CSIRO PUBLISHING
Emu, 2012, **112**, 167–172
http://dx.doi.org/10.1071/MU11068

Short Communication

Variation in the size of eggs of Chubut Steamer Ducks (*Tachyeres leucocephalus*)

Walter S. Svagelj[A,C], *María Laura Agüero*[A] *and Pablo García Borboroglu*[A,B]

[A]Biología y Manejo de Recursos Acuáticos, Centro Nacional Patagónico – CONICET, Boulevard Brown 2915, Puerto Madryn (U9120ACD), Chubut, Argentina.
[B]University of Washington, Department of Biology, Box 351800, Seattle, WA 98195-1800, USA.
[C]Corresponding author. Email: tito@cenpat.edu.ar

Abstract. Although several studies have analysed spatial or temporal variation in the size of eggs in waterfowl (Anseriformes), no study has analysed variation throughout the breeding range of a species. Chubut Steamer Ducks (*Tachyeres leucocephalus*) are flightless marine waterfowl endemic to a small section of coastline in Patagonia, Argentina. We partitioned and analysed sources of variation in the size of 989 Chubut Steamer Duck eggs, from 175 clutches, obtained during the breeding seasons of 1998 and 2004–08 at 31 islands throughout the range of the species. In relation to other Anseriformes, we found a low level of variation (coefficient of variation = 6.4%) at the species level. Most variation in the size of eggs were within clutches (59.0%) and among clutches (34.5%); variation between islands within geographical areas accounted for only 6.5% of variation, and there was no variation among geographical areas. Variation in size of eggs was not related to year, apparent clutch-size or latitude. The low variation at the species level and the lack of variation in size of eggs between geographical areas could be a consequence of the low genetic diversity and restricted distribution of the species. This study highlights the potential importance of variation in egg-size for understanding ecological processes linked to the natural history of avian species.

Additional keywords: coefficient of variation, endemic, flightless marine duck, near threatened.

Received 26 August 2011, accepted 5 December 2011, published online 14 May 2012

Introduction

The size of eggs is an important life-history trait influencing the quality of offspring and their survival (Williams 1994; Christians 2002; Krist 2011). Because large eggs contain more nutrients than smaller eggs (Ankney 1980; Badzinski *et al*. 2002; Arnold and Green 2007), hatchlings from large eggs are generally larger and have larger absolute nutrient reserves than those of hatchlings from smaller eggs (Ankney 1980; Badzinski *et al*. 2002). The size of eggs is a particularly important character in precocial birds, in which most of the total parental investment is confined to maternal investments in the egg (Lack 1968). Waterfowl (throughout this paper restricted to members of the Anseriformes) have highly precocial young that leave the nest shortly after hatching and secure their own food. Several studies of waterfowl have shown that the size of eggs is positively related to hatchling size, resistance to cold weather, endurance, resistance to starvation, swimming speed and feeding rate (Ankney 1980; Anderson and Alisauskas 2001), all characteristics ultimately affecting survival of ducklings.

The study of intraspecific variation in the size of eggs is of biological interest because, although the size of eggs affects offspring survival (see above), it also varies greatly within species, with the largest egg in a population generally being 50–100% bigger than the smallest (Christians 2002). Such large variation in size can be partitioned, allowing for an estimation of the relative importance of the various determinants of the size of eggs. For example, the variation in size of eggs across the distributional range of a species can be partitioned over different spatial scales. Spatial variation can be discrete (e.g. among populations or areas) or clinal (e.g. latitudinal), where differences may reflect differential phenotypic expression of traits in different environments. If the size of eggs has fitness consequences (Krist 2011), differences in the size of eggs among geographical areas or populations may be indicators of different pressures and limitations across the range of a species. Documenting that variation has important implications for evolutionary studies and for conservation efforts (Avise and Hamrick 1996).

Chubut Steamer Ducks (*Tachyeres leucocephalus*) are flightless marine waterfowl endemic to a 700-km section of coast of Chubut Province, Central Patagonia, Argentina; the total population is <3700 individuals (Humphrey and Thompson 1981; Agüero *et al*. 2010, 2011). The species is classified as near threatened globally (BirdLife International 2011; IUCN 2011) owing to the combination of its restricted distribution, small population size, flightlessness and the potential threats to which it is exposed (see Agüero *et al*. 2011). Despite this, there is little knowledge of its basic ecology. Indeed, even much basic information about key breeding parameters as clutch-size and

Journal compilation © BirdLife Australia 2012

measurements of eggs is anecdotal (Boswall 1973; Daciuk 1976; Boswall and MacIver 1979; Humphrey and Livezey 1985).

