Inter-Nest Variability in the Egg to Hatchling Mass Ratio in the Common Pochard Aythya ferina: Does Female Body Mass Matter?

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Inter-nest variability in the egg to hatchling mass ratio in the Common Pochard *Aythya ferina*: Does female body mass matter?

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Abstract. Offspring survival and subsequent fitness are assumed to increase with offspring size. Although the relationship between egg size and young size in birds has attracted considerable scientific attention, to our knowledge no study so far has investigated differences among nests with respect to this relationship. The aim of this study was to find out 1) whether some inter-nest variation in the egg mass — young mass relationship exists among nests of Common Pochards, and 2) whether such a variation could be attributed to the body mass of the female measured in the last 5 days of incubation. Egg mass explained a higher portion of the variability in young mass in nests of heavier females. Those females produced smaller young for eggs of a given size. We suggest a trade-off between current and future reproduction as being the evolutionary mechanism underlying the relationship between female body mass and hatchling body mass.

INTRODUCTION

Offspring survival and subsequent fitness are assumed to increase with offspring size (Smith & Fretwell 1974). This premise has been supported by much empirical evidence (reviewed by Bernardo 1996a, but see also Moran & Emlet 2001). In oviparous animals such as birds, egg size is a reliable predictor of hatchling size (reviewed by Williams 1994). Correspondingly, larger eggs are considered favourable because they contain higher amounts of nutrients (Nager et al. 2000, Lessells et al. 2002, Pelayo & Clark 2002). Young hatched from large eggs, therefore, have several advantages over conspecifics hatched from small eggs. They have higher energetic reserves in the form of yolk (Dawson & Clark 1996), more efficient thermal isolation (Alisauskas 1986, Rhymer 1988), better moving performance (Anderson & Alisauskas 2001) and/or faster body tissue growth (Anderson & Alisauskas 2002). Although the relationship between egg size and young size in birds (hereafter EYR) has attracted considerable attention (Williams 1994), to our knowledge no study thus far has investigated how variation explained by EYR differs among nests. Such differences, however, may reflect energy allocation which is part of the female reproductive tactics. Theoretically, the shape of EYR can be determined by thermal conditions in the nest because they influence energy consumption and development of embryos (Lourens et al. 2005). To maintain a stable thermal environment, the female has to put considerable effort into incubation, which requires a high amount of energy. Hence, the benefit of providing adequate thermal conditions for developing offspring might be offset by reduced female body condition and consequently the probability of

future reproduction (Visser & Lessells 2001). In ducks, which are capital breeders using mostly endogenous reserves for breeding (Alisauskas & Ankney 1992), it has been shown that enhanced incubation effort will manifest in a lowering of the female body condition (Hanssen et al. 2005). The role of egg size in determining offspring quality should be more pronounced in precocial than in altricial birds, since the former allocate a higher portion of energy acquired into egg formation (Sotherland & Rahn 1987). In addition, EYR in precocial birds cannot be modified by feeding care by parents (Reed et al. 1999).

The Common Pochard is a precocial species which does not provide young with any demanding parental care during the post-hatching period, except of the selection of feeding habitat and anti-predator defence. As a consequence, parental allocation of energy during clutch formation and incubation is one of the major sources of variation in initial young body condition, even though other factors may be highly influential (gender, genetics, within-patch variation in food supply etc.).

The aim of this study was to 1) describe the among nest variability in the relationship between egg mass and young mass, and 2) find out whether such variability can be attributed to late-incubation body mass of the female (measured during the last 5 days of incubation). We hypothesised that if female body mass loss during incubation increases with incubation effort (Hanssen et al. 2005), then eggs in nests of lighter females should be exposed to better thermal conditions. Then, EYR in these nests will be weaker because egg size related differences in energy consumption by embryo are obscured by good thermal conditions (Lourens et al. 2006).

METHODS

Field work was carried out in 2001 and 2002 in the Třeboň Basin Biosphere Reserve, the Czech Republic (Southern Bohemia 49°00′N, 14°46′E). From mid-May to mid-July, we searched for Pochard nests in suitable breeding habitats. Since pochards are representatives of the Aythyini tribe, in which conspecific brood parasitism occurs frequently (Geffen & Yom-Tov 2001), we used visual criteria (Dugger & Blums 2001) to determine the presence of parasitism in nests. Only those classified as non-parasitic were included in the analyses. During the incubation period, we measured

the length and width of all eggs in localised nests to the nearest 0.1 mm using a calliper. We used these measurements for egg mass estimation according to the following equation (Rohwer 1988):

$$\text{egg mass [g]} = \text{egg length [cm]} \times \text{egg width [cm]}^2 \times 0.55$$

