

Jordi Figuerola · Andy J. Green

## A comparative study of egg mass and clutch size in the Anseriformes

Received: 1 December 2004 / Revised: 2 August 2005 / Accepted: 24 August 2005 / Published online: 18 October 2005  
© Dt. Ornithologen-Gesellschaft e.V. 2005

**Abstract** The factors explaining interspecific differences in clutch investment in precocial birds are poorly understood. We investigated how variations in clutch characteristics are related to environmental factors in a comparative study of 151 extant species of ducks, geese and swans (Anseriformes). Egg mass was negatively related to clutch size in a phylogenetic regression, a relationship that was much stronger when controlling for female mass. Nest placement was related to both egg size and clutch size, with cavity-nesting species laying more but smaller eggs. Egg size was positively correlated with incubation period and with female mass, and also with sexual size dimorphism (i.e. male mass relative to that of the female). Clutch size was not related to female mass. Species with long term pair bonds laid smaller clutches and larger eggs. The size of the breeding range was strongly positively correlated with clutch size and clutch mass, and its inclusion in multivariate models made other biogeographical variables (hemisphere, breeding latitude or insularity) non-significant. The small clutches in insular species appear to be a product of small range size rather than insularity per se. Our results suggest there is an evolutionary trade-off between clutch and egg size, and lend support to Lack's resource-limitation hypothesis for the waterfowl.

**Keywords** Clutch mass · Clutch size · Egg size · Sexual dimorphism · Waterfowl

### Introduction

Clutch size varies widely both among and within bird species (Lack 1947; Klomp 1970). Variation in clutch size is an important factor related to the fitness of

individuals (Rockwell et al. 1987; Briskie and Sealy 1989; but see Hôrak et al. 1997) and the life history of a species (Martin 1995). Different ecological factors can potentially determine interspecific differences in clutch size in waterfowl (Anseriformes) and other birds (see Winkler and Walters 1983; Rohwer 1992; Monaghan and Nager 1997 for reviews).

Firstly, the number of eggs in species not providing food directly to the chicks may be limited by the capacity to cover and incubate the eggs effectively (Rice and Kenyon 1962). Some support for this hypothesis has been found for shorebirds (Winkler and Walters 1983; Székely et al. 1994), but in waterfowl and other groups hatching rates are often not affected in experimentally increased clutches (Rohwer 1992; Leopold 1951; Hilden 1964; Fredrickson 1969; Heusmann 1972; Rohwer 1988).

Secondly, clutch size could be limited by predation pressure during nesting (Slagsvold 1982; Arnold et al. 1987), i.e. the more eggs are laid the longer they are exposed to predation before the start of incubation. Although indirect support for this hypothesis is provided in passerines by the larger clutch size in species nesting in cavities, which are less exposed to nest predation (Lima 1987), to our knowledge no such analyses have been done on any group of nidifugous birds (but see Blackburn (1991a) for general analyses on precocial and altricial birds). Laurila (1988) reported a significant effect of nest placement on clutch size in waterfowl, due to a larger clutch size, both in species breeding in cavities and in species that make concealed nests on the ground, in comparison with unconcealed nests on the ground. Geffen and Yom-Tov (2001) confirmed the differences in clutch size between open and cavity nesters controlling for the phylogenetic relationships between species, but failed to explore the relevance of other potential factors related to clutch size. Perrins (1977) showed that, if predation pressure is high enough, natural selection could favour clutch size limitation. However, in most species of waterfowl, predation levels required for this mechanism are very high (95% of clutches predated;

Communicated by C. Rahbek

J. Figuerola (✉) · A. J. Green  
Department of Applied Biology, Estación Biológica de Doñana,  
CSIC, Avda. María Luisa s/n, 41013 Sevilla, Spain  
E-mail: jordi@ebd.csic.es

Winkler and Walters 1983), although some authors still consider such a possibility as realistic (Arnold et al. 1987). Milonoff (1989, 1991) proposed the re-nesting hypothesis where clutch size is determined by predation rates and the capacity to lay replacement clutches. Unlike the traditional nest-predation hypothesis, the re-nesting hypothesis does not require such high nest predation rates (Milonoff 1989).

Thirdly, clutch size could be limited by a decrease in offspring survival after hatching, for example due to an increased risk of detection by predators of larger broods. However, Rohwer (1992) in his review concluded that survival of waterfowl young is largely independent of brood size in waterfowl (see also Bustnes and Erikstad 1991; Milonoff et al. 1995). Furthermore, if parental care were so costly, brood amalgamation would not be so common in waterfowl (Afton and Paulus 1992; Beauchamp 1997). Nevertheless, some studies of waterfowl have found that predation risk (Hilden 1964; Cooch 1961; Lessells 1986) or parental vigilance (Forslund 1993) increased with brood size.

Finally, clutch size may be limited by the amount of resources available to the laying female (Lack 1947). This resource-limitation hypothesis remains controversial, particularly in the case of waterfowl (Ankney et al. 1991; Arnold and Rohwer 1991). Food shortages result in a reduction of clutch or egg size in several duck species (Bengtson 1971; Pehrsson 1991), although this could potentially reflect an adjustment of investment according to reduced expectations of the resources available later during brood rearing. The resource-limitation hypothesis is supported by the trade-off between egg size and clutch size at an interspecific level (Klomp 1970; Blackburn 1991a; Lack 1968; Blackburn 1991b), although this relationship is considered weak in waterfowl (Rohwer 1992, 1988, 1991), perhaps because of the influence of other factors such as breeding phenology (e.g. species breeding later may accumulate more reserves to invest in their clutch; Green et al. 1999). Further support for the resource-limitation hypothesis comes from the finding that female common eiders (*Somateria mollissima*) or mallards (*Anas platyrhynchos*) do not extend egg-laying if eggs are removed experimentally (Rohwer 1984; Swennen et al. 1993), whilst females in better body condition lay larger clutches (Erikstad et al. 1993). However, egg removal affected neither the final clutch size nor survival of female goldeneyes (*Bucephala clangula*) (Milonoff and Paananen 1993).

Insular species of waterfowl tend to lay fewer but larger eggs than mainland species, without a marked change in relative clutch mass (Rohwer 1988; Williams et al. 1991; Livezey 1993). This has usually been suggested to reflect a switch from  $r$  to  $k$  selection on islands, to increase the size and survivorship of hatchlings, but it may also reflect difficulties in nutrient allocation (i.e. island diets may demand delays of several days between laying of each egg; see Rohwer 1992, 1988; Williams et al. 1991). Furthermore, clutch size may not only be limited by the resources available for laying or for

parental care in a given year, but by the optimisation of reproductive effort over the whole life history of individuals, taking the costs of reproduction into account (Stearns 1992). For species with low life expectancy, it pays to invest more in current reproduction, while for long lived species reproductive effort in a given year should be limited so as to ensure future opportunities in later years. According to this life-time reproduction model, species living in more stable environments with high life expectancy (e.g. living on islands and/or in the tropics) are expected to lay smaller clutches (Blondel 2000; Johnston et al. 1997; but see Karr et al. 1990).

More attention has been paid to explaining interspecific variation in clutch size than in egg size (but see Laurila 1988). Large eggs produce large chicks better able to stand cold climates (Koskimies and Lahti 1964). At the intraspecific level, egg size is a good predictor of future chick growth and survival (Galbraith 1988; Dawson and Clark 1996; see also Williams 1994). Clutch size has typically been used as an estimate of investment in reproduction instead of focussing on clutch mass (see Martin 1995; Ricklefs 1977). However, as we will show, interspecific variability in egg size in relation to clutch size is an important component of interspecific variability in laying investment.

In this paper, we explore how variations in clutch characteristics (egg mass and clutch size) are related to environmental factors using comparative data for almost all living species of ducks, geese and swans ( $n=151$ ). Although numerous previous works cited above have tested hypotheses for clutch size determination in this group, the hypotheses have been tested separately without controlling for other, confounding, variables and have not adequately controlled for the phylogenetic relationships between species. We use a comparative, multivariate approach controlling for variables related to clutch or egg size variation, including breeding latitude, breeding range, mating system and insularity (see Klomp 1970; Gaston and Blackburn 1996), to establish which variables are most related to clutch and egg size variation.