Although several studies have analysed spatial or temporal variation in the size of eggs in various species of waterfowl (Sjöberg and Sjöberg 1992; Robertson *et al*. 2001; Chaulk *et al.* 2004), few have partitioned or quantified the relative importance of sources of variation (Leblanc 1989; Swennen and van der Meer 1992; Flint *et al*. 2001). Moreover, there have been no studies partitioning and analysing sources of variation in the size of eggs throughout the entire breeding range of any species of waterfowl. In this paper, we analysed data on variation in egg size in Chubut Steamer Ducks collected over 6 years throughout their entire breeding range. Our main objectives were to quantify the variation in egg-size at the species level, to partition the variation at different spatial scales, and to assess the effects of year, clutch-size and geographical latitude on the size of eggs.

Materials and methods

We collected data over six breeding seasons (September–December) of 1998 and 2004–08. We surveyed 337 km of mainland coast and 104 km of island coast throughout the distribution of Chubut Steamer Ducks looking for nests (Fig. 1), from Playa Unión, Rawson (43°21′S, 65°03′W) to the Chubut–Santa Cruz provincial border (46°00′S, 67°36′W; for details, see Agüero *et al*. 2011). Nests were found from Punta Tombo (44°03′S, 65°12′W) to the Vernaci Islands (45°11′S, 66°30′W; Fig. 1). When nests were found, their location was recorded (see Agüero *et al*. 2010, 2011 for methodology) and we measured the length and width of the eggs using vernier calipers (to the nearest 0.5 mm). Owing to logistical restrictions, nests were not monitored over the laying period and clutch-size and laying order were not known. As nests were only visited once, and as such laying date and incubation stage of eggs were not known, egg weight was not recorded. We measured a total of 993 eggs from 175 clutches. Four eggs – two runt and two abnormally large eggs – were excluded from all analyses, leaving 989 eggs, still from 175 clutches.

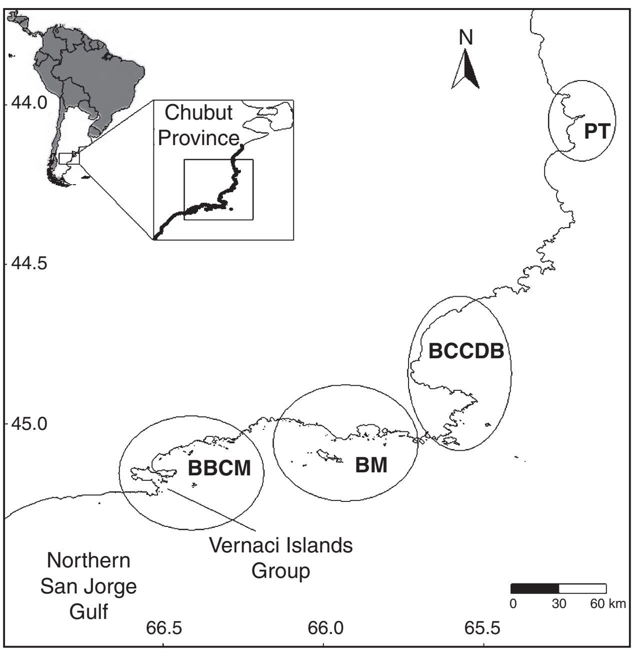

Fig. 1. Geographical areas used in the analysis of components of variance (see Methods). BM, Bahía Melo; BCCDB, Bahía Camarones–Cabo Dos Bahías; BBCM, Bahía Bustamante–Caleta Malaspina; PT, Punta Tombo. In the inset map, the breeding distribution of Chubut Steamer Ducks is shown as thick dark line.

Statistical analysis

Using the length and width of eggs, we estimated the mass of eggs using the formula: $Egg\ Mass = K_w \times Length \times Width^2$ (Hoyt 1979), where K_w is a species-specific mass coefficient. Because there is no figure of K_w for Chubut Steamer Ducks, we used a general coefficient value ($K_w = 5.55 \times 10^{-4}$ g mm^{-3}) considered representative for Anseriformes (Rohwer 1988). To quantify the level of variation in size of eggs at the species level, we estimated the coefficient of variation (CV) as (s.d. / mean) × 100.

