni-adjusted $\alpha = 0.025$ as significant. In all other analyses, we considered p -values ≤ 0.05 as significant.

3. RESULTS

(a) Nestling mass

Figure 1a,b shows mean nestling mass from brood day 0–12 of nestlings that hatched from clutches of small and large eggs in early- and late-season broods, respectively. In early-season broods, mean nestling mass was significantly positively correlated with the mean mass of eggs from which they hatched (original-egg mass) from brood day 0 through brood day 6, after which the correlation was not significant (table 2). In contrast, mean nestling mass in late-season broods was significantly positively correlated with original-egg mass from brood day 0 through brood day 10, and marginally significantly correlated on brood day 12 (table 2). Mean nestling mass was not correlated with parental quality (as expressed by foster-mother-egg mass) at any point during the nestling period in either early- or late-season broods (table 2).

Figure 1. Foster nestling mass (mean $\pm$ 2 s.e.) in relation to brood day for nestlings from cross-fostered clutches of small and large eggs in (a) early-season broods, and (b) late-season broods. Brood day 0 is the day the first egg of a clutch hatched. Open circles denote large-egg nestlings and filled circles represent small-egg nestlings.

Finally, there was no difference in nestling mass on brood day 12 between early- and late-season broods ($t_{74} = 1.57$, $p = 0.12$).

(b) Nestling growth

The partial correlation analyses of nestling mass indicate that small-egg nestlings caught up in mass with large-egg nestlings by brood day 12 in early-season broods (table 2, see also figure 1a). However, the growth rate constant, g , was not correlated with original-egg mass or parental quality (foster-mother-egg mass) in either early- or late-season broods (table 2). Further, nestlings of late-season broods grew significantly more slowly than did nestlings of early-season broods ($t_{75} = 3.14$, $p = 0.002$), even though late-season nestlings hatched from larger eggs.

(c) Nestling survival

The mean number of nestlings that survived to leave the nest was 5.6 (n broods = 47, s.e. = 0.16) in early-season broods and 4.9 (n broods = 32, s.e. = 0.22) in late-season

Table 2. Mean mass at two-day intervals, growth (g), and survival to nest leaving of nestlings in relation to original-egg mass and foster-mother quality (as reflected in egg mass) in early- and late-season house wren broods, 1997

(Presented are Pearson (except where noted) partial correlation coefficients (see §2 for partial correlation procedures). Original-egg mass refers to the mass of the eggs from which the nestlings hatched. Foster-mother-egg mass refers to the mass of the eggs produced by the foster mother.)

brood	brood day	n broods ^a	original-egg mass		foster-mother-egg mass	
			<i>r</i>	<i>p</i> ^b	<i>r</i>	<i>p</i> ^b
early season	0	44	0.644	<0.001	−0.215	0.178
	2	40	0.373	0.012	−0.043	0.800
	4	46	0.362	0.008	−0.075	0.634
	6	48	0.332	0.013	−0.075	0.623
	8	48	0.225	0.068	−0.096	0.530
	10	47	0.085	0.291	−0.207	0.177
	12	45	0.171	0.140	−0.040	0.804
	growth (g)	46	0.194	0.101	−0.056	0.714
	survival	47	0.094 ^c	0.534	0.160 ^c	0.288
late season	0	27	0.530	0.004	−0.102	0.634
	2	30	0.391	0.022	−0.186	0.352
	4	32	0.368	0.025	−0.182	0.344
	6	30	0.417	0.015	0.050	0.804
	8	30	0.502	0.004	−0.134	0.506
	10	30	0.551	0.001	−0.275	0.166
	12	31	0.353	0.033	−0.079	0.690
	growth (g)	31	−0.159	— ^d	0.094	0.628
	survival	31	−0.032 ^c	— ^d	0.001 ^c	0.995

^a Sample size varies because of missed nest visits and losses to predators.

^b As per our predictions, *p*-values associated with original-egg mass are one-tailed, whereas *p*-values associated with foster-mother-egg mass are two-tailed. The Bonferroni-adjusted $\alpha = 0.025$ (see §2 for explanation); significant *p*-values are in bold print.

^c *r*-value is the Spearman correlation coefficient.