We verified this for the Common Pochard by plotting the fresh egg mass of a test sample of eggs (107 eggs collected within the study area) against the estimated egg mass obtained from the above equation. The regression model explained 93% of variation (linear regression: $r^2 = 0.93$, $F_{1,105} = 1297.184$, $p < 0.001$). Hence, we considered this equation as appropriate for estimating fresh egg mass in Common Pochards. To accurately assess the date of hatching, we estimated the incubation stage of all eggs in a clutch by candling (Weller 1956). Eggs were numbered with water-proof ink, which enabled them to be individually identified. Before hatching, piping eggs were placed into separate net-sacks (Hořák & Albrecht, in press). On the day of hatching, we checked the nests and collected data on the structural size and mass of young. We estimated structural measurements (bill length, tarsus length) and body mass of young with calliper (to the nearest 0.1 mm) and spring scale (to the nearest 0.5 g), respectively. After concluding this procedure, we put all ducklings together into a paper sack to keep them safe in the nest until the flushed female returned (Korschgen et al. 1996). Females were caught at the nests using drop-door traps (Weller 1957) or mist nets during the last 5 days of incubation and released away from the nests. Their mass was estimated by spring scale to the nearest 1.0 g. Structural size characteristics of females were measured in a similar way as in young.

Statistical analyses

As the regression coefficient of the relationship between body mass (dependent variable) and structural size characteristics (independent variable) approached zero, we used pure body mass instead of regression residuals as a better estimate of female and young body condition (Green 2001). We suggest that the approximation is appropriate because variability in structural characteristics is very low in studied sub-populations of Common Pochard (D. Hořák et al., unpubl.). Information on female body mass was available only for 11 nests, thus only those were included in the analyses.

As a measure of variability explained by EYR within particular nests, we used the coefficient of determination (r^2). Before analyses, the possible effect of the value spread on the coefficient of determination was removed by taking residuals from the regression between the coefficient and sum of squares of deviations from mean egg mass. Common statistical procedures were used to test hypotheses. All tests were two-tailed and data were checked for normality before analyses. Statistical analyses were performed in R 2.2.1 package (http://r-project.org).

RESULTS

In total, 106 young from 6 and 12 nests were measured during breeding seasons 2001 and 2002, respectively. The clutch size in studied nests was 9.5 ± 0.746 on average. We found no differences in mean young mass within the nests between the two study years (ANOVA: $F_{1,16} = 0.418$, p = 0.53) and data were pooled for further calculations. Our data showed a positive relationship between estimated egg mass and young mass (ANCOVA: $F_{1,70} = 346.426$, p < 0.001), and young mass differed significantly among nests (ANCOVA: $F_{17,70} = 6.796$, p < 0.001). The overall variability in egg mass explained ca. 61% of variation in young mass. Additionally, we found significant differences in EYR among nests (ANCOVA: $F_{17,70} = 1.938$, p < 0.03). Variation explained by EYR in particular nests varied from 0% to 100% among nests. To evaluate the causes of such variation, we constructed a linear model with female body mass and clutch size as explanatory variables. The minimum adequate model (Crawley 2003) included only female body mass as the most influential factor (elimination of clutch size and interaction from the model caused no significant change in deviance; both p > 0.40). We found a positive trend in the relationship between female body mass and variability explained by relationships between egg mass and young mass in particular nests. This was not significant, however ($r^2 = 0.25$, $F_{1,9} = 2.922$, p = 0.12, Y = -270.260 + 0.350*X , Fig. 1). Nevertheless, after removing the most influential point (a nest in which EYR was based on three young and explained 100% of variability, Cook's distance D = 0.40) the positive trend remained unchanged but the relationship became significant ($r^2 = 0.48$, $F_{1,8} = 7.515$, p = 0.025, Y = -373.443 + 0.475*X , Fig. 1). Further, we examined the relationship between female body mass and mean
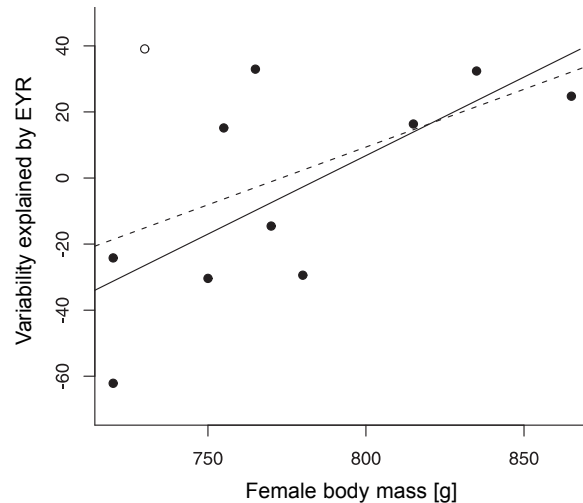