We analysed variation in the size of eggs of Chubut Steamer Ducks using general linear mixed models (Pinheiro and Bates 2000; Crawley 2007). We partitioned total variance in egg-size in different variance components (Flint *et al*. 2001), evaluating also the effects of the geographical area (see below), year, apparent clutch-size and latitude. Total variance was partitioned into three hierarchical components: islands (i.e. among islands within geographical areas), clutches (i.e. among clutches within islands), and within clutches (residual variation). Based on the highest concentrations of Chubut Steamer Ducks within their range, Agüero *et al*. (2011) identified three major geographical areas for the species: Bahía Melo (BM), Bahía Camarones/Cabo Dos Bahías (BCCDB), and Bahía Bustamante/Caleta Malaspina (BBCM). In this study, we used this classification but also included a fourth, more northerly area, Punta Tombo (PT; see Fig. 1). Thus, geographical area (i.e. four areas), year (i.e. six breeding seasons, 1998 and 2004–08), apparent clutch-size (i.e. number of eggs in a nest when it was found) and latitude were included as fixed covariates. Intraspecific brood parasitism is frequent in Anseriformes (Yom-Tov 2001), although there has been no report of it in the four species of steamer ducks (*Tachyeres* spp.) (Geffen and Yom-Tov 2001; M. L. Agüero and P. García Borboroglu, pers. comm.). Even though there is no evidence of brood parasitism in Chubut Steamer Ducks (M. L. Agüero and P. García Borboroglu, pers. coms.), we excluded one abnormally large clutch (containing 11 eggs) from our analyses. We employed a backward selection procedure removing non-significant terms from the model one by one, in decreasing order of probability (Crawley 2007). The significance of random effects was tested with a likelihood ratio test (Pinheiro and Bates 2000; Crawley 2007). Statistical analyses were carried out using R software, Version 2.13.1 (R Development Core Team 2011). Values are reported as means ± s.e., except where noted. All tests were two-tailed, and differences were considered significant at $P < 0.05$.

Results

Most of nests (172 of 175) were found on the coast of 30 islands; only 3 nests were found on the mainland coast at Punta Tombo. The mean length of eggs was 82.3 mm (s.d. = 2.8, range = 71.0–91.0 mm, $n = 989$ eggs from 175 clutches from

30 islands and 1 mainland coastal area of all four geographical areas) and mean width 54.9 mm (s.d. = 1.5, range = 50.0–60.0 mm, $n = 989$ eggs). The estimated mean mass of eggs was 137.8 g (s.d. = 8.9, CV = 6.4%, $n = 989$ eggs). Estimated mass of eggs ranged from 106.6 to 179.8 g, the largest egg being 69% heavier than the smallest. After excluding one abnormally large clutch (containing 11 eggs), which may have been the result of brood parasitism (see Methods), apparent clutch-size was 5.7 eggs (s.d. = 1.6, range = 2–9, $n = 174$ clutches).

After elimination of fixed effects not included in the final model, general linear mixed models showed that differences between clutches within islands accounted for 34.5% of the variation in the size of eggs, with the residual variance (differences within clutches) accounting for 59.0% (Table 1). Just 6.5% of the variance in the size of eggs was attributed to differences between islands within geographical areas (Table 1). Mean mass of eggs did not differ between geographical areas or across years (Table 1 and Fig. 2) and there was no relationship between either clutch-size ($\beta = -0.19 \pm 0.33$) or latitude ($\beta = 12 \pm 18$) with mean size of eggs (Table 1).

Discussion

This study analyses the spatial and temporal variation in the size of Chubut Steamer Duck eggs throughout the breeding range of the species. Until now the only published measurements of the eggs of this flightless marine duck were of 15 eggs from four clutches found at one location (Boswall 1973; Daciuk 1976; Boswall and MacIver 1979; Humphrey and Livezey 1985; see Table 2).

