Trade-offs between egg size and number in waterfowl: an interspecific test of the van Noordwijk and de Jong model

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Summary

1. Van Noordwijk & de Jong proposed a model to predict the sign of an intraspecific correlation between two life-history traits, given that a trade-off between the two traits exists. In this paper, the model is adapted to egg size/number trade-offs.

2. The predictions of the model are tested within various clades of waterfowl. Although the relationship between egg mass and clutch size in this group has been examined previously, prior analyses have either failed to take phylogenetic structure into account or relied upon phylogenies that lack resolution. Phylogenetic structure is adjusted for using recently constructed phylogenies and the method of phylogenetically independent contrasts.

3. Van Noordwijk and de Jong's model was successful in explaining between-clade variation in the relationship between egg mass and clutch size. Even if a trade-off between egg size and number exists, a negative relationship will only be observed if the variation in the pattern of allocation (i.e. few large eggs *vs* many small eggs) is high relative to the variation in the amount of resources invested in the clutch. Thus, this model may be useful for understanding interspecific relationships as well as intraspecific patterns.

Key-words: Clutch size, functional constraints, life-history trade-offs, phylogenetically independent contrasts, propagule size

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Introduction

Reproduction requires resources to be allocated among competing demands (Stearns 1992). If resources limit the production of propagules, there will be a trade-off between the number of propagules produced and the investment in each (Bernardo 1996). However, a trade-off within individuals will not necessarily result in a negative relationship between propagule size and number within species if individuals differ in their access to resources (van Noordwijk & de Jong 1986; Flint, Grand & Sedinger 1996). 'High-quality' individuals (i.e. those with more resources) will be able to produce more propagules and larger propagules than 'low-quality' individuals. Many species do not show negative correlations between propagule size and number (Bernardo 1996), perhaps as a result of variation in resource acquisition.

Van Noordwijk & de Jong (1986) proposed a model to predict the sign of the correlation between two life-history traits, given that a trade-off between the two traits exists. In the model, the investment in the two traits is measured in the same units (e.g. energy).

Hence, it is not immediately obvious how this model can be applied to the trade-off between egg size (measured in mass or volume) and clutch size (measured in number of eggs). Furthermore, the model was developed to explain intraspecific correlations, and certain assumptions of the model (see Results and Discussion) may not be realistic in interspecific relationships.

In this paper, it is shown how van Noordwijk & de Jong's (1986) model can be adapted to the egg size/number trade-off. The predictions of this model are then tested to see if they hold for interspecific relationships by examining the correlations between egg mass and clutch size in various clades of waterfowl (Order Anseriformes; geese, swans and ducks). Although egg size/number trade-offs in this group of birds have been examined previously by Rohwer (1988), his analyses ignored phylogenetic relationships among species, which can lead to misleading interpretations of comparative data (Felsenstein 1985). Blackburn (1991b) reanalysed Rohwer's data, adjusting for phylogenetic structure, but the phylogeny he used (i.e. Livezey 1986a) lacked resolution, such that most

of Rohwer's (1988) data were discarded (data from 151 species were reduced to 37 points). As a result, Blackburn (1991b) could only test for a relationship across the entire order, and not within lower taxonomic groups. Here recently constructed phylogenies (see below) and the method of phylogenetically independent contrasts (Felsenstein 1985) are used to examine the relationship between egg mass and clutch size across the Anseriformes and within a number of tribes and subfamilies.

THE PREDICTIONS OF VAN NOORDWIJK & DE JONG'S MODEL WITH REGARDS TO THE EGG SIZE/NUMBER TRADE-OFF

In the van Noordwijk & de Jong (1986) model, an amount (A) of resource is acquired for two life-history traits (R and S) such that

$$A = R + S. \qquad \text{eqn 1}$$

Although investment in egg mass (E) and clutch size (C) is multiplicative, i.e.

$$A' = E \times C, \qquad \text{eqn 2}$$

rather than additive, an egg size/number trade-off can easily be fit to the model by logarithmically transforming the variables, i.e.

