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Covariation between egg size and rearing condition determines offspring quality: an experiment with the alpine swift

Abstract A positive correlation between egg size, early growth and nestling survival has been frequently reported in the ornithological literature. Albeit of interest, most of these studies did not determine whether the relationship between egg size, early growth and nestling survival was confounded by the quality of rearing conditions. However, this is of importance in order to assess the extent to which a life-history trait like egg size causally affects fitness. In a colony of the alpine swift *Apus melba*, we cross-fostered complete clutches between nests to determine the relative contribution of egg size and rearing condition on nestling growth and survival. In foster nests, nestlings that hatched out of larger eggs were significantly heavier at birth and at the age of 10 days; at 25 days, however, the relationship was no longer significant. The likelihood of a chick surviving from birth to 25 days of age was not correlated with its original egg size, but with the size of the eggs laid by its foster parents. This experiment therefore lends support to the hypothesis that in the alpine swift the relationship between egg size and nestling growth and survival is mainly due to a covariation between egg size and parental care rather than to a direct contribution of egg size.

Keywords *Apus melba* · Coloniality · Cross-fostering experiment · Egg volume · Parental quality

Introduction

In a wide range of bird species, egg size is positively correlated with hatchling size, nestling growth and

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survival (Williams 1994). Two hypotheses can explain how such correlations can arise. First, since larger eggs usually contain a larger yolk sac, embryos have access to larger amounts of energy during early development (Birkhead and Nettleship 1982). At least in the first days after hatching, nestlings issued from larger eggs may therefore grow more rapidly and achieve a higher survival (Nisbet 1973). Second, egg size may be correlated with parental or territory quality so that nestlings originating from larger eggs may be in better condition because parental care was of higher quality (Reid and Boersma 1990; Bolton 1991; Amundsen et al. 1996). For instance, more experienced females may have improved foraging abilities allowing them to simultaneously lay larger eggs and provision offspring at a higher rate. The relative importance of the two hypotheses can be determined only through an experimental approach where eggs are swapped between randomly chosen nests (Williams 1994; Bernardo 1996). Indeed, cross-fostering experiments permit the separation of the potential covariation between egg size and parental, territory or nest site quality from the effect of egg size on nestling growth and survival (Amundsen and Stokland 1990; Reid and Boersma 1990; Bolton 1991; Meathrel et al. 1993; Smith et al. 1995; Blomqvist et al. 1997; Hipfner and Gaston 1999; Styrsky et al. 1999; Hipfner 2000; Risch and Rohwer 2000).

In the present study, we investigated the contribution of egg size and parental care to offspring growth and survival after having cross-fostered complete clutches between alpine swift *Apus melba* nests. Swifts are altricial, and hence post-hatching parental care is crucial to ensure a high breeding success. We therefore predict that the eggs out of which nestlings hatched (hereafter referred to as 'original-egg volume') make a minor contribution to nestling growth and survival. In addition, if we assume that egg size reflects the quality of parental care, as shown in five other bird species (Amundsen and Stokland 1990; Reid and Boersma 1990; Bolton 1991; Magrath 1992; Risch and Rohwer 2000), we also predict that offspring growth and survival should correlate with the size of the

Table 1 Relationships between egg volume and hatching success, nestling survival, and body mass. Original-egg volume refers to the mean volume of the eggs out of which nestlings hatched, and foster-parents-egg volume refers to the mean volume of eggs laid by their foster mother. Changes in deviance of a logistic regression (Δ), standardised coefficients of a multiple linear regressions (β) and statistical significance (P-values) are presented.

Trait	Age (days)	Sample size	Original-egg volume		Foster-parents-egg volume	
			Coeff	P	Coeff	P
Hatching success	0	41	Δ=−0.85	0.40	Δ=0.09	0.93
Nestling survival	0–25	41	Δ=0.95	0.42	Δ=3.82	0.007
Nestling mass[a]	0	41	β=0.60	<0.001	β=0.02	0.90
	10	41	β=0.38	0.01	β=0.01	0.23
	25	41	β=0.16	0.26	β=−0.24	0.11

[a] We controlled for brood size because it varied throughout the experiment due to the death of some nestlings and because mean nestling body mass was inversely correlated with brood size (Pearson's coefficients of correlation between brood size and nestling mass: $r=-0.28$ and $P=0.07$ at day 0, $r=-0.20$ and $P=0.22$ at day 10, and $r=-0.48$ and $P<0.01$ at day 25)

eggs laid by foster parents (hereafter referred to as 'foster-parents-egg volume').

Materials and methods

The alpine swift

The socially monogamous alpine swift is a trans-Saharan migrant insectivorous bird that spends most of its lifetime on the wing. It reproduces in colonies of a few to several hundred pairs in holes in cliffs or under the rooves of tall buildings. A single clutch is produced per year containing 1–4 eggs laid at 1-day intervals. Both parents incubate the clutch for 20 days, and then feed the offspring up to fledging at an age of 50–70 days. The clutch requires 1–2 days to hatch (mean=1 day, SD=0.8 day, $n=52$ clutches; unpublished data). Adults are sexually mature at the age of 2–3 years. The oldest recaptured individual reported was 26 years old (Arn 1960).

