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Limited male incubation ability and the evolution of egg size in shorebirds

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In bird species where males incubate but are smaller than females, egg size may be constrained by male body size, and hence ability to incubate the eggs. Using data from 71 such shorebird species, we show that egg size decreases as the degree of female-biased sexual size dimorphism increases, after controlling for female body mass. Relative egg size was not related to mean clutch size. However, when controlling for mating system, the relationship between female-biased sexual size dimorphism and relative egg size was only significant in polyandrous species. The relatively small eggs of socially polyandrous shorebirds have previously been explained as an energy-saving strategy associated with the production of multiple clutches. Our findings suggest that egg size evolution is better explained by male incubation limitation in these birds.

1. INTRODUCTION

Offspring performance is typically positively related to egg size in birds (Williams 1994), and females should therefore be selected to lay eggs that are as large as possible. However, nutritional resources available to females may constrain egg formation, as egg size is often positively correlated with female body condition, and increases if birds are given supplementary food (e.g. Nager *et al.* 2000; Christians 2002). Accordingly, the relatively small eggs (adjusted for female body size) in socially polyandrous shorebirds (Charadrii) may be explained as an energy-saving adaptation to the production of multiple clutches (Ross 1979; Sæther *et al.* 1986; Liker *et al.* 2001).

An additional factor that possibly limits the size of bird eggs is parental incubation ability. Eggs need to be kept in relatively stable thermal environments in order to secure optimal conditions for embryo development (White & Kinney 1974; Deeming 2002). If the total egg surface area in a nest is too large to be efficiently covered by a parent's brood patch, this should result in sub-optimal incubation conditions (Bortolotti & Wiebe 1993), and might lead to selection for smaller clutches (Lack 1947; Arnold

1999) or for smaller eggs. In the following, we refer to this idea as the incubation limitation hypothesis.

Most shorebirds lay four eggs, and larger clutches are rarely found (Maclean 1972; Walters 1984). Eggs are typically pear-shaped, a feature presumably reducing heat loss by optimizing the volume to surface area, and by making the eggs fit well to the parents' brood patch (Andersson 1978). Many shorebirds exhibit female-biased, or reversed, sexual size dimorphism (RSD), and males often incubate (see electronic supplemental material). The relatively small males may be poor incubators if egg size is simply allometrically determined by the larger body size of females. To compensate for this, egg size could have evolved in response to the body size differences between the sexes. If so, we predict that relative egg size should decrease as the degree of RSD increases. Importantly, this provides an explanation for the variation in relative egg size among polyandrous shorebirds, unlike the energy limitation hypothesis. Here, we test the incubation limitation hypothesis in shorebirds using phylogenetic comparative methods. We include the effect of clutch size, since this factor may be traded off against egg size, and since incubation limitation should be less severe in species normally laying less than four eggs.

2. MATERIAL AND METHODS

We collected information on average body mass (g) measured in the breeding season from both sexes, male incubation behaviour (incubate or not), average fresh egg mass (g), average clutch size, and social mating system (monogamous and polygynous species were scored as 0, polyandrous species were scored as 1) from 115 shorebird species (see electronic supplemental material). Egg size should not be adjusted to sexual size dimorphism when males are larger than females, because female body size would then be the limiting factor. Consequently, as we were only interested in how egg size has evolved in species where males both (i) incubate and (ii) are smaller than females, we reduced the dataset according to these criteria before performing the analyses. Males are reported to incubate until eggs hatch in all remaining species. Prior to analyses, measurements of egg mass and body mass were natural log-transformed. We calculated RSD as ln (male body mass)–ln (female body mass).

To account for non-independence arising through phylogenetic relationships amongst species, we always used the generalized least squares method in which the phylogeny describes the expected variance and covariance between species under a non-directional random walk (Brownian) model of trait evolution (Pagel 1999; Freckleton *et al.* 2002). The phylogeny was taken from Thomas *et al.* (2004). Egg size is positively correlated with both female body size and male body size (regression coefficients=0.67 and 0.69, respectively, $p < 0.001$ and $n=71$ in both cases). Our prediction of male incubation limitation can be tested in a multiple regression with egg size as dependent variable, and either male body size or RSD as a predictor along with female size. The interpretation would remain the same, e.g. for a given female size, egg size decreases in association with reductions in male size. Male and female sizes are highly correlated in our dataset ($r=0.99$, $p < 0.001$, $n=71$), but female size and RSD are not ($r=-0.13$, $p=0.30$, $n=71$). Results from regressions where predictors are highly intercorrelated are likely to be confounded (Zar 1998). Hence, we use RSD instead of male size here.

Using multiple regressions, we first tested for a relationship between RSD and egg size, controlling for female body size (model 1). Following this, we added clutch size and mating system to the model (model 2). Finally, we tested for a difference in the slope of RSD and egg size between polyandrous and non-polyandrous species by adding social mating system by RSD as a first-order interaction term (model 3). Note that residual egg mass is only used for illustrative purposes in figure 1, not as a variable in the regressions. In all analyses, we simultaneously estimated and implemented the appropriate degree of phylogenetic correction as described by Freckleton *et al.* (2002). We repeated all analyses on
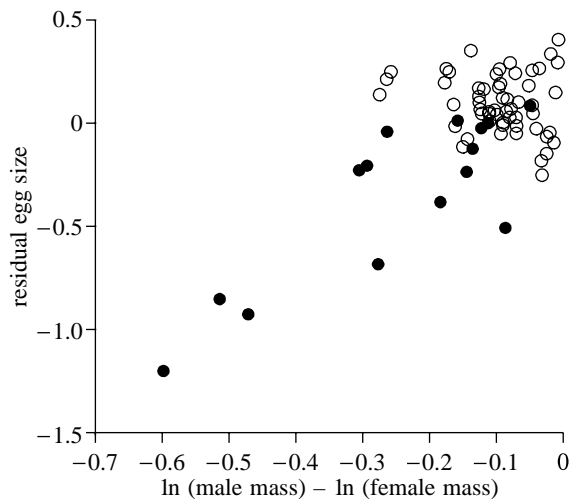
Figure 1. As predicted by the incubation limitation hypothesis, egg mass decreases as the degree of reversed sexual size dimorphism increases in shorebirds where males incubate but are smaller than their mates. For visual purposes, egg size is displayed as the residuals from a regression between egg size (dependent) and female body size. Taking social mating system into account, the relationship only remains significant in polyandrous species (filled circles) and not monogamous and polygynous species (open circles).