The coefficient of variation in the size of eggs that we observed for Chubut Steamer Ducks (6.4%) was low compared with figures reported for other species of birds, either in general (see Arnold and Green 2007) or for Anseriformes (Table 3). Also, most variation in the size of eggs was a result of differences within clutches (59%), with between-clutch variation accounting for only 35% of variation, a finding that deviates from most other species of Anseriformes. In waterfowl, between-clutch variation in the size of eggs is usually greater than that within clutches (Rohwer 1986; Leblanc 1989; Rohwer and Eisenhauer 1989; Flint *et al*. 2001), although some studies have found levels of variation between and within clutches to be similar (Swennen and van der Meer 1992; Pelayo and Clark 2003).

Corbin *et al*. (1988) estimated genetic variation and heterozygosity in steamer ducks by using allozyme markers from liver proteins. They reported that Chubut Steamer Ducks had low genetic variation and reduced heterozygosity in relation to other steamer ducks. Thus, the low levels of variation in the size of eggs at the species level and the low levels of variation between clutches observed in our study could be a consequence of their low genetic variation. It must be noted, however, that Corbin *et al*. (1988) only sampled nine Chubut Steamer Ducks from a single area (Bahía Melo), so their results need to be interpreted with caution.

Table 1. Components of variation in the size of eggs of Chubut Steamer Ducks, partitioned between islands, clutches within islands, and within clutches (residual variation)

In total, we included measurements of 978 eggs from 174 clutches found in the four geographical areas occupied during the 1998 and 2004–08 breeding seasons. LRT, Likelihood Ratio Test

Fixed effects	*F*		*P*
Intercept	$F_{1,804} = 44124$		<0.0001
Geographical area[A]	$F_{3,27} = 0.62$		0.61
Year[A]	$F_{5,138} = 1.03$		0.40
Clutch-size[A]	$F_{1,137} = 0.34$		0.56
Latitude[A]	$F_{1,136} = 0.41$		0.53
Random effects	**Variance (±s.d.)**	**%**	**LRT**
Island	2.28 ± 5.22	6.5	$\chi^2_1 = 5.5$, $P = 0.019$
Island (Clutch)	5.25 ± 27.52	34.5	$\chi^2_1 = 179$, $P < 0.0001$
Residual	6.86 ± 47.05	59.0	

[A]Non-significant fixed effects were excluded from the final model. One abnormally large clutch (containing 11 eggs) was excluded from this analysis (see Methods for details). Variance, standard deviation and proportion of total variance explained by random effects are given.

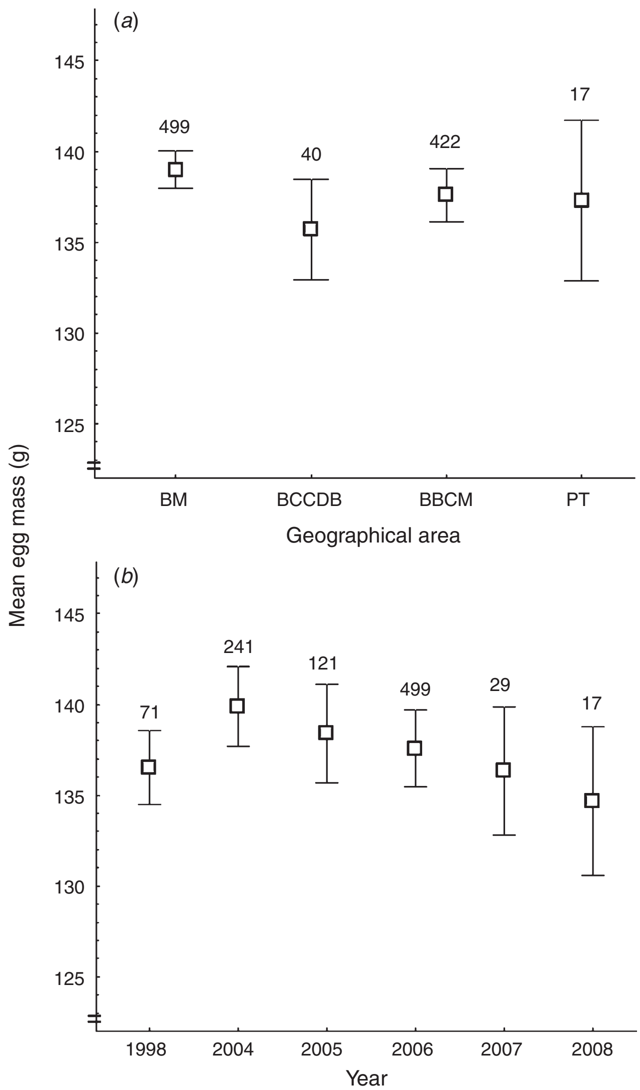

Fig. 2. Mean estimated mass of eggs of Chubut Steamer Ducks : (*a*) within geographical breeding areas (see Fig. 1, and Methods) and (*b*) by year. Numbers indicate sample size; whiskers show standard error.