Fig. 1. The association between variability explained by egg mass-young mass relationship (coefficient of determination controlled for values' spread, for details see Results) within nests and female body mass at the end of incubation. The positive trend (dashed line, p = 0.122) became significant (solid line, p = 0.025) after removing the possible outlier (unfilled circle). Y = -270.260 + 0.350*X and Y = -373.443 + 0.475*X, respectively.

relative young mass (mean young mass controlled for estimated mean egg mass) at hatch. The minimum adequate model again contained only female body mass as the most influential variable (clutch size and interaction removed from the
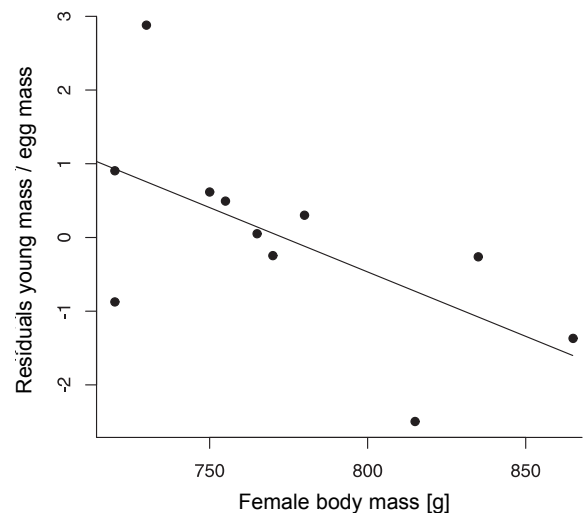

Fig. 2. Relationship between mean young mass in the nest (controlled for respective mean estimated egg mass — residuals from regression between mean young mass and mean egg mass) and female body mass at the end of incubation (p < 0.05). Y = 13.502 - 0.017*X.

model, both p > 0.28). We found that mean relative young mass was negatively correlated with female body mass (r^2 = 0.36, $F_{1,9}$ = 5.163, p = 0.049, Y = 13.502 - 0.017*X , Fig. 2).

DISCUSSION

EYR shows a positive trend for most studied species. However, the percentage of variability it explains differs distinctly among studies (see Williams 1994 for review). In our study, estimated egg mass explained approximately 61% of variability in young body mass, which is lower than values reported for other duck species such as Lesser Scaup *Aythya affinis* (77%, Dawson & Clark 1996), Common Eider *Somateria mollissima* (83%, Erikstad et al. 1998), and King Eider *S. spectabilis* (69%, Anderson & Alisauskas 2002). It lies inside the range reported by Williams (1994) for precocial species (21–94%, average = 65%) but this provides no meaningful information because of the wide range of EYR estimates in precocial species. It is obvious that there are clear differences in EYR between species even at the sub-family level. The sources of these differences might lie in species-specific life histories, but some variation can be also expected within species as a result of variance in energy allocation among individuals. In order to describe variation in EYR at a sub-population level, we compared variability in young mass explained by estimated egg mass among nests of Common Pochards. Our data indicate that variability explained by EYR varies highly among nests. We supposed that clutch size and female body mass were factors strongly determining the shape of EYR. Interestingly, we found no evidence that clutch size affects the variation in EYR. Although there is evidence that clutch size influences incubation behaviour characteristics (Hepp et al. 2005), these effects might be relatively slight and therefore not detectable in our data set. Despite of many factors that possibly influence size of young and eggs (Tryjanowski et al. 2004), parental quality has recently been considered one of the most important factors modifying the relationship between size of egg and young (Williams 1994, Bernardo 1996b). Body condition is a fundamental characteristic of duck reproductive tactics and at least partly reflects the amount of energy available to the female (Alisauskas & Ankney 1992). We examined the relationship between female body mass and the shape of EYR. Our results show a positive relationship between female body mass and strength of EYR (Fig. 1). Furthermore, we found that light females produce heavier young from eggs of respective size if compared with heavy females (Fig. 2). Body mass characteristics of females were taken at the end of incubation, when a majority of energy has already been invested into reproduction. Sources of body mass change in incubating females still remain enigmatic but some evidence has accumulated for the downward trend in body mass during incubation in ducks (Zicus & Riggs 1996, Kellet et al. 2005). Moreover, mass loss is reported to increase with incubation effort (Hanssen et al. 2005). Accordingly, we suppose that the lower mass of lighter females is a consequence of higher incubation effort. If this holds true, a higher portion of the variability explained by EYR in heavier females might be generated by suboptimal and/or unstable thermal conditions in the nest. Such a thermal environment might accentuate differences in energy consumption between embryos in small and large eggs. We suggest that egg-size-related differences in relative egg surface area generate differences in thermal radiation. A higher amount of energy invested into thermoregulation by developing embryos in smaller eggs will then result in stronger EYR, because smaller eggs will produce young with a relatively smaller yolk sack and larger eggs will produce young with a relatively larger yolk sack. On the other hand, an optimal thermal environment in nests of lighter females could lead to similar energy consumption by developing embryos in eggs of all sizes, as has been reported by Lourens et al. (2006) for eggs incubated under stable artificial conditions. Our second finding indicates that yolk reserve consumption in eggs of lighter females could be lower, because those females produced heavier young from eggs of respective mass (Fig. 2). The influence of thermal conditions during incubation on the phenotype of young has recently been demonstrated by Hepp et al. (2006). They have shown that embryos incubated at lower temperatures use a greater proportion of egg proteins then those incubated at higher temperatures. Such evidence partially supports our above-mentioned explanation; however, the effect of egg size and incubation effort on energy consumption in developing embryos remains unknown and should be a focus of future studies. We believe that our results shed new light on the mechanism that presumably forms a relationship between young and female quality. During incubation, energy available to young can be saved, for