---

## Methods

In our analyses, we included 13 variables likely to correlate with egg mass, clutch size and clutch mass (see appendix for data sources). These variables were: (1) female body mass; (2) size dimorphism (see below for calculation); (3) incubation period; (4) breeding latitude estimated from distribution maps (Madge and Burn 1988) as the mean of the most northerly and southerly points (positive values were given to all species by considering breeding latitude in degrees north of 55°S, to facilitate the use of second and third order polynomials so as to allow for non-linear relationships); (5) absolute breeding latitude calculated as the number of degrees from the equator irrespective of the direction (i.e. 10°S and 10°N are equivalent); (6) migration distance,

calculated as the number of degrees between breeding and wintering latitudes (the latter calculated in the same way as the former); (7) breeding range, estimated as the number of squares occupied during the breeding season in the WORLDMAP grid, a projection of the world divided in equal-area grid squares of ca. 611,000 km<sup>2</sup> (Gaston and Blackburn 1996; Williams 1996); (8) hemisphere, a categorical variable indicating in which hemisphere (North or South) most of the breeding area of the species occurs; (9) migratory behaviour, a categorical variable for migratory and sedentary species, classifying a species as migratory when distance between mean breeding and wintering latitudes exceeds one degree of latitude; (10) nest placement, a categorical variable indicating whether or not the species nests mainly in cavities; (11) mating system, a categorical variable for species pairing less than, or at least, once a year (after Scott and Clutton-Brock 1989); (12) sexual dichromatism, scoring species as sexually dimorphic in coloration or not, based on the colour plates of Madge and Burn (Madge and Burn 1988); (13) insularity, a categorical variable with species endemic to islands with an area of less than 20,000 km<sup>2</sup>, and those with a wider distribution (after Green 1996). Body mass, egg and clutch mass and breeding range were log transformed previous to analyses. The original data used in these analyses and the data sources are listed in the appendix.

### Statistical analyses

Data from different species do not constitute independent data points, owing to their shared ancestry. Consequently, regular statistical methods should not be used without accounting for the phylogenetic relationships between species. Phylogenetically independent contrasts (Harvey and Pagel 1991) were calculated using a working phylogeny for 156 waterfowl species based on Livezey's analyses of morphological data (Livezey 1986, 1991, 1995a, b, c, 1996a, b, 1997a, b; Livezey and Humphrey 1992). This phylogeny was presented by Figuerola and Green (2000). Since no compatible estimates of branch length were available for each of the original sources, node height was considered proportional to the number of species included in the node, then branch length was calculated as the difference in height between its upper and lower nodes (Grafen 1989). Only data based on the measurement of at least five individuals of each sex were considered for analyses. To calculate size dimorphism we used independent contrasts calculated using the CAIC programme (Purvis and Rambaut 1995). We first regressed the independent contrast in log transformed male mass (dependent variable) against independent contrasts in log transformed female mass, and calculated the slope of the regression through the origin. A line with this same slope was fitted to the species data and the residuals from this line were used as estimates of size dimorphism in

further analyses (see Purvis and Rambaut 1995). Size dimorphism was not calculated directly from raw data (e.g. as the residuals of a regression of male against female mass) because the slope of this regression could be biased due to the phylogenetic relationship between species (Harvey and Pagel 1991).

To determine the factors related to interspecific differences in egg mass, clutch size and clutch mass, we used the Grafen phylogenetic regression (Grafen 1989, 1992). Unlike independent contrasts, the Grafen regression is appropriate to analyse continuous and discrete variables because it does not assume a Brownian motion model of evolution and is based on general lineal modelling. When the phylogeny and branch lengths are known, the Grafen regression and independent contrasts give identical results (Martins and Hansen 1996). However, for this phylogeny, no estimates of branch length (i.e. time since divergence of species) are available and branch length were calculated according to Grafen's (Grafen 1989) method.

The significance of the different variables was tested separately and the variable best fitting the data was first added to the model. The significance of the remaining variables was then tested again, and this forward stepwise procedure was repeated until no additional variable significantly increased the fit of the model and all the variables included contributed significantly to the fit of the model (see Sokal and Rohlf 1995, p. 656, for a more detailed description of the procedure, and Bustamante 1997 for an example using similar methods). We also provide the significance of univariate analyses in order to illustrate what correlational relationships disappear after controlling for other ecological factors. To determine the extent to which our results were dependent on the phylogeny used, all the above analyses were repeated incorporating an alternative phylogeny for the tribe Anatini based on molecular data (Johnson and Sorenson 1999). The results of these analyses are only discussed below when differing significantly from the first set of analyses, but further details are available from the authors on request.

---

## Results

The influence of each variable on clutch and egg parameters was analysed both individually (Table 1) and collectively in a multivariate model (Table 2).

### How clutch characteristics relate to female characteristics

In a phylogenetic regression, egg mass was strongly correlated with female mass both in univariate and multivariate analyses ( $P < 0.0001$ ; Table 1, 2). Size dimorphism was unrelated to egg mass in univariate analysis (Table 1), but after controlling for other variables related to egg size species with bigger males

**Table 1** Results of a Grafen phylogenetic regression testing the significance of different variables to explain the evolutionary changes in egg size, clutch size and clutch mass in ducks, geese and swans

	Egg mass				Clutch size				Clutch mass			
	Estimate	<i>F</i>	<i>df</i>	<i>P</i>	Estimate	<i>F</i>	<i>df</i>	<i>P</i>	Estimate	<i>F</i>	<i>df</i>	<i>P</i>
Female mass (log)	0.4894	206.60	139	<0.0001	0.8241	0.79	134	0.38	0.5495	157.44	138	<0.0001
Size dimorphism	0.2565	1.64	134	0.20	-0.7596	0.07	130	0.79	0.2677	0.98	133	0.32
Incubation length (days)	0.01475	14.96	130	0.0002	-0.02953	0.66	126	0.42	0.01541	7.09	129	0.009
Breeding latitude (degrees)	-0.000391	1.91	139	0.17	0.01210	9.09	134	0.003	0.000193	0.46	138	0.50
Breeding latitude	-0.0000021	0.87	139	0.35	0.000068	4.85	134	0.03	0.0000019	0.34	138	0.56
Breeding latitude	-0.00000002	0.68	139	0.41	0.0000004	2.66	134	0.11	0.00000001	0.12	138	0.73
Abs.breeding latitude	0.000711	2.13	139	0.15	-0.00779	0.83	134	0.36	0.000303	0.46	138	0.50
Migration distance	-0.00239	3.97	139	0.05	0.01049	0.59	134	0.44	-0.00352	1.38	138	0.24
Breeding range (log)	-0.00052	0.00	139	1.00	0.8934	11.21	134	0.001	0.06236	6.86	138	0.01
Hemisphere (factor)	0.01521	0.17	139	0.68	-0.8429	6.10	134	0.01	-0.02708	1.11	138	0.29
Migratory behaviour (factor)	-0.00312	0.02	139	0.89	0.4563	2.49	134	0.12	0.02692	1.19	138	0.28
Nest placement (factor)	-0.1279	21.16	139	<0.0001	1.233	11.13	134	0.001	-0.05196	2.19	138	0.14
Mating system (factor)	-0.04901	1.80	138	0.18	0.9054	3.29	133	0.07	0.002805	0.00	137	1.00
Colour dimorphism (factor)	0.001074	0.04	139	0.84	-0.02514	0.01	134	0.92	-0.01847	0.07	138	0.79
Insularity (factor)	0.02616	0.34	139	0.56	-1.794	9.36	134	0.003	-0.09425	3.10	138	0.08

The significance of each variable was tested individually without controlling for the effects of the other variables (i.e. univariate analyses)

(relative to female mass) laid relatively bigger eggs ( $P=0.002$ ; Table 2). Clutch size was not significantly related to female mass or to sexual size dimorphism (Table 1). Female mass was the variable best explaining the interspecific variation in clutch mass ( $P<0.0001$ ; Table 1). There was no relationship between size dimorphism and clutch mass (Table 1). These relationships remained unchanged in the multivariate model of clutch mass (Table 2).

explained only 3.7% of the original deviance in egg mass. However, given that body mass covaries with egg mass but not with clutch size (see above), the relationship between clutch size and egg mass was recalculated while controlling for female mass. As a result, the variance in egg mass explained by clutch size increased dramatically ( $F_{1,137}=32.67$ ,  $P<0.0001$ ) to 19.1% of the original deviance.

How are clutch size and egg mass related?

Does clutch size increase with latitude?