the raw species data. The results were fully consistent and here we report only the results from the phylogenetic analyses. All analyses were performed in R 2.1.0 (Ihaka & Gentleman 1996) using code written by R. P. Freckleton.

3. RESULTS

Of the species in our dataset ($n = 71$), 54 are regarded socially monogamous, two polygynous and 15 are polyandrous. Average clutch sizes per species vary between 1.7 and 4 eggs (mean $= 3.66 \pm 0.59$ (s.d.)). Egg size decreased with increasing RSD (table 1). This relationship holds after controlling for female body size (model 1, table 1; figure 1) as well as clutch size and social mating system (model 2, table 1). In addition, smaller eggs are associated with polyandrous species compared to non-polyandrous species (model 2, table 1; figure 1). There is no association between clutch size and egg size (model 2, table 1). The significant interaction between mating system and RSD, indicates that the slope of RSD on egg size differs between polyandrous and non-polyandrous species. Indeed, RSD remains significant (regression coefficient $= 1.1184$, $p = 0.014$, $n = 15$) when excluding non-polyandrous species from a model with RSD and female body mass as predictors, but is non-significant when polyandrous species are excluded (regression coefficient $= -0.3550$, $p = 0.273$, $n = 56$).

4. DISCUSSION

We have shown that, in cases when males incubate and are smaller than females, the relative size of shorebird eggs declines with increasing differences in sexual size dimorphism. This relationship does not depend on clutch size, but is significant only in polyandrous species when mating system is controlled for. Our results are consistent with the hypothesis that egg size evolution is constrained by the relative

Table 1. Associations amongst egg size (dependent variable), reversed sexual size dimorphism, female mass, clutch size and social mating system analysed in three different phylogenetically corrected linear models (see §2). For each model regression coefficients $\pm$ s.e. are given with r^2.

model (covariate d.f., error d.f.)	regression coefficient ($\pm$s.e.)	p
model 1 (2, 68)		
female mass	0.688 ± 0.032	< 0.0001
RSD	0.976 ± 0.223	< 0.0001
r^2	0.871	
model 2 (4, 66)		
female mass	0.667 ± 0.032	< 0.0001
RSD	0.722 ± 0.233	0.0016
mating system	-0.135 ± 0.050	0.0109
r^2	0.882	
excluded from final model: clutch size		
model 3 (4, 66)		
female mass	0.663 ± 0.031	< 0.0001
RSD	0.206 ± 0.353	not tested
mating system	-0.028 ± 0.068	not tested
mating system $\times$ RSD	0.937 ± 0.440	0.0368
r^2	0.894	

body size of incubating males. The lack of clutch size effects in this dataset is likely to be due to the low number of polyandrous species normally laying less than four eggs (*Charadrius montanus* and *Eudromias morinellus*). The influence of RSD suggests an indirect effect of sexual selection on egg size evolution, since a recent comparative study demonstrated that the direction and strength of sexual size dimorphism in shorebirds is mediated by the interaction between social mating system and male display type (Székely *et al.* 2004). We suggest two possible reasons for the effect of mating system. First, the more pronounced levels of RSD exhibited by several polyandrous species should make incubation limitation more important in these species, and consequently strengthen the correlation between RSD and egg size. Second, as predicted by the energy limitation hypothesis, egg size in polyandrous species is reduced to compensate for increases in the number of clutches laid. However, the energy limitation hypothesis cannot explain the influence of RSD unless the number of clutches laid by polyandrous females increases with increased RSD. At present, there is insufficient data on clutch numbers in polyandrous shorebirds to perform a robust test of this hypothesis. We conclude that incubation limitation is a plausible factor in the evolution of egg size in polyandrous shorebirds. It may also play a role in other avian taxa showing relatively small eggs (e.g. polyandrous coucals *Centropus* spp.; Slotow 1996).

The proximate forces making it maladaptive for polyandrous shorebirds to lay relatively large eggs may be similar to those involved in limiting clutch sizes in birds. If parents are not able to cover the clutch sufficiently with their brood patches, this could result in a lowered hatching success due to an overall reduction in egg temperature (Monaghan & Nager 1997; Arnold 1999), or an elevated evaporation rate

(Reid *et al*. 2000). However, reduced incubation ability may also negatively influence the performance of bird embryos in more subtle ways. In northern lapwings (*Vanellus vanellus*), newly hatched chicks from experimentally enlarged clutches were in poorer body condition than controls, perhaps increasing their risk of mortality (Larsen *et al*. 2003). Further, prenatal developmental conditions can have long-term effects on zebra finch (*Taeniopygia guttata*) reproductive performance later in life, without producing a clear effect on growth and development (Gorman & Nager 2004). In order to advance our knowledge of how egg size evolution could be affected by incubation limitation, more experiments and comparative analyses are needed to: (i) test how egg sizes alter incubation conditions in bird nests; (ii) investigate whether the fairly modest decrease in relative egg size observed in polyandrous shorebirds is sufficient to enhance incubation conditions; and (iii) test whether these changes in incubation conditions influence embryo development.

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