Table 2. Length and width of eggs of Chubut Steamer Ducks
Figures are means, with ranges given in parentheses

Length (mm)	Width (mm)	Sample size Eggs	Sample size Clutches	Source
84.0 (83.0–85.0)	55.3 (54.2–56.1)	6	1	Boswall (1973), Boswall and MacIver (1979)
78.4 (72.3–83.2)	54.7 (53.7–55.6)	3	1	Daciuk (1976)
81.2 (72.3–85.6)[A]	54.2 (51.2–56.1)[A]	15[A]	4[A]	Humphrey and Livezey (1985)[A]
82.3 (71.0–91.0)	54.9 (50.0–60.0)	989	175	This study

[A]These values include data of Boswall (1973), Daciuk (1976), and Boswall and MacIver (1979).

Table 3. Coefficients of variation (CV) of size of eggs for species of waterfowl (Anseriformes)
Studies are ordered in decreasing level of variation in size

Species	CV (%)	Source
Northern Pintail (*Anas acuta*)	11	Flint and Grand (1996, 1999)
Common Eider (*Somateria mollisima borealis*)	10.5	Chaulk *et al*. (2004)
Canada Goose (*Branta canadensis maxima*)	9.4	Cooper (1978)
Blue-winged Teal (*Anas discors*)	9.3	Rohwer (1986)
Canada Goose (*Branta canadensis maxima*)	8.7	Thomas and Peach Brown (1988)
Snow Goose (*Chen caerulescens caerulescens*)	7.5	Newell (1988)
Common Eider (*Somateria mollisima sedentaria*)	7.4	Robertson and Cooke (1993)
Canada Goose (*Branta canadensis moffitti*)	7.3–7.4	Leblanc (1989)
Canada Goose (*Branta canadensis interior*)	7.2	Manning (1978)
Common Eider (*Somateria mollisima mollisima*)	7.1	Swennen and van der Meer (1992)
Brant Goose (*Branta bernicla nigricans*)	6.8	Flint and Sedinger (1992)
Ruddy Duck (*Oxyura jamaicensis*)	6.4	Pelayo and Clark (2003)
Chubut Steamer Duck (*Tachyeres leucocephalus*)	6.4	This study
Snow Goose (*Chen caerulescens caerulescens*)	5.8	Ankney (1980)

Our protocol for recording nests did not allow us to detect possible intraspecific brood parasitism or to exclude incomplete clutches, two factors that could potentially bias our results. Intraspecific brood parasitism is frequent in Anseriformes (Yom-Tov 2001) but there is no evidence for such parasitism in the four species of steamer ducks (Geffen and Yom-Tov 2001; M. L. Agüero and P. García Borboroglu, pers. comm.). As for the inclusion of incomplete clutches, which would result in an underestimate of within-clutch variation, we found a very high level of within-clutch variation. Finally, two studies (Rohwer 1986; Pelayo and Clark 2003) analysing variation between and within clutches found that the inclusion of incomplete clutches and clutches suspected to contain dumped eggs did not substantially bias the estimators obtained in relation to complete clutches without dumped eggs. It is thus likely that our analysis might not be severely affected by our study protocol.

We found a low level of variation among islands (6.5%), but no variation among geographical areas. To our knowledge, all the studies that have considered multiple sites or populations in waterfowl found spatial differences in the mean size of eggs (Sjöberg and Sjöberg 1992; Robertson *et al*. 2001; Chaulk *et al*. 2004). Contrary to those studies, we did not find geographical differences in mean size of eggs, probably as consequence of the low genetic variation within the species (Corbin *et al*. 1988), which could result in similar morphological traits among females across the range. Clearly, further studies analysing gene flow and possible genetic structuring between geographical areas are needed in this species.