In a phylogenetic regression, a negative and weakly significant relationship was detected between egg mass and clutch size ( $F_{1,138}=4.54$ ,  $P=0.03$ ). Clutch size

Clutch size significantly increased with breeding latitude ( $P=0.003$ ; Table 1), but not with absolute breeding latitude (Table 1). An effect of hemisphere was also

**Table 2** Results of a Grafen phylogenetic regression testing the significance of different variables to explain the evolutionary changes in egg size, clutch size and clutch mass in ducks, geese and swans

	Egg mass				Clutch size				Clutch mass			
	Estimate	<i>F</i>	<i>df</i>	<i>P</i>	Estimate	<i>F</i>	<i>df</i>	<i>P</i>	Estimate	<i>F</i>	<i>df</i>	<i>P</i>
Female mass (log)	0.4446	260.3	120	<0.0001	–	3.18	135	0.08	0.5453	179.6	127	<0.0001
Size dimorphism	0.3448	9.92	120	0.002	–	1.48	130	0.23	–	0.20	122	0.66
Incubation length (days)	0.01091	21.05	120	<0.0001	–	0.05	125	0.82	0.00791	7.69	127	0.007
Breeding latitude (degrees)	–	0.00	119	1.00	–	1.50	135	0.22	–	0.89	126	0.35
Breeding latitude	–	0.00	119	1.00	–	0.40	135	0.53	–	0.12	126	0.73
Breeding latitude	–	0.05	119	0.82	–	0.05	135	0.82	–	0.03	126	0.86
Abs.breeding latitude	–	0.26	119	0.61	–	0.87	135	0.35	–	1.85	126	0.18
Migration distance	–	0.52	119	0.47	–	0.06	135	0.81	–	0.48	126	0.49
Breeding range (log)	–	0.49	119	0.49	0.7386	7.78	131	0.007	0.05890	10.86	127	0.001
Hemisphere (factor)	–	0.02	119	0.89	–	1.79	135	0.18	–	1.78	126	0.18
Migratory behaviour (factor)	–	0.05	119	0.82	–	0.79	135	0.38	–	0.19	126	0.66
Nest placement (factor)	-0.07547	16.68	120	0.0001	1.3400	12.88	136	0.0005	–	0.15	126	0.70
Mating system (factor)	-0.05829	8.03	120	0.005	1.0070	5.59	136	0.02	–	0.25	125	0.62
Colour dimorphism (factor)	0.03818	5.54	120	0.02	–	0.47	135	0.49	–	1.58	126	0.21
Insularity (factor)	–	0.22	119	0.64	–	2.92	135	0.09	–	0.21	126	0.65
Initial deviance	10.16	291	893.60	291	9.26	289						
Final deviance	1.61	257	592.71	286	2.92	268						

A forward stepwise procedure was followed until no additional variable significantly increased the fit of the model (i.e. multivariate analysis). Model estimates are presented for variables retained in the final model. For other variables, we give their significance when added to the final model

detected, with larger clutches in the north ( $P=0.01$ ; Table 1). Breeding latitude<sup>2</sup> was also positively related to clutch size ( $P=0.03$ ; Table 1). However, after controlling for the effect of other variables explaining more variance in the model, these four variables were unrelated to clutch size (Table 2).

Does clutch size increase in cavity nesting species?

Cavity nesting species laid larger clutches ( $P=0.001$ ; Table 1), composed of smaller eggs ( $P<0.0001$ ; Table 1). However, clutch mass did not vary with nest placement (Table 1). The effect of nest placement on clutch size and egg mass remained highly significant in multivariate models (Table 2).

Other variables related to egg and clutch characteristics

Species breeding on small islands produced smaller clutches than those with a wider distribution ( $P=0.003$ ; Table 1). However, this effect was not significant in the multivariate model ( $P=0.09$ ; Table 2), probably because insularity was confounded with breeding range, which was strongly correlated with clutch size ( $P=0.007$ ; Table 2). No effect of insularity was detected on egg size or clutch mass (Table 1, 2). Breeding range was positively correlated with clutch size ( $P=0.001$ ) and clutch mass ( $P=0.01$ ), but was not related to egg mass (Table 1). Similar results were obtained in multivariate models (Table 2).

Egg mass was correlated with migration distance ( $P=0.05$ ), but not with migratory behaviour (Table 1). The egg mass-migration distance relationship disappeared when controlling for other variables (Table 2). Clutch size and clutch mass were unrelated to migration distance or migratory behaviour (Table 1). When using the Johnson and Sorenson (1999) molecular phylogeny, a significant relationship between egg size and breeding latitude was detected ( $F_{1,134}=4.30$ ,  $P=0.04$ ), but this relationship was not significant after controlling for other variables more correlated with egg mass ( $F_{1,116}=0.02$ ,  $P=0.89$ ).

Mating system had no significant effect on egg mass or clutch mass when tested in univariate analyses (Table 1). There was a trend for larger clutch size in species that mate more frequently ( $P=0.07$ ; Table 1), a statistically significant relationship when controlling for other variables ( $P=0.02$ ; Table 2). After controlling for other variables, species with more frequent matings also had smaller eggs ( $P=0.005$ ). When repeating the analyses with the Johnson and Sorenson (1999) phylogeny, a significant positive effect of mating frequency on clutch size and negative effect on egg mass was detected in both the univariate (egg mass,  $F_{1,134}=5.79$ ,  $P=0.02$ ; clutch size,  $F_{1,129}=6.24$ ,  $P=0.02$ ) and multivariate analyses (egg mass,  $F_{1,117}=7.78$ ,  $P=0.006$ ; clutch size,  $F_{1,132}=7.82$ ,  $P=0.006$ ).

Colour dimorphism had no significant effect on clutch size or clutch mass (Table 1, 2). In multivariate analyses, colour dimorphic species laid larger eggs ( $P=0.02$ , Table 2), although this result was not supported by univariate analyses or analyses done with Johnson and Sorenson (1999) phylogeny ( $F_{1,116}=1.52$ ,  $P=0.22$ ).

## Discussion

In this study, we have analysed the ecological factors potentially explaining interspecific differences in clutch and egg size among waterfowl. In other groups of birds, body mass usually explains a low but significant proportion of the variation in clutch size (Blackburn 1991a; Newton 1977), a pattern reported in previous studies with waterfowl (Laurila 1988; Rahn et al. 1975). When we analysed our data set with standard regression techniques, a significant negative relationship was found ( $R=-0.35$ ,  $F_{1,149}=20.31$ ,  $P<0.0001$ ), but this becomes non-significant when controlling for phylogeny, i.e. closely related swans and geese all tend to have smaller clutches than their smaller-bodied cousins, the true ducks. A recent analysis based on mean values for bird families and orders concluded that female mass was correlated with egg mass, but not with clutch size or other measures of reproductive effort (Bennett and Owens 2002).

Our study illustrates how female size should be controlled for when examining the trade-off between egg and clutch size, as this improves the relationship between these parameters. Rohwer (1992, 1988, 1991) and Blackburn (1991a, b) debated the significance of inverse correlations between egg and clutch size in the light of the resource-limitation hypothesis. We suggest that the biological significance of this correlation cannot simply be assessed by the relative amount of variance explained, since a number of factors independent of the resource-limitation hypothesis are likely to influence this relationship. For example, the relationship between independent contrasts in egg and clutch size ( $R=-0.19$ ,  $F_{1,125}=4.82$ ,  $P=0.03$ ) is weaker than that between the changes in egg and clutch size associated with a shift in the type of nest used ( $R=-0.69$ ,  $F_{1,15}=13.31$ ,  $P=0.002$ ). This suggests that, when some ecological factor influences reproductive parameters, the changes occurring in egg and clutch size are strongly correlated.

Unlike field studies, where experimental manipulations can demonstrate the existence of trade-offs between variables such as egg and clutch size (see Stearns 1992), no such opportunity for manipulation exists in comparative analyses such as ours. However, we suggest that the correlated changes in egg mass and clutch size associated with changes in species ecology such as nest placement provide further support for the existence of an egg size-number trade-off. Lack (1968) considered that clutch size in species that do not feed

their chicks was limited by the amount of resources available to the laying female. The costs of egg laying are not only limited to the energy stored in the egg, but include the energetic costs of acquiring the necessary resources, producing and incubating the egg and the additional costs of chick-rearing (Monaghan and Nager 1997). Our results support the view that resource-limitation has a direct influence on clutch mass in waterfowl, producing a trade-off between clutch and egg size. They are consistent with the correlations between clutch size and duckling mass recently demonstrated at the intraspecific level in ducks (Blums et al. 2002). Unfortunately, no information is available on the survival rates of most species. Consequently, we have been unable to analyse the relationship between survival rates and clutch size, and how well interspecific variation in clutch characteristics is compatible with the life-time reproduction model. However, it is noteworthy that the species with the highest clutch size in the Old World (the marbled teal *Marmaronetta angustirostris*) appears to have an extremely low survival rate (Green 1998; Green et al. 2005).

We have found that, at the interspecific level, egg size in waterfowl is not only related to female size, but also to the extent of sexual size dimorphism, increasing in species with relatively larger males. Thus, egg size is influenced by adult size, whether male or female, not simply by female size. Egg size has an important impact on chick development, survival and adult size (Galbraith 1988; Ankney 1980; Rhymer 1988; Grant 1991), and thus selection for larger adult size of either sex will translate into selection for laying larger eggs that are likely to produce larger offspring at maturity. Egg size is probably correlated with relative male size owing to the greater mating success of larger males in dimorphic species (Andersson 1994). Our results contrast with a previous analysis by Sigurjónsdóttir (1981) that failed to detect any relationship between size dimorphism and 'reproductive effort', a combination of egg size, clutch size and incubation length standardised as a function of species size. However, this author did not examine the influence of size dimorphism on more simple variables, like egg size, and did not control adequately for the effects of body size and phylogeny in her analyses (see Ranta et al. 1994).