$$\log(A') = \log(E \times C), \qquad \text{eqn 3}$$

$$A = \log(E) + \log(C). \qquad \text{eqn 4}$$

Van Noordwijk & de Jong (1986) refer to A as the 'acquisition' of resources, but in an egg size/number scenario it more properly refers to the amount of resources invested in a clutch (i.e. log[clutch mass]). The model of van Noordwijk & de Jong (1986) incorporates an additional parameter, B, the fraction of resources allocated to R, such that

$$R = B \times A, \qquad \text{eqn 5}$$

and

$$S = (1 - B) \times A. \qquad \text{eqn 6}$$

In an egg size/number trade-off, resources invested in egg size and clutch size are not mutually exclusive. However, the following parameter can be used as an index of allocation (i.e. few large eggs *vs* many small eggs):

$$B = \log(E) [\log(E \times C)]^{-1}, \qquad \text{eqn 7}$$

or

$$B = \log(C) [\log(E \times C)]^{-1}. \qquad \text{eqn 8}$$

This parameter satisfies the condition of van Noordwijk & de Jong's (1986) model that $0 \leq B \leq 1$ as long as $E > 1$. The latter condition is easily achieved by using appropriate units for egg mass.

The model predicts that, given a trade-off between egg size and number, there will be a negative correlation between egg mass (i.e. $\log[E]$) and clutch size (i.e. $\log[C]$) when the variation in allocation of resources (i.e. $B = \log[\text{egg mass}] \{\log[\text{clutch mass}]\}^{-1}$) is large relative to the variation in investment of resources (i.e. $A = \log[\text{clutch mass}]$), and vice versa (van Noordwijk & de Jong 1986).

Methods

ANALYSIS

Egg mass, clutch size and female mass data were obtained from Rohwer (1988) and were logarithmically (base 10) transformed prior to analysis. The phylogenetic structure of the data (i.e. the non-independence of data points due to relatedness between species) was taken into account using phylogenies described below. The independent contrasts method (Felsenstein 1985) involves calculating the difference (i.e. contrast) between sister species, whether they be extant species (tips in the phylogeny) or ancestors (nodes), for each variable (i.e. egg mass, clutch size, female mass, investment and allocation in this analysis). Ancestral trait values are estimated from extant species. Each contrast is adjusted for the lengths of the branches between the two species and, in the case of ancestral species, the lengths of the branches between the ancestor and extant descendants. This standardization takes into account the expected amount of change between taxa, as well as uncertainty in the estimation of ancestral values. Standardized contrasts (i.e. the change between two taxa) are thus independent of one another, assuming that each character evolves under a Brownian motion model (Felsenstein 1985).

Calculation of standardized contrasts was performed using COMPARE version 4·0.2 (Martins 1999); these calculations assumed that variation within species is negligible compared with variation between species. To correct egg mass and clutch size for body size, the contrasts in these reproductive parameters were each regressed on the contrasts in female mass using ordinary least squares (OLS) regression (see Blackburn 1991b) through the origin (Garland, Harvey & Ives 1992). The residuals of these regressions provided size-adjusted contrasts of egg mass and clutch size. To test the strength of the relationship (i.e. r^2) between egg mass and clutch size, adjusted for female mass and phylogenetic structure, the residual standardized contrasts in clutch size were regressed on the residual standardized contrasts in egg mass using OLS regression, again through the origin (Garland *et al.* 1992). However, to estimate the slope of the regression of clutch size on egg mass, major (or principal) axis regression was performed (Pagel & Harvey 1988) using equations from Sokal & Rohlf (1995, p. 589). Major axis regression was used since both variables were subject to measurement error and since the distinction between dependent and independent variables was not appropriate for this analysis.

The standardized contrasts in investment and allocation were each regressed on the contrasts in female mass using OLS regression through the origin. The variance in the residuals of these regressions provided estimates of the variation in these variables.

Analyses were performed to examine the relationship across all of the Anseriformes, as well as within subfamilies and tribes. All regressions were performed using SAS (SAS Institute 1988). Power analyses were performed using PASS (Hintze 1996).

TOPOLOGY OF THE PHYLOGENIES

The phylogeny of Anseriform genera proposed by Livezey (1997b), with increased resolution from Livezey (1996c, Fig. 5 therein), provided a general topology. Resolution below the genus level was provided by Livezey (1986b; genus *Tachyeres* – steamer-ducks; Livezey 1991; tribe Anatini – dabbling ducks; Livezey 1995a; subfamily Dendrocygninae – whistling and white-backed ducks; Livezey 1995b; tribe Oxyurini – stiff-tailed ducks; Livezey 1995c; tribe Mergini – seaducks; Livezey 1996a; subfamily Anserinae – geese and swans; Livezey 1996b; tribe Aythyini – pochards; Livezey 1997a; tribe Tadornini – sheldgeese and shelducks). All of these phylogenies are based on morphological characters (i.e. not the characters of interest in this study). Combining phylogenies was straightforward since there was little conflict in topologies. The position of the Cairineae differed between Livezey (1991, 1997b) and Livezey (1996c), but since the placement of this group was ambiguous (Livezey 1996c), the topology of Livezey (1991, 1997b) was arbitrarily adopted. Polytomies were rare, and were arbitrarily resolved to bifurcations by adding short branches between groups (Felsenstein 1985). Combining the phylogenies of Livezey (1986b, 1991, 1995a,b,c, 1996a,b,c, 1997a,b) in this way produced a working topology which included 146 of the 152 species listed by Rohwer (1988).