Year, apparent clutch-size and latitude were not related to variation in the mean size of eggs. Our results agree with most studies in waterfowl that have shown little annual variation in the size of eggs (Sjöberg and Sjöberg 1992; Swennen and van der Meer 1992; Pelayo and Clark 2003; but see Flint and Sedinger 1992). Also, although the existence of a negative relationship between the size of eggs and clutch-size is predicted by life-history theory (Stearns 1992), there is little evidence for such a trade-off at both intraspecific and interspecific levels for Anseriformes (Rohwer 1988; Rohwer and Eisenhauer 1989; Flint and Sedinger 1992; Flint and Grand 1996). Finally, some studies in birds have found significant latitudinal variation in the size of eggs (Hõrak *et al*. 1995; Encabo *et al*. 2002). The lack of latitudinal variation in the size of Chubut Steamer Duck eggs could be a consequence of the low genetic variation, high endemism and restricted breeding range of this flightless species (see Agüero *et al*. 2011).

In summary, we suggest that the low intraspecific variation in egg-size, low level of variation in egg-size between females and the lack of variation in egg-size along the distribution range of Chubut Steamer Ducks could be consequence of the low genetic variation of the species.

Acknowledgements

Research was funded by grants from the OAK Foundation Grant in Marine Conservation – Duke University Marine Laboratory, Rufford Small Grants Foundation, Wildlife Conservation Society, Chubut Province Government and the Neotropical Bird Club. We thank Centro Nacional Patagónico

(CONICET) for institutional support and Soriano SA, Dirección de Fauna y Flora Silvestre, Secretaría de Turismo de la Provincia del Chubut for logistical support. The manuscript benefited from the constructive comments of Daniel Hanley and two anonymous referees.

References

Agüero, M. L., García Borboroglu, J. P., and Esler, D. (2010). Nesting habitat of Chubut Steamer Ducks in Patagonia, Argentina. *Emu* **110**, 302–306. doi:10.1071/MU09096

Agüero, M. L., García Borboroglu, P., and Esler, D. (2011). Distribution and abundance of Chubut Steamerducks: an endemic species to Central Patagonia, Argentina. *Bird Conservation International* **21**, in press.

Anderson, V. R., and Alisauskas, R. T. (2001). Egg size, body size, locomotion, and feeding performance in captive King Eider ducklings. *Condor* **103**, 195–199. doi:10.1650/0010-5422(2001)103[0195:ESBSLA]2.0.CO;2

Ankney, C. D. (1980). Egg weight, survival, and growth of Lesser Snow Goose goslings. *Journal of Wildlife Management* **44**, 174–182. doi:10.2307/3808363

Arnold, T. W., and Green, A. J. (2007). On the allometric relationship between egg size and composition of avian eggs: a reassessment. *Condor* **109**, 705–714. doi:10.1650/7902.1

Avise, J. C., and Hamrick, J. L. (1996). 'Conservation Genetics.' (Chapman and Hall: London.)

Badzinski, S. S., Ankney, C. D., Leafloor, J. O., and Abraham, K. F. (2002). Egg size as a predictor of nutrient composition of eggs and neonates of Canada Geese (*Branta canadensis interior*) and Lesser Snow Geese (*Chen caerulescens caerulescens*). *Canadian Journal of Zoology* **80**, 333–341. doi:10.1139/z02-010

BirdLife International (2011). White-headed Steamerduck *Tachyeres leucocephalus*. (BirdLife International: Cambridge, UK.) Available at http://www.birdlife.org/datazone/speciesfactsheet.php?id=405 [Verified 29 March 2012].

Boswall, J. (1973). Supplementary notes on the birds of Point Tombo, Argentina. *Bulletin of the British Ornithologists*' *Club* **93**, 33–36.

Boswall, J., and MacIver, D. (1979). Nota sobre el Pato Vapor Volador (*Tachyeres patachonicus*). *Hornero* **12**, 75–78.

Chaulk, K. G., Robertson, G. J., and Montevecchi, W. A. (2004). Regional and annual variability in Common Eider nesting ecology in Labrador. *Polar Research* **23**, 121–130. doi:10.1111/j.1751-8369.2004.tb00002.x

Christians, J. K. (2002). Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews of the Cambridge Philosophical Society* **77**, 1–26. doi:10.1017/S1464793101005784

Cooper, J. A. (1978). The history and breeding biology of the Canada Geese of Marshy Point, Manitoba. *Wildlife Monographs* **61**, 3–87.