^d *p*-value omitted because *r*-value opposite from that predicted.

broods (two-sample equal variance *t*-test; $t_{77} = 2.56$, $p = 0.01$). Nestling survival (from hatching to nest leaving) was high in both early- (92.1%) and late-season (92.6%) broods. Not surprisingly, mean nestling survival was not correlated with original-egg mass or parental quality (foster-mother-egg mass) in either early- or late-season broods (table 2).

4. DISCUSSION

As predicted by the egg-size hypothesis, the cross-fostering experiments reveal that nestling mass was positively correlated with the mass of the eggs from which nestlings hatched. However, the pattern of association between nestling mass and egg mass differed between early- and late-season broods. Nestling mass in early-season broods was positively correlated with egg mass through to only brood day 6, but nestling mass in late-season broods was positively correlated with egg mass until nestlings achieved asymptotic mass. The pattern of correlations in late-season broods differs from that of previous studies of passerines in which nestling mass in European blackbirds (Magrath 1992) and European starlings (Smith *et al.* 1995) was correlated with egg mass *per se* only early in post-hatching development.

Smith & Bruun (1998) suggested that previous studies of both passerine and non-passerine species failed to detect a lasting association between fitness-related traits of nestlings and egg size *per se* because such experiments were performed in optimal habitats. Smith & Bruun

(1998) investigated this hypothesis in European starlings by testing for correlations of egg mass with nestling mass and survival based on the proportion of pasture (the preferred foraging substrate of starling parents) available in agricultural landscapes. Nestling survival, mediated through the effect of egg mass on nestling mass, was related to egg mass only in areas with a low proportion of pasture, presumably because of decreased food availability. Thus, egg mass *per se* may have a more pronounced effect on fitness-related traits of nestlings when food availability is low than when food is abundant (Smith & Bruun 1998). We propose that this is why the mass of house wren nestlings was correlated with egg mass only early in the nestling period in early-season broods, but was correlated throughout the nestling period in late-season broods.

Based on a 38-year study, Kendeigh (1979) found that in forests of central Illinois lepidopteran larvae, gryllids (Orthoptera) and araneid spiders (Arachnida) reach peak abundance in May, June and July, respectively. These three taxa represent the majority of arthropod prey delivered to nestling house wrens (Morton 1984). However, most late-season broods do not hatch until the last week of July, well after the peak abundance of preferred food items. With preferred food resources abundant early during the breeding period, parents of early-season broods may provision nestlings adequately so that the initial effect of egg mass on nestling mass is lost as nestlings age. Late in the season, however, the initial effect of egg mass on nestling mass may be sustained throughout

the nestling period because the provisioning of nestlings is constrained by limited food resources. To compensate, females may invest instead in heavier eggs in late-season clutches when food is more abundant than it will be two to three weeks later during the nestling period (see Visser *et al.* 1998). Murton & Westwood (1977) proposed a similar hypothesis to explain the seasonal increase in egg size in great tits (*Parus major*), but, to date, no empirical data exist to support this hypothesis (see Perrins 1996).

In addition to Kendeigh's (1979) 38-year data set on arthropod abundance, there is other evidence that breeding conditions deteriorate on our study area as the season progresses. First, the increased investment in larger eggs in late-season clutches does not offset the decrease in clutch size, either in total mass of the clutch or in the number of nestlings produced (this study; see also Finke *et al.* 1987; Drilling & Thompson 1991). Second, nestling growth (*g*) is significantly slower in late-season than in early-season broods despite a higher *per capita* provisioning rate (K. P. Eckerle, unpublished data), which suggests that parents provide low-quality prey to their late-season broods.

A decline in abundance of preferred arthropod food resources has potentially substantial consequences for the fitness of adult house wrens through effects on nestling mass in late-season broods. Asymptotic mass (i.e. brood day 12 mass) in house wrens is positively correlated with juvenile survival and recruitment (C. F. Thompson, unpublished data), as has often been reported for other passerines (e.g. Tinbergen & Boerlijst 1990; Hochachka & Smith 1991; Magrath 1991). Allocating resources to produce larger eggs but fewer eggs in late-season clutches may be advantageous because nestlings that hatch from larger eggs weigh more at nest leaving, leading to increased juvenile survival and recruitment. Nestlings of late-season broods achieved the same asymptotic mass as did nestlings of early-season broods, which may be a consequence of increased investment in eggs in late-season clutches. Considering these results, we propose that female house wrens in this population trade off clutch size for larger egg size to maximize reproductive success in late-season broods.

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