Cavity nesting is an important factor affecting interspecific variation in clutch size (Lack 1948; Sæther 1996). We have demonstrated that cavity nesting waterfowl lay larger clutches than open nesters, even after controlling for a number of potentially confounding ecological variables. These results are consistent with those for passerines (Slagsvold 1982; Blackburn 1991a). Intraspecific nest-parasitism is common in Anseriformes, and was considered more common in cavity nesting species (Yom-Tov 1980), although further analyses suggested that both characters have evolved independently (Geffen and Yom-Tov 2001). We have used estimates of clutch size based on detailed intraspecific studies which have usually

controlled for the effect of intraspecific nest parasitism. We found egg size to change in an opposing manner to clutch size, so that overall clutch mass does not differ between cavity and open nesters. In a previous analysis, Geffen and Yom-Tov (2001) concluded that cavity nesting had no significant effect on egg size. However, their and our study have important differences that can explain these contrasting results. Firstly, the number of species included in our study is slightly larger, but this seems unlikely to explain the differences given that the number of evolutionary changes in nest site selection is the same. Secondly, the methods used to control for phylogenetic effects are different (phylogenetic regression vs independent contrasts), and thirdly and probably most importantly, we used a multivariate approach controlling for a number of other factors potentially related to egg size. To our knowledge, such analyses have not been published with other birds so it is not clear if the pattern of larger clutches of smaller eggs in cavity nesting species also occurs in altricial species. Our results suggest a change in the distribution of resources during laying in cavity nesters (more eggs at the cost of a small size) instead of an overall increase in resources devoted to clutch formation. The smaller egg size in cavity nesting species is important given the direct relationship between egg size and fitness (Hôrak et al. 1997). The fitness benefits derived from a larger clutch may overcome the costs of smaller eggs in terms of reduced chick survival. Alternatively, nests in cavities offer a more stable environment than open nests, and this could reduce the risk of egg (or chick) chilling, one possible cost of smaller eggs (O'Connor 1979; Potti and Merino 1996). The reduced risk of predation in cavity nesting species is often considered to have allowed an increase in clutch size via prolonging laying for a few days. Perrins (1977) model does not support this hypothesis in waterfowl, because the required levels of predation are unrealistically high (Winkler and Walters 1983), but this model has been severely criticised (Arnold et al. 1987; Laurila 1988).

Alternatively, Beissinger and Waltman (1991) and Martin (1993) suggested that the scarcity of cavities could be the factor responsible for the higher investment in egg laying by cavity nesting species. Cavity availability will limit the opportunity to breed. According to this hypothesis, only cavity nesters that cannot excavate their own nests will lay larger clutches, predictions supported in North American and European Picidae and Sittidae (Martin 1993) but not in Parids (Mönkkönen and Orell 1997). Given that no waterfowl excavate their own cavities, we cannot test this explanation directly. However, our finding that clutch mass does not increase in cavity nesters is evidence against this hypothesis, since it would predict that cavity nesting waterfowl would invest more in a clutch given the difficulty in acquiring cavities in future breeding seasons. Much work is needed to identify the evolutionary factors related to larger clutches in cavity nesting species,

examining both the demographic and behavioural predictions derived from each hypothesis (Beissinger 1996).

Incubation length was positively related to egg size in waterfowl, as observed in birds in general (Rahn and Ar 1974). Experimental increase in clutch size increased incubation time in shorebirds (Székely et al. 1994; Sandercock 1997) and blue-winged teal *Anas discors* (Feldheim 1997). However, we found that clutch size was unrelated to incubation length at the interspecific level. This suggests that incubation length has not directly limited the evolution of clutch size in waterfowl.

Breeding range showed a very important correlation with clutch size and clutch mass, closely resembling the results of Gaston and Blackburn (1996). In the case of clutch size, breeding range absorbed the variance explained by insularity, hemisphere and breeding latitude when considered together in the multivariate model. This suggests that the smaller clutches of waterfowl endemic to islands reflect the extreme of a continuous relationship between clutch size and breeding range. The small clutch size in island breeding waterfowl has been considered to result from a shift towards the *k* end of the *r-k* continuum in reproductive strategies (Pianka 1970), or towards a prudent breeding system on the life-time reproduction model (Blondel 2000). Our results suggest that, once controlling for breeding range, insularity may not have a unique influence on reproductive parameters in waterfowl, contrary to previous suggestions (Rohwer 1988; Lack 1970; Weller 1980).

Breeding range may also explain the smaller clutches in the southern hemisphere, which is occupied by waterfowl species with much more reduced breeding ranges than northern species ( $F_{1,139} = 10.92$ ,  $P = 0.001$ ). Thus, the relationship we observed between breeding latitude and clutch size could be explained by a strong relationship between breeding latitude and breeding range (already reported by Gaston and Blackburn 1996). We are unable to establish the causality of these relationships, which could even be due to some other variable not included in our analyses. In British birds, egg mass and total clutch mass were positively correlated with species abundance (Blackburn et al. 1996), and abundance and breeding range size are positively correlated in all animals (Gaston 1996; Gaston et al. 1997). We suggest that our relationship between clutch size and breeding range reflects an overall positive relationship between investment in reproduction, abundance and breeding range in waterfowl. It may ultimately be a consequence of environmental stability, since the species with the largest breeding ranges use boreal continental parts of the northern hemisphere that are isolated from oceanic influences. These areas have higher seasonal variation and may cause lower survival rates in waterfowl.

Waterfowl species with long term pair bonds laid significantly smaller clutches, tending to lay larger eggs ( $P = 0.09$  or  $P = 0.005$  depending on the phylogeny used). These tend to be *k* selected species investing more

in parental care and with lower mortality rates and consequently investing less in current reproduction according to the life-time reproduction model (Scott and Clutton-Brock 1989; Sigurjónsdóttir 1981). A possible relationship between colour dimorphism and egg size was found, although this result dependent on the phylogeny used in the analyses, probably because of the different grouping of species with different colour dichromatism patterns, making necessary further research to confirm the soundness of this result.

In conclusion, interspecific analyses suggest that incubation length is not likely to have limited the evolution of clutch size in waterfowl. Clutch size and egg size are negatively correlated, but a number of other factors affect this relationship. A number of other variables are related to clutch characteristics, breeding range, nest placement, sexual dimorphism and mating system being especially important. Our findings bring into question the uniqueness of insular taxa in their response to the clutch size-egg size trade-off.

---

## Zusammenfassung

Vergleichende Analyse der Eimasse und Gelegegröße bei Anseriformes

Welche Faktoren die artspezifischen Unterschiede in der Gelegegröße von Nestflüchtern bedingen, ist kaum bekannt. Deshalb untersuchten wir, in wie weit Gelegetherkmale durch Umweltfaktoren beeinflusst sind. Dazu verglichen wir die Gelegetherkmale von 151 Arten von Enten, Gänsen und Schwänen. In einer phylogenetischen Regression war die Eimasse negativ korreliert mit der Gelegegröße und dieser Zusammenhang war noch ausgeprägter, wenn die Körpermasse der Weibchen berücksichtigt wurde. Der Neststandort war positiv korreliert mit Eigröße und Gelegegröße. Höhlenbrüter legen mehr aber kleinere Eier. Die Eigröße war positiv korreliert mit der Bebrütungszeit, der Körpermasse der Weibchen und dem Ausmaß des sexuellen Dimorphismus (Körpermasse des Männchens in Relation zu der des Weibchens). Die Gelegegröße stand in keinem Bezug zur Körpermasse der Weibchen. Arten mit langer Paarbindung legen kleinere Gelege und größere Eier. Die Ausdehnung des Brutareals war positiv korreliert mit der Gelegegröße und der Gelegemasse. Bei Einschluss der Gelegemasse in einem multivariaten Modell zeigten sich alle andere biogeografischen Variablen (Erdeil, geografische Länge des Brutgebiets, Insularität) als nicht signifikant bedeutsam. Die kleineren Gelege von Inselarten scheinen damit eher die Folge des kleinen Brutareals zu sein als durch die Insellage selbst bedingt. Unsere Ergebnisse deuten einen evolutionären Konflikt zwischen Gelegegröße und Eigröße an und unterstützen die Hypothese von Lack, nach der Wasservögel Ressourcen limitiert sind.