BRANCH LENGTHS OF THE PHYLOGENIES

For within-subfamily or -tribe analysis, branch lengths were estimated using the number of character changes between taxa (Garland *et al.* 1992). Square-root transformation of the branch lengths was necessary for effective standardization of the contrasts (see Garland *et al.* 1992). In the case of the working phylogeny for the entire Anseriform order, the numbers of character changes from different references were not comparable and so, where possible, branch lengths were estimated using the numbers of character changes from Livezey (1986a). For branches not described by Livezey (1986a) (e.g. branches within genera), lengths were assumed to be one. Because of the coarse nature of this estimation, the sensitivity of the results to branch lengths was investigated using random sets of branch lengths. Two thousand trees with the topology described above and random branch lengths (uniformly distributed between 0 and 2) were generated using a program written by the author. Standardized contrasts were calculated using these trees and the CONTRAST program of the PHYLIP package (Felsenstein 1995). These contrasts were analysed as described above.

Results and discussion

Given an underlying trade-off between egg size and number, van Noordwijk & de Jong's (1986) model predicts that a negative correlation between egg mass and clutch size will be observed when the variation in allocation of resources (i.e. log[egg mass] {log[clutch mass]}$^{-1}$) is large relative to the variation in investment of resources (i.e. log[clutch mass]). Among tribes and subfamilies of waterfowl, the ratio of variation in allocation to variation in investment, adjusted for body mass and phylogenetic structure, is highest in the Anatini and the Aythyini (Table 1). As predicted, negative correlations between egg mass and clutch size are only observed within these two tribes (Table 1)

Table 1. Variation in investment (i.e. log[clutch mass]) and allocation (i.e. log[egg mass] {log[clutch mass]}$^{-1}$), and the relationships between clutch size and egg mass in the Anseriformes and within lower taxonomic groups. Relationships were considered significant at type I error level, $\alpha = 0.05$

Group	Taxonomic level	n^a	$\sigma^2_{investment}$ ($\times 10^{-3}$)	$\sigma^2_{allocation}$ ($\times 10^{-3}$)	$\sigma^2_{allocation}/\sigma^2_{investment}$	r^2	Major axis slope	P
Anatini	Tribe	49	4·91	1·12	0·23	0·51	−0·49	0·0001
Anseriformes	Order	145	3·68	0·42	0·11	0·18	−0·51	0·0001
Anserinae	Subfamily	23	2·34	0·11	0·05	0·00	−0·14	NS
Aythyini	Tribe	14	0·51	0·11	0·22	0·57	−1·21	0·001
Dendrocygninae[b]	Subfamily	8	–	–	–	0·32	−2·52	NS
Mergini	Tribe	15	3·30	0·17	0·05	0·01	0·02	NS
Oxyurini[b]	Tribe	6	–	–	–	0·26	−0·27	NS
Tadornini	Tribe	13	2·56	0·09	0·04	0·04	−6·16	NS

[a] n = number of contrasts = (number of species – 1).
[b] Variance in allocation and investment was not calculated for these clades since the sample size (and hence the statistical power to detect a relationship between clutch size and egg mass) was so low.
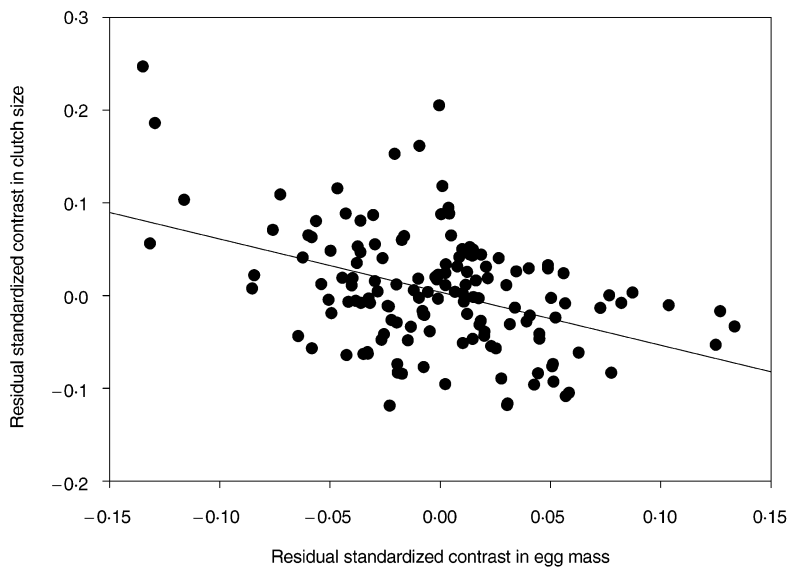
Fig. 1. Regression of residual standardized contrasts in clutch size on residual standardized contrasts in egg mass (i.e. adjusted for body mass and phylogenetic structure) across the entire order Anseriformes.