General field procedures

The field study was conducted in 2000 in Bienne (Switzerland: 47°10′N, 7°12′E) in a colony of 115 breeding pairs located in a building. At the beginning of April, nests were checked every other day to determine the date of clutch initiation and completion. The laying date of each egg was recorded and its position in the laying sequence written on the shell with a pen. Egg length (L) and breadth (B) were measured to the nearest 0.1 mm. Egg volume (V) was then determined with the formula $V=LB^2\pi/6$. Egg volume was highly correlated with egg mass ($r=0.98$, $P<0.001$, $n=41$). In the statistical analyses, we considered egg volume to be an index of egg size instead of egg mass because egg mass was missing for one clutch. Close to hatching, we checked nests every day between 1300 and 1600 hours to determine hatching date (=day 0). Nestlings were weighed to the nearest 0.1 g at day 0, 10 and 25. We did not measure nestlings after 25 days of age because they start to invade neighbouring nests and are frequently adopted by foster families (Arn 1960).

Cross-fostering experiments

Within 48 h after clutch completion, we swapped complete clutches between nests. We did not carry out a partial cross-fostering experiment (e.g. half of the eggs are swapped between nests) to avoid altering subtle adaptation of intra-clutch egg size variation (Vinuela 1997) and to avoid the possibility that parents feed preferentially larger or smaller chicks of different origins (Slagsvold 1997). For our experiment, we considered only modal clutches of three eggs, because not enough clutches of other sizes (21% of 75 easily accessible nests) were available for cross-fostering experiments. In total, 42 clutches were matched in pairs with the criterion that two clutches of the same pair were laid at the same date. If several pairs completed their clutch on the same day, we randomly allocated nests to a given pair. Within pairs of nests, mean egg size was not correlated (Pearson correlation, $r=0.10$, $n=42$, $P=0.52$). Laying date was not correlated with egg size (for each clutch a mean value was calculated; Spearman rank correlation, $r=-0.024$, $n=42$ nests, $P=0.88$).

Statistical analyses

We investigated the relative contribution of original-egg volume and foster-parents-egg volume to hatching success and nestling survival via logistic regression analyses, and nestling mass via multiple linear regression analyses. Logistic regression analyses were performed with binomial errors and a logit link, with the number of hatchlings or nestlings as the dependent variable, and clutch size or brood size at hatching as the binomial denominator. Siblings were not considered as independent data points, and to avoid pseudoreplication we therefore used mean body mass of siblings in the statistical analyses. One clutch was excluded from the analyses because we accidentally broke one egg, which reduced sample size to 41 experimental clutches. Statistical tests are two-tailed and mean values are given ±1 SE.

Results

One to three chicks hatched per clutch (mean=2.8±0.1, $n=41$); no clutch failed, and overall hatching success was high (114 out of 123 eggs hatched, 93%). The proportion of eggs that hatched in a nest was neither associated with original-egg volume nor with foster-parents-egg volume (Table 1). From hatching to the age of 25 days, 8 out of 114 nestlings (7%) died in 6 out of 41 nests (15%). The proportion of nestlings in a brood that survived up to 25 days of age was not correlated with original-egg volume, but with the volume of the eggs laid by the foster mother (Table 1). After controlling for brood size, nestlings issued from larger eggs were heavier at both hatching and 10 days of age but not at 25 days (Table 1). Egg volume of foster parents was not significantly correlated with body mass of their foster offspring at hatching, 10 and 25 days later (Table 1).

Discussion

In line with previous similar experiments in other bird species, hatching success was neither correlated with original-egg nor with foster-mother-egg size (Reid and Boersma 1990; Smith et al. 1995; Risch and Rohwer 2000; but see Amundsen et al. 1996). Furthermore, hatchling body mass was correlated with original-egg volume but not with foster-parents-egg volume (Reid and Boersma 1990; Bolton 1991; Smith et al. 1995; Blomqvist et al. 1997; Styrsky et al. 1999; Hipfner 2000). This suggests that hatchling body mass depends on the amount of energy packed into eggs (larger eggs contain a larger yolk sac; Rofstad and Sandvik 1987) but not on incubation efficiency, which might be correlated with the size of the eggs foster parents laid. The absence of a significant relationship between original egg size and nestling survival until 25 days after hatching is difficult to interpret because nestling mortality was low in the year 2000. It cannot be excluded that a positive relationship between egg size and nestling survival is detectable in years when nestling mortality is high. In alpine swifts, 7–99% of the nestlings die every year before fledging (mean=28%, n=24 years; Arn 1960). Finally, we found that the positive relationship between original-egg size and nestling body mass decreased from hatching to half way through the rearing period, as already reported in other altricial birds (Williams 1994; but see Reid and Boersma 1990; Styrsky et al. 1999). This probably reflects the fact that at hatching, body mass depends mainly on the amount of energy stored in eggs (larger eggs have larger stores), whereas at later stages body mass also depends on other factors like parental feeding rate or environmental quality (Smith and Bruum 1998; Styrsky et al. 1999; but see Styrsky et al. 2000).

The observation that nestling survival was positively correlated with the size of eggs laid by foster parents indicates that egg size covaries with parental or territory quality as already documented in five other bird species (Amundsen and Stokland 1990; Reid and Boersma 1990; Bolton 1991; Magrath 1992; Risch and Rohwer 2000). As in most colonial birds, alpine swift parents do not defend a territory but only the surroundings of their nest. Therefore, the effect of foster egg size on nestling survival may be due to either the quality of parents or of the nest site. These two alternatives are plausible because maternal age (review in Saether 1990), experience (Thomas 1983; Weimerskirch 1990; Sydeman and Emslie 1992), and condition (Murphy 1986; Smith et al. 1993) all correlate with egg size. Furthermore, females may also produce larger eggs when mated with higher-quality males (Cunningham and Russell 2000). Finally, nest quality can vary within the same colony, since in the alpine swift ectoparasites are not randomly distributed within a colony, with some parts of it being more infested (Roulin et al. 1998). Further studies are required to determine whether nest site also reflects parental quality (Hoi et al. 1994; Grubbauer and Hoi 1996).

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