**Acknowledgements** We are grateful to G. Callard, the late J. Kear, K. Kilpatrick, A. Marshall, H.G. Young and Oxford University Press for their help in compiling the data on which our analyses are based. Two anonymous referees provided helpful comments on an earlier version of the manuscript

## Appendix

Table 3

**Table 3** Data used in the analyses

Species	a	b	c	d	e	f	g	h	i	j	k	l
<i>Aix galericulata</i>	628	512	29	38.7	9.3	41.5	7	0.16051	2	2	2	1
<i>A. sponsa</i>	681	635	30	42.6	11.1	32.5	15	0.1046	2	2	2	1
<i>Alopochen aegyptiacus</i>	2,075	1,650	29	95.7	8.5	-4	42	0.1848	2	1	1	1
<i>Amazonetta brasiliensis</i>	430	370	25	33.3	7	-13.5	22	0.1334	2	1	2	1
<i>Anas acuta</i>	1,035	986	23	40.3	6.9	52.5	84	0.1004	1	2	2	1
<i>A. americana</i>	792	719	25	44.1	8.5	57	22	0.1177	1	2	2	1
<i>A. aucklandica</i>	521	410	32.5	70.5	4	-50	1	0.1733	1	1	2	2
<i>A. bahamensis</i>	503	569	25	40.5	8.4	-2	15	-0.0195	1	1	1	1
<i>A. bernieri</i>	380	344	26.5	28.6	6.3	-18	3	0.1105	2	1	1	1
<i>A. capensis</i>	419	380	25.5	35.9	8.4	-11.5	23	0.1108	1	1	1	1
<i>A. carolinensis</i>	322	309	22	25.2	8.6	55.5	30	0.0839	1	2	2	1
<i>A. castanea</i>	660	590	25.5	44	9.7	-34	7	0.1221	2	1	2	1
<i>A. chlorotis</i>	579	479	29.5	60.8	5.5	-40.5	5	0.1535	1	2	2	1
<i>A. clypeata</i>	636	590	23	39.1	10.2	54	70	0.1061	1	2	2	1
<i>A. crecca</i>	364	318	22	29	9.5	55	59	0.1250	1	2	2	1
<i>A. cyanoptera</i>	408	363	25	30.8	9.7	37.5	28	0.1187	1	2	2	1
<i>A. diazi</i>	1,010	902	26			21	3	0.1275	1	2	1	1
<i>A. discors</i>	409	363	23	28.1	10.4	48.5	19	0.1197	1	2	2	1
<i>A. eatoni</i>	497	441		39.6	5	-49	1	0.1221	1	2	2	2
<i>A. erythrorhyncha</i>	617	566	26	40.1	9	-13.5	23	0.1105	1	1	1	1
<i>A. falcata</i>	713	585	24.5	49.7	8	50.5	15	0.1593	1	2	2	1
<i>A. flavirostris</i>	429	394	24	34.3	6.5	-23	20	0.1058	2	1	1	1
<i>A. formosa</i>	437	431	25	30.9	7.3	68	6	0.0759	1	2	2	1
<i>A. fulvigula</i>	1,030	968	26	50	10	27	3	0.1061	1	2	1	1
<i>A. georgica</i>	632	535	26	37	4.2	-28.5	17	0.1446	1	1	1	1
<i>A. gibberifrons</i>	508	469	24.5	36	7.9	-20.5	33	0.1055	2	1	1	1
<i>A. hottentata</i>		240	26	26.6	7.1	-10.5	26		1	2	1	1
<i>A. laysanensis</i>	463	427	27	44.1	3.4	24	1	0.1049	1	2	2	2
<i>A. luzonica</i>	906	779	25.5	50.4	10	-7	3	0.1423	1	2	1	1
<i>A. melleri</i>	1,010	911	28.5	50.1	8.15	-19.5	3	0.1233	1		1	1
<i>A. penelope</i>	819	724	24.5	46.4	9	62	38	0.1294	1	2	2	1
<i>A. platalea</i>	608	523	25	41.3	6.5	-41.5	12	0.1375	1	1	2	1
<i>A. platyrhynchos</i>	1,279	1,123	25	49.9	9.7	44.5	107	0.1374	1	2	2	1
<i>A. poecilorhyncha</i>	1,365	1,025	27	55.6	8.5	31.5	35	0.1246	2	2	1	1
<i>A. querquedula</i>	342	310	22	28	8.5	50.5	40	0.1087	1	2	2	1
<i>A. rubripes</i>	1,400	1,100	27	61.5	9.5	47.5	15	0.1853	1	2	1	1
<i>A. sibilatrix</i>	939	828	26	57.2	6.5	-46.5	8	0.1321	1	1	1	1
<i>A. smithii</i>	688	597	27.5	44.7	9.4	-29	4	0.1352	1	2	2	1
<i>A. sparsa</i>	1,086	914	28	67.7	5.9	-11.5	26	0.1534	2	1	1	1
<i>A. strepera</i>	990	849	26	45.9	9.5	48	53	0.1444	1	2	2	1
<i>A. superciliosa</i>	1,089	981	29	54.1	9.1	-21	41	0.2042	2	1	1	1
<i>A. undulata</i>	954	817	27	52.4	7.8	-11.5	18	0.1445	1	2	1	1
<i>A. versicolor</i>	442	373	25.5	30.6	8.5	-32	16	0.1419	1	1	1	1
<i>A. wyvilliana</i>	644	585	28	32.1	8.3	24	1	0.1151	1	2	1	2
<i>Anser albifrons</i>	2,703	2,456	27.5	128	4.9	68.5	24	0.1315	1	1	1	1
<i>A. anser</i>	3,509	3,108	27.5	165	5.9	50.5	37	0.1453	1	1	1	1
<i>A. brachyrhynchus</i>	2,770	2,520	26.5	122.5	4.3	70	5	0.1313	1	1	1	1
<i>A. caeruleus</i>	2,744	2,517	23	122	4	66.5	13	0.1277	1	1	1	1
<i>A. canagicus</i>	2,812	2,766	25	120.4	4.8	65.5	2	0.0984	1	1	1	1
<i>A. cygnoides</i>	3,500	3,150	28	142.7	5.5	48	4	0.1386	1	1	1	1
<i>A. erythropus</i>	1,870	1,725	26.5	103	5	68	17	0.1208	1	1	1	1
<i>A. fabalis</i>	3,198	2,843	28	146.2	5	62.5	38	0.1427	1	1	1	1
<i>A. indicus</i>	2,505	2,230	27	142.2	5	42	7	0.1393	1	1	1	1
<i>A. rossii</i>	1,679	1,500	22	91.5	3.8	66.5	4	0.1332	1	1	1	1
<i>Anseranas semipalmata</i>	2,766	2,071	28	112.2	8.6	-15.5	12	0.2136	1	1	1	1
<i>Aythya affinis</i>	850	790	26	48.2	10.2	54	22	0.1086	1	2	2	1
<i>A. americana</i>	1,100	990	24	62.9	9.4	52	17	0.1252	1	2	2	1
<i>A. australis</i>	902	838	31	55.8	10	-26.5	8	0.1095	1	2	1	1
<i>A. baeri</i>	880	680	27	40.9	10	47	5	0.1871	1	2	2	1

Table 3 (Contd.)