Table 2. Correlations between investment (i.e. log[clutch mass]) and allocation (i.e. log[egg mass] {log[clutch mass]}$^{-1}$) in the Anseriformes and within lower taxonomic groups. Relationships were considered significant at $\alpha = 0.05$

Group	r	P
Anatini	−0·68	0·0001
Anseriformes	−0·51	0·0001
Anserinae	−0·59	0·003
Aythyini	0·09	NS
Mergini	−0·66	0·007
Tadornini	−0·10	NS

when body mass and phylogenetic relatedness are taken into account. Similar results were obtained when phylogenetic structure was not taken into account (Rohwer 1988). The lack of a significant negative correlation within the Tadornini, Mergini and Anserinae (Table 1) is not simply due to small sample sizes; if the 'real' strength of the correlation between clutch size and egg mass in these three groups was as strong as that observed in the Anatini ($r^2 = 0.51$), the statistical power to detect the relationship (with type I error level, $\alpha = 0.05$) would be high (0·83, 0·89 and 0·98, respectively). The lack of relationship within the Dendrocygninae and the Oxyurini (Table 1) may be due to small sample sizes.

The ratio of variation in allocation to variation in investment across the entire Anseriform order (0·11) is intermediate between the ratios in clades with significant negative correlations (≈ 0.22 in the Anatini and the Aythyini) and the ratios in clades without (≈ 0.05 in the Anserinae, Mergini and Tadornini) (Table 1). Similarly, the strength of the negative relationship between clutch size and egg mass in the Anseriformes ($r^2 = 0.18$) is intermediate between these two groups (Table 1, Fig. 1). The negative correlation across the entire order is highly significant, and is robust with regards to the branch lengths used; the r^2 of the relationship ranges from 0·092 to 0·298 in 95% of simulated trees, while the slope varies from −0·70 to −0·34. The strength of the trade-off between egg size and number in Anseriformes is similar to that found by Rohwer (1988; $r^2 = 0.13$), even though his analysis considered species as statistically independent. Blackburn's (1991b) analysis, which took phylogeny into account but included only a subset of Rohwer's (1988) data, provided an estimate that is

at the upper end of the range found in this study ($r^2 = 0.29$).

Van Noordwijk & de Jong's (1986) model assumes that variation in investment and allocation are independent of one another. However, the model appears to be robust to violation of this assumption; these two parameters are highly correlated in all but two groups of waterfowl (Table 2). Specifically, large clutch mass tends to be associated with clutches of many small eggs. Despite the correlation between investment and allocation, the model successfully explains between-clade variation in the relationship between egg mass and clutch size. This study has therefore shown (1) how van Noordwijk & de Jong's (1986) model can be extended to egg size/number trade-offs, and (2) that this model may be useful above the species level.

The trade-off between egg mass and clutch size is reflected by a negative correlation between these two life-history parameters within Anseriformes (this study) and among birds in general (Blackburn 1991a), despite many potentially confounding variables (see Blackburn 1991a). However, there is often no such inverse relationship within tribes and subfamilies (this study), and generally none within species of waterfowl (Rohwer 1988; Lessells, Cooke & Rockwell 1989; Rohwer & Eisenhauer 1989; Flint et al. 1996). A similar situation is observed in other taxa: interspecific trends often suggest trade-offs (Godfray, Partridge & Harvey 1991; Bernardo 1996; Polishchuck & Tseitlin 1999) while intraspecific correlations do not (Bernardo 1996). The results of this study suggest that van Noordwijk & de Jong's (1986) model may prove useful in understanding the heterogeneity between taxonomic levels in the relationship between egg size and number. Trade-offs between egg size and number will not be reflected by a negative correlation between these two parameters if the variation in investment is high relative to the variation in the patterns of allocation.

Acknowledgements

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