instance, by higher incubation constancy from the female. On the one hand, this might result in higher young body mass at hatching (more yolk reserves saved) and, on the other hand, it requires higher energy expenses from the female. We suggest that there is a conflict between female body mass maintenance during incubation and quality of young at hatching. As a possible general explanation for this observed conflict we suggest the "current reproduction — condition trade-off" hypothesis (Stearns 1992). Even though the EYR is relatively well-described and in fact uniform across various animal taxa, some mechanisms leading to its formation should be more precisely investigated. Especially, the issue of differences in energy allocation among individuals is of particular importance in birds, and future research providing plausible results is essential. At a population level, variation in energy allocation can be interpreted as an outcome of individual optimisation of reproductive tactics. Alternatively, it can be explained by non-adaptive variation in physiological processes. The first step in distinguishing between these two explanations is to combine first-rate data on body mass change of incubating females and their incubation effort with information on variation in EYR.

ACKNOWLEDGEMENTS

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STRESZCZENIE

[Czy u głowienki ciężar cała samic wpływa na zależność pomiędzy masą jaj a masą piskląt?]

Zakłada się, że wielkość jaj odzwierciedla wielkość wykluwających się z nich piskląt, natomiast przeżywanie młodych zwiększa się wraz ze wzrostem ich wielkości. W ostatnich latach zależność między rozmiarami jaj i piskląt (opisywana w pracy jako EYR) jest często badana, jednak jak dotąd nie były analizowane różnice występujące pomiędzy poszczególnymi gniazdami. Celem pracy było stwierdzenie istnienia zmienności tej zależności pomiędzy gniazdami głowienki, oraz zbadanie czy to zróżnicowanie może być związane z ciężarem ciała wysiadujących samic.

Autorzy założyli, że wraz ze spadkiem ciężaru ciała samicy podczas wysiadywania, zwiększane są nakłady ponoszone na ogrzewanie jaj, tym samym jaja lżejszych samic znajdują się w lepszych warunkach termicznych. Dlatego też zależność między wielkością jaj a wielkością piskląt w takich gniazdach powinna być słabsza, gdyż jest maskowana przez dobre warunki termiczne panujące w gnieździe.

Badania prowadzono w rezerwacie Biosfery "Trebon" w 2001 i 2002 roku. Masę jaj głowienek obliczano w oparciu o pomiary, natomiast pisklęta były ważone w dniu wyklucia. Samice chwytano, ważono i mierzono podczas ostatnich 5 dni wysiadywania.

Wykazano istotne różnice w zależności EYR pomiędzy poszczególnymi gniazdami. Stwierdzono związek miedzy masą ciała samic a zmiennością EYR (Fig. 1) — masa jaj tłumaczyła większą część zmienności ciężaru ciała piskląt w gniazdach cięższych samic. Stwierdzono, że relatywna wielkość młodych była negatywnie skorelowana z ciężarem ciała samic (Fig. 2).

Autorzy sugerują istnienie kompromisu pomiędzy obecną i przyszłą reprodukcją, który jest mechanizmem ewolucyjnym leżącym u podstaw zależności między masą samic a masą piskląt.