Species	a	b	c	d	e	f	g	h	i	j	k	l
<i>A. collaris</i>	730	680	26	49.9	9.5	54.5	16	0.1059	1	2	2	1
<i>A. ferina</i>	849	807	25	68	8.3	51	41	0.0991	1	2	2	1
<i>A. fuligula</i>	723	680	25	55.5	9.6	58	51	0.1017	1	2	2	1
<i>A. innotata</i>						-19.5	2				2	1
<i>A. marila</i>	932	957	27	66.1	9.7	66.5	42	0.0675	1	2	2	1
<i>A. novaeseelandiae</i>	677	687	30	59.7	7	-41	4	0.0688	1	2	2	1
<i>A. nyroca</i>	583	520	26	42.5	9	46	22	0.1217	1	2	2	1
<i>A. valisineria</i>	1,248	1,190	24	70.5	8.2	55	9	0.1022	1	2	2	1
<i>Biziura lobata</i>	2,398	1,551	24	127.9	2.8	-34	8	0.2738	1	2	1	1
<i>Branta bernicla</i>	1,370	1,230	25	91	4	70.5	29	0.1287	1	1	1	1
<i>B. canadensis</i>	3,814	3,314	28	169	5.6	54	37	0.1543	1	1	1	1
<i>B. hrota</i>	1,395	1,090	24	84	3.9	70.5	12	0.1877	1	1	1	1
<i>B. leucopsis</i>	1,788	1,586	24	104	4.5	73	3	0.1370	1	1	1	1
<i>B. ruficollis</i>	1,375	1,094	24	78.2	4.5	71	4	0.1799	1	1	1	1
<i>B. sandvicensis</i>	2,010	1,930	29	144	4.2	19	1	0.1047	1	1	1	2
<i>Bucephala albeola</i>	473	334	29	36.7	8.8	55.5	20	0.2181	2	2	2	1
<i>B. clangula</i>	1,000	800	31	64.1	8.7	57	69	0.1739	2	2	2	1
<i>B. islandica</i>	1,090	730	32	67.7	7.9	56.5	19	0.2500	2	2	2	1
<i>Cairina moschata</i>	2,915	2,022	35	78.7	8.8	-3	36	0.2465	2	2	1	1
<i>C. scutulata</i>	3,400	2,600	34	89	10	11	3	0.2070	2	1	1	1
<i>Callonetta leucophrys</i>	423	321	27	32.4	9	-24.5	3	0.1863	2	1	2	1
<i>Cereopsis novaehollandiae</i>	5,290	3,770	35.5	126.9	4.1	-37.5	3	0.2420	1	1	1	1
<i>Chenonetta jubata</i>	815	800	34	55.8	10	-31	17	0.0851	2	1	2	1
<i>Chloephaga hybrida</i>	2,611	2,043	30	141.5	5.3	-47.5	5	0.1943	1	1	2	1
<i>C. melanoptera</i>	2,730	3,640	30	113.5	7	-21	7	-0.0305	1	1	1	1
<i>C. picta</i>	3,170	2,690	30	128	6.1	-44.5	7	0.1622	1	1	2	1
<i>C. poliocephala</i>	2,267	2,200	30	97.1	5	-47	5	0.1017	1	1	1	1
<i>C. rubidiceps</i>	1,750	1,400	30	102.8	5	-52.5	4	0.1803	1	1	1	1
<i>Clangula hyemalis</i>	661	636	26.5	44.1	7.9	68.5	58	0.0910	1	2	2	1
<i>Coscoroba coscoroba</i>	4,600	3,800	35	178.4	6.8	-41	10	0.1779	1	1	1	1
<i>Cyanochen cyanopterus</i>	2,180	1,420	32	97.1	7.5	10.5	5	0.2698	1	1	1	1
<i>Cygnus atratus</i>	6,200	5,100	40	267	5.5	-31	22	0.1831	1	1	1	1
<i>C. bewickii</i>	6,400	5,700	29.5	257.9	5.1	70	13	0.1499	1	1	1	1
<i>C. buccinator</i>	11,400	10,300	35	366.5	5.2	63	7	0.1505	1	1	1	1
<i>C. columbianus</i>	7,100	6,200	29.5	273.2	4.3	64	11	0.1595	1	1	1	1
<i>C. cygnus</i>	14,000	8,750	35	333.9	5.2	60	41	0.3086	1	1	1	1
<i>C. melanocoryphus</i>	5,400	4,000	36	247.4	4.6	-49	8	0.2258	1	1	1	1
<i>C. olor</i>	11,800	9,670	35.5	353	7.5	50.5	27	0.1922	1	1	1	1
<i>Dendrocygna arborea</i>		1,150	30	48.8	10	18	4		2	1	1	1
<i>D. arcuata</i>	741	732	29	38.7	10	-4	20	-0.0812	2	1	1	1
<i>D. autumnalis</i>	813	849	31	44.3	13	-2	41	0.0589	2	1	1	1
<i>D. bicolor</i>	675	690	29	49.1	9.7	-3	66	0.0658	1	1	1	1
<i>D. eytoni</i>	788	792	29	34.5	11	-25	13	0.0747	2	1	1	1
<i>D. guttata</i>		800	31	41.7	11	-3	8		2	1	1	1
<i>D. javanica</i>		525		35.3	10	10.5	25		2	1	1	1
<i>D. viduata</i>	686	662	27	38	10.5	-6	69	0.0902	2	1	1	1
<i>Heteronetta atricapilla</i>	460	605	24.5	60.2		-31	8	-0.0452	1	2	2	1
<i>Histrionicus histrionicus</i>	687	558	28	54.4	5.7	52.5	38	0.1632	1	2	2	1
<i>Hymenolaimus malacorhynchus</i>	897	768	31.5	73	5.4	-42	4	0.1439	1	1	1	1
<i>Lophodytes cucullatus</i>	680	540	31	57.6	10.2	45.5	19	0.1725	2	2	2	1
<i>Lophonetta specularioides</i>	1125	900	30	56.9	6.5	-32	13	0.1753	1	1	1	1
<i>Malacorhynchus membranaceus</i>	404	344	27	35.2	6.7	-25.5	14	0.1371	2	1	1	1
<i>Marmaronetta angustirostris</i>	562	492	26	30.2	11.8	38.5	11	0.1291	1	2	1	1
<i>Melanitta fusca</i>	1,794	1,730	27.5	92	8.43	59	51	0.1017	1	2	2	1
<i>M. nigra</i>	1,100	800	30.5	74.2	8.7	66	31	0.2153	1	2	2	1
<i>M. perspicillata</i>	1,000	900		63.2	6	63	20	0.1241	1	2	2	1
<i>Merganetta armata</i>	440	327	43.5	62	3.3	-21.5	19	0.1957	2	1	2	1
<i>Mergus albellus</i>	652	568	27	41.7	8	63	22	0.1329	2	2	2	1
<i>M. australis</i>						-19	1		2	1	1	1
<i>M. merganser</i>	1,709	1,232	31	79.2	9.4	53	78	0.2240	2	2	2	1
<i>M. octosetaceus</i>						-51	2				1	2
<i>M. serrator</i>	1,135	908	31.5	73.3	9.5	63	76	0.1753	1	2	2	1
<i>M. squamatus</i>	1,232	956			10.5	46	4	0.1891	2	2	2	1
<i>Neochen jubata</i>		1,250	30	64.5	9	-6	14		2	1	1	1
<i>Netta erythrophthalma</i>	788	766	26	60.3	9	-12	16	0.0888	1	2	2	1
<i>N. peposaca</i>	1,181	1,004	28	58.3	9	-33.5	5	0.1501	1	2	2	1
<i>N. rufina</i>	1,130	1,100	27	56.8	9.9	44.5	24	0.0923	1	2	2	1

Table 3 (Contd.)

Species	a	b	c	d	e	f	g	h	i	j	k	l
<i>Nettapus auritus</i>	285	260	23.75	22.9	8.5	-9.05	41	0.1038	2	2	2	1
<i>N. coromandelianus</i>	282	220		32	10	5.5	30	0.1699	2	2	2	1
<i>N. pulchellus</i>	310	304		25	10	-15.5	8	0.0743	2	2	2	1
<i>Nomonyx dominicus</i>	406	339	28	50.5	6	-7.5	42	0.1454	1	2	2	1
<i>Oxyura australis</i>	812	852	24	84.4	5.5	-34.5	9	0.0569	1	2	2	1
<i>O. jamaicensis</i>	590	499	24	71.3	7.6	4.5	50	0.1443	1	2	2	1
<i>O. leucocephala</i>	737	593	25.5	97	6	42	16	0.1679	1	2	2	1
<i>O. maccoa</i>	820	554	25	88	6	-7.5	18	0.2430	1	2	2	1
<i>O. vittata</i>	690	590	23.5	78.7	4	-37.5	9	0.1414	1	2	2	1
<i>Plectropterus gambensis</i>	6,100	4,700	31	138.8	9.4	-7.5	42	0.2106	1	2	1	1
<i>Polysticta stelleri</i>	773	842	26.5	55.1	8	67.5	15	0.0405	1	2	2	1
<i>Pteronetta hartlaubi</i>	976	788	32	53.8	8.3	0.5	10	0.1697	2	1	1	1
<i>Salvadorinia waiguensis</i>	462	469		57	3	-5.5	5	0.0642	1	1	1	1
<i>Sarkidornis melanotos</i>	1,863	1,069	30	64.3	9.5	-2.5	77	0.3215	2	2	1	1
<i>Somateria fischeri</i>	1,432	1,304	24	77.1	3.7	69.5	10	0.1232	1	2	2	1
<i>S. mollissima</i>	2,218	1,915	26	111	4.3	63.5	55	0.1508	1	2	2	1
<i>S. spectabilis</i>	1,668	1,567	23	66.7	5	68	46	0.1118	1	2	2	1
<i>Speculanus specularis</i>	1,460	1,531	30	69	4.5	-45.5	6	0.0638	1	1	1	1
<i>Stictonetta naevosa</i>	969	842	28	77.2	7.4	-33.5	5	0.1386	1	1	1	1
<i>Tachyeres brachypterus</i>	4,200	3,450	34	145.4	6	-51	1	0.1792	1	1	2	2
<i>T. leucocephalus</i>	3,808	3,013		132.4	4.6	-41	1	0.1939	1	1	2	1
<i>T. patachonicus</i>	2,958	2,346		116.6	6.2	-46	5	0.1901	1	1	1	1
<i>T. pteneres</i>	5,394	4,228		146.5	6.6	-46	4	0.2019	1	1	1	1
<i>Tadorna cana</i>	1,758	1,417	30	97.1	9.5	-27.5	5	0.1772	2	1	2	1
<i>T. ferruginea</i>	1,360	1,100	30	83.4	8.5	39.5	34	0.1727	2	1	1	1
<i>T. radjah</i>	934	839	30	57.8	9	-13	11	0.1240	2	1	1	1
<i>T. tadorna</i>	1,261	1,043	30	80.9	8.9	54.5	32	0.1624	2	1	1	1
<i>T. tadornoides</i>	1,559	1,291	31.5	90	10.4	-34	7	0.1644	2	1	2	1
<i>T. variegata</i>	1712	1,387	32.5	88.1	9.4	-42.5	4	0.1747	2	1	2	1
<i>Thalassornis leucotis</i>	720	695	31	82.6	8	-7.5	36	0.0907	1	1	1	1

a Male mass, b female mass, c incubation length, d egg mass, e clutch size, f breeding latitude, g breeding range, h size dimorphism, i nest type, j. Open nest, 2. Cavity nest; j mating system, l. Pairing less than once a year, 2. Pairing at least once a year, k dichromatism, l monomorphic, 2 dimorphic; l Insularity, 1 non insular, 2 endemic to small islands. Data sources: (Rohwer 1988; Scott and Clutton-Brock 1989; Cramp and Simmons 1977; Johnsgard 1978; Bellrose 1980; Brown et al. 1982; Marchant and Higgins 1991; Johnsgard and Carbonell 1996; Kear 2005)

## References

- Afton AD, Paulus SL (1992) Incubation and brood care. In: Batt BDJ, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL (eds) Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, pp 62–108
- Andersson M (1994) Sexual selection. Princeton University Press, Princeton
- Ankney CD (1980) Egg weight, survival, and growth of lesser snow goose goslings. *J Wildl Manage* 44:174–182
- Ankney CD, Afton AD, Alisauskas RT (1991) The role of nutrient reserves in limiting waterfowl reproduction. *Condor* 93:1029–1032
- Arnold TW, Rohwer FC, Armstrong T (1987) Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. *Am Nat* 130:643–653
- Arnold TW, Rohwer FC (1991) Do egg formation costs limit clutch size in waterfowl? A skeptical view. *Condor* 93:1032–1038
- Beauchamp G (1997) Determinants of intraspecific brood amalgamation in waterfowl. *Auk* 114:11–21
- Beissinger SR (1996) On the limited breeding opportunities hypothesis for avian clutch size. *Am Nat* 147:655–658
- Beissinger SR, Waltman JR (1991) Extraordinary clutch size and hatching asynchrony of a Neotropical parrot. *Auk* 108:863–871
- Bellrose FC (1980) Ducks, geese and swans of North America. Stackpole Books, Harrisburg
- Bengtson SA (1971) Variations in clutch-size in ducks in relation to the food supply. *Ibis* 113:523–526
- Bennett PM, Owens IPF (2002) Evolutionary ecology of birds. Oxford Series in ecology and evolution. Oxford University Press, Oxford
- Blackburn TM (1991a) An interspecific relationship between egg size and clutch size in birds. *Auk* 108:973–977
- Blackburn TM (1991b) The interspecific relationship between egg size and clutch size in wildfowl. *Auk* 108:209–211
- Blackburn TM, Lawton JH, Gregory RD (1996) Relationships between abundances and life histories of British birds. *J Anim Ecol* 65:52–62
- Blondel J (2000) Evolution and ecology of birds on islands: trends and prospects. *Vie Milieu* 50:205–220
- Blums P, Clark RG, Mednis A (2002) Patterns of reproductive effort and success in birds: path analyses of long-term data from European ducks. *J Anim Ecol* 71:280–295
- Briskie JV, Sealy SG (1989) Determination of clutch size in the least flycatcher. *Auk* 106:269–278
- Brown LH, Urban EK, Newman K (1982) The birds of Africa, vol 1. Academic, London
- Bustamante J (1997) Predictive models for lesser Kestrel *Falco naumanni* distribution, abundance and extinction in southern Spain. *Biol Conserv* 80:153–160
- Bustnes JO, Erikstad KE (1991) Parental care in the common eider *Somateria mollissima*: factors affecting abandonment and adoption of young. *Can J Zool* 69:1538–1545
- Cooch G (1961) Ecological aspects of the blue snow goose complex. *Auk* 78:72–89

- Cramp S, Simmons KEL (1977) The birds of the western Palearctic, vol 1. Oxford University Press, Oxford
- Dawson RD, Clark RG (1996) Effects of variation in egg size and hatching date on survival of Lesser Scaup *Aythya affinis* ducklings. *Ibis* 138:693–699
- Erikstad KE, Bustnes JO, Moum T (1993) Clutch-size determination in precocial birds: a study of the common eider. *Auk* 110:623–628
- Feldheim CL (1997) The length of incubation in relation to nest initiation date and clutch size in dabbling ducks. *Condor* 99:997–1001
- Figuerola J, Green AJ (2000) The evolution of sexual dimorphism in relation to mating patterns, cavity nesting, insularity and sympatry in the Anseriformes. *Funct Ecol* 14:701–710
- Forslund P (1993) Vigilance in relation to brood size and predator abundance in the barnacle goose, *Branta leucopsis*. *Anim Behav* 45:965–973
- Fredrickson LH (1969) An experimental study of clutch size of the American coot. *Auk* 86:541–550
- Galbraith H (1988) Effects of egg size and composition on the size, quality and survival of lapwing *Vanellus vanellus* chicks. *J Zool* 214:383–398
- Gaston KJ (1996) The multiple forms of the interspecific abundance–distribution relationship. *Oikos* 75:211–220
- Gaston KJ, Blackburn TM, Lawton JH (1997) Interspecific abundance–range size relationships: an appraisal of mechanisms. *J Anim Ecol* 66:579–601
- Gaston KJ, Blackburn TM (1996) Global macroecology: interactions between population size, geographic range size and body size in the Anseriformes. *J Anim Ecol* 65:701–714
- Geffen E, Yom-Tov Y (2001) Factors affecting the rates of intra-specific nest parasitism among Anseriformes and Galliformes. *Anim Behav* 62:1027–1038
- Grafen A (1989) The phylogenetic regression. *Philos Trans R Soc B* 326:119–157
- Grafen A (1992) The uniqueness of the phylogenetic regression. *J Theor Biol* 156:405–423
- Grant MC (1991) Relationships between egg size, chick size at hatching, and chick survival in the Whimbrel *Numenius phaeopus*. *Ibis* 133:127–133
- Green AJ (1996) Analyses of globally threatened Anatidae in relation to threats, distribution, migration patterns and habitat use. *Conserv Biol* 10:1435–1445
- Green AJ (1998) Clutch size, brood size and brood emergence in the marbled teal *Marmaronetta angustirostris* in the Marismas del Guadalquivir, southwest Spain. *Ibis* 140:670–675
- Green AJ, Navarro JD, Dolz JC, Aragonese J (1999) Brood emergence patterns in a Mediterranean duck community. *Bird Study* 46:116–118
- Green AJ, Fuentes C, Figuerola J, Viedma C, Ramón N (2005) Survival of marbled teal (*Marmaronetta angustirostris*) released back into the wild. *Biol Conserv* 121:595–601
- Harvey PH, Pagel MD (1991) The comparative method in evolutionary biology. Oxford University Press, Oxford
- Heusmann HW (1972) Survival of wood duck broods from dump nests. *J Wildl Manage* 36:620–624
- Hilden O (1964) Ecology of duck populations in the island group of Valasaaret, Gulf of Bothnia. *Ann Zool Fenn* 1:153–279
- Hórák P, Mänd R, Ots I (1997) Identifying targets of selection: a multivariate analysis of reproductive traits in the great tit. *Oikos* 78:592–600
- Johnsgard PA (1978) Ducks, geese, and swans of the world. University of Nebraska Press, Lincoln
- Johnsgard PA, Carbonell M (1996) Ruddy ducks and other stiff-tails. University of Oklahoma Press, Norman
- Johnson KP, Sorenson MD (1999) Phylogeny and biogeography of the dabbling ducks (Genus: *Anas*): a comparison of molecular and morphological evidence. *Auk* 116:792–805
- Johnston JP, Peach WJ, Gregory RD, White SA (1997) Survival rates of tropical and temperate passerines: a Trinidadian perspective. *Am Nat* 150:771–789
- Karr JR, Nichols JD, Klimkiewicz MK, Brawn JD (1990) Survival rates of birds of tropical and temperate forests: will the dogma survive? *Am Nat* 136:277–291
- Kear J (2005) Ducks, geese, swans and screamers. Oxford University Press, Oxford
- Klomp H (1970) The determination of clutch-size in birds: a review. *Ardea* 58:1–124
- Koskimies J, Lahti L (1964) Cold-hardiness of the newly-hatched young in relation to ecology and distribution in ten species of European ducks. *Auk* 81:281–307
- Lack D (1947) The significance of clutch size, parts I and II. *Ibis* 89:302–352
- Lack D (1948) The significance of clutch size, parts III. *Ibis* 90:25–45
- Lack D (1968) Ecological adaptation for breeding in birds. Chapman and Hall, London
- Lack D (1970) The endemic ducks of remote islands. *Wildfowl* 21:5–10
- Laurila T (1988) Reproductive strategies in waterfowl: the effect of ultimate environmental factors, size and phylogeny. *Ornis Fennica* 65:49–64
- Leopold F (1951) A study of nesting wood ducks in Iowa. *Condor* 53:209–220
- Lessells CM (1986) Brood size in Canada geese: a manipulation experiment. *J Anim Ecol* 55:669–689
- Lima SL (1987) Clutch size in birds: a predation perspective. *Ecology* 68:1062–1070
- Livezey BC (1986) A phylogenetic analysis of recent anseriform genera using morphological characters. *Auk* 103:737–754
- Livezey BC (1991) A phylogenetic analysis and classification of recent dabbling ducks (Tribe Anatini) based on comparative morphology. *Auk* 108:471–508
- Livezey BC (1993) Comparative morphometrics of *Anas* ducks, with particular reference to the Hawaiian duck *Anas wyvilliana*, laysan duck *A. laysanensis*, and Eaton's pintail *A. eatoni*. *Wildfowl* 44:75–100
- Livezey BC (1995a) Phylogeny and comparative ecology of stiff-tailed ducks (Anatidae: Oxyurini). *Wilson Bull* 107:214–234
- Livezey BC (1995b) Phylogeny and evolutionary ecology of modern seaducks (Anatidae: Mergini). *Condor* 97: 233–255
- Livezey BC (1995c) A phylogenetic analysis of the whistling and white-backed ducks (Anatidae: Dendrocygninae) using morphological characters. *Ann Carnegie Mus* 64:65–97
- Livezey BC (1996a) A phylogenetic analysis of geese and swans (Anseriformes: Anserinae), including selected fossil species. *Syst Zool* 45:415–450
- Livezey BC (1996b) A phylogenetic analysis of modern pochards (Anatidae: Aythyini). *Auk* 113:74–93
- Livezey BC (1997a) A phylogenetic classification of waterfowl (Aves: Anseriformes), including selected fossil species. *Ann Carnegie Mus* 66:457–496
- Livezey BC (1997b) A phylogenetic analysis of modern sheldgeese and shelducks (Anatidae, Tadornini). *Ibis* 139:51–66
- Livezey BC, Humphrey PS (1992) Taxonomy and identification of steamer-ducks (Anatidae: Tachyeres). University of Kansas, Museum of Natural History Monographs 8:1–125
- Madge S, Burn H (1988) Wildfowl: an identification guide to the ducks, geese and swans of the world. Helm, London
- Marchant S, Higgins PJ (1991) Handbook of Australian, New Zealand and Antarctic birds, vol 1. Oxford University Press, Oxford
- Martin TE (1993) Evolutionary determinants of clutch size in cavity-nesting birds: nest predation or limited breeding opportunities? *Am Nat* 142:937–946
- Martin TE (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol Monogr* 65:101–127
- Martins EP, Hansen TF (1996) The statistical analysis of interspecific data: a review and evaluation of phylogenetic comparative methods. In: Martins PE (ed) Phylogenies and the comparative method in animal behavior. Oxford University Press, Oxford, pp 22–75

- Milonoff M (1989) Can nest predation limit clutch size in precocial birds? *Oikos* 55:424–427
- Milonoff M (1991) Renesting ability and clutch size in precocial birds. *Oikos* 62:189–194
- Milonoff M, Pöysä H, Virtanen J (1995) Brood-size-dependent offspring mortality in common goldeneyes reconsidered: fact or artifact? *Am Nat* 146:967–974
- Milonoff M, Paananen P (1993) Egg formation, brood survival, and cost of reproduction as clutch-size-determining factors in common goldeneyes. *Auk* 110:943–946
- Monaghan P, Nager RG (1997) Why don't birds lay more eggs? *Trends Ecol Evol* 12:270–274
- Mönkkönen M, Orell M (1997) Clutch size and cavity excavation in parids (Paridae): the limited breeding opportunities hypothesis tested. *Am Nat* 149:1164–1174
- Newton I (1977) Breeding strategies in birds of prey. *Living Bird* 16:51–82
- O'Connor RJ (1979) Egg weights and brood reduction in the European swift (*Apus apus*). *Condor* 81:133–145
- Pehrsson O (1991) Egg and clutch size in the mallard as related to food quality. *Can J Zool* 69:156–162
- Perrins CM (1977) The role of predation in the evolution of clutch size. In: Stonehouse B, Perrins CM (eds) *Evolutionary ecology*. MacMillan, London, pp 181–191
- Pianka ER (1970) On r- and K-selection. *Am Nat* 104:592–597
- Potti J, Merino S (1996) Causes of hatching failure in the pied flycatcher. *Condor* 98:328–336
- Purvis A, Rambaut A (1995) Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comput Appl Biosci* 11:247–251
- Rahn H, Paganelli CV, Ar A (1975) Relation of avian egg weight to body weight. *Auk* 92:750–765
- Rahn H, Ar A (1974) The avian egg: incubation time and water loss. *Condor* 76:147–152
- Ranta E, Laurila A, Elmberg J (1994) Reinventing the wheel: analysis of sexual dimorphism in body size. *Oikos* 70:313–332
- Rhymer JM (1988) The effect of egg size variability on thermoregulation of mallard (*Anas platyrhynchos*) offspring and its implications for survival. *Oecologia* 75:20–24
- Rice DW, Kenyon KW (1962) Breeding cycles and behaviour of Laysan and black-footed albatrosses. *Auk* 79:517–567
- Ricklefs RE (1977) On the evolution of reproductive strategies in birds: reproductive effort. *Am Nat* 111:453–478
- Rockwell RF, Findlay CS, Cooke F (1987) Is there an optimal clutch size in snow geese. *Am Nat* 130:839–863
- Rohwer FC (1984) Patterns of egg-laying in prairie ducks. *Auk* 101:660–668
- Rohwer FC (1988) Inter- and intraspecific relationships between egg size and clutch size in waterfowl. *Auk* 105:161–176
- Rohwer FC (1991) Response to T.M. Blackburn. *Auk* 108:211–213
- Rohwer FC (1992) The evolution of reproductive patterns in waterfowl. In: Batt BDJ, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL (eds) *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, pp 486–539
- Sandercocock BK (1997) Incubation capacity and clutch size determination in two calidrine sandpipers: a test of the four-egg threshold. *Oecologia* 110:50–59
- Scott DK, Clutton-Brock TH (1989) Mating systems, parasites and plumage dimorphism in waterfowl. *Behav Ecol Sociobiol* 26:261–273
- Sigurjónsdóttir H (1981) The evolution of sexual size dimorphism in gamebirds, waterfowl and raptors. *Ornis Scandinavica* 12:249–260
- Slagsvold T (1982) Clutch size variation in passerina birds: the nest predation hypothesis. *Oecologia* 54:159–169
- Sokal RR, Rohlf FJ (1995) *Biometry*. Freeman, New York
- Stearns SC (1992) *The evolution of life histories*. Oxford University Press, Oxford
- Swennen C, Ursem JCH, Duiven P (1993) Determinate laying and egg attendance in common eiders. *Ornis Scandinavica* 24:48–52
- Székely T, Karsai I, Williams TD (1994) Determination of clutch-size in the Kentish plover *Charadrius alexandrinus*. *Ibis* 136:341–348
- Sæther B-E (1996) Evolution of avian life histories—does nest predation explain it all? *Trends Ecol Evol* 11:311–312
- Weller MW (1980) *The island waterfowl*. Iowa State University Press, Ames
- Williams TD (1994) Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biol Rev* 68:35–59
- Williams P (1996) *WORLDMAP*, priority areas for biodiversity: using version 4. Privately distributed software and manual, London
- Williams M, McKinney F, Norman FI (1991) Ecological and behavioural responses of Austral teal to island life. *Proc Int Ornithol Congr* 20:876–884
- Winkler DW, Walters JR (1983) The determination of clutch size in precocial birds. *Curr Ornithol* 1:33–68
- Yom-Tov Y (1980) Intraspecific nest parasitism in birds. *Biol Rev Cambridge Philos Soc* 55:93–108.