Corbin, K. W., Livezey, B. C., and Humphrey, P. S. (1988). Genetic differentiation among Steamer-ducks (Anatidae : *Tachyeres*): an electrophoretic analysis. *Condor* **90**, 773–781. doi:10.2307/1368834

Crawley, M. J. (2007). 'The R Book.' (Wiley: Chichester, UK.)

Daciuk, J. (1976). Notas faunísticas y bioecológicas de Península Valdés y Patagonia. XVIII. Comportamiento del "Pato Vapor Volador" observado durante el ciclo reproductivo en costas e islas de Chubut (Rep. Argentina) – (Anserif., Anatidae). *Neotropica* **22**, 27–29.

Encabo, S. I., Barba, E., Gil-Delgado, J. A., and Monrós, J. S. (2002). Geographical variation in egg size of the Great Tit *Parus major*: a new perspective. *Ibis* **144**, 623–631. doi:10.1046/j.1474-919X.2002.00099.x

Flint, P. L., and Grand, J. B. (1996). Variation in egg size of the Northern Pintail. *Condor* **98**, 162–165. doi:10.2307/1369519

Flint, P. L., and Grand, J. B. (1999). Patterns of variation in size and composition of Greater Scaup eggs: are they related? *Wilson Bulletin* **111**, 465–471.

Flint, P. L., and Sedinger, J. S. (1992). Reproductive implications of egg-size variation in the Black Brant. *Auk* **109**, 896–903.

Flint, P. L., Rockwell, R. F., and Sedinger, J. S. (2001). Estimating repeatability of egg size. *Auk* **118**, 500–503. doi:10.1642/0004-8038(2001)118[0500:EROES]2.0.CO;2

Geffen, E., and Yom-Tov, Y. (2001). Factors affecting the rates of intraspecific nest parasitism among Anseriformes and Galliformes. *Animal Behaviour* **62**, 1027–1038. doi:10.1006/anbe.2001.1855

Hõrak, P., Mänd, R., Ots, I., and Leivits, A. (1995). Egg size in the Great Tit *Parus major*: individual, habitat and geographic differences. *Ornis Fennica* **72**, 97–114.

Hoyt, D. F. (1979). Practical methods of estimating volume and fresh weight of bird eggs. *Auk* **96**, 73–77.

Humphrey, P. S., and Livezey, B. C. (1985). Nest, eggs, and downy young of the White-headed Flightless Steamer-duck. *Ornithological Monographs* **36**, 944–953.

Humphrey, P. S., and Thompson, M. C. (1981). A new species of steamer-duck (Tachyeres) from Argentina. *University of Kansas Musuem of Natural History Occasional Papers* **95**, 1–12.

IUCN (2011). 'IUCN Red List of Threatened Species.' Version 2011.1. (International Union for Conservation of Nature and Natural Resources: Cambridge, UK.) Available at http://www.iucnredlist.org [Verified 5 December 2011].

Krist, M. (2011). Egg size and offspring quality: a meta-analysis in birds. *Biological Reviews of the Cambridge Philosophical Society* **86**, 692–716. doi:10.1111/j.1469-185X.2010.00166.x

Lack, D. (1968). 'Ecological Adaptations for Breeding in Birds.' (Methuen: London.)

Leblanc, Y. (1989). Variation in size of eggs of captive and wild Canada Geese. *Ornis Scandinavica* **20**, 93–98. doi:10.2307/3676874

Manning, T. H. (1978). Measurements and weights of eggs of the Canada Goose, *Branta canadensis*, analyzed and compared with those of other species. *Canadian Journal of Zoology* **56**, 676–687. doi:10.1139/z78-095

Newell, L. C. (1988). Causes and consequences of egg weight variation in the Lesser Snow Goose (*Anser caerulescens caerulescens*). M.Sc. Thesis, Queen's University, Kingston, Ontario, Canada.

Pelayo, J. T., and Clark, R. G. (2003). Consequences of egg size for offspring survival: a cross-fostering experiment in Ruddy Ducks (*Oxyura jamaicensis*). *Auk* **120**, 384–393. doi:10.1642/0004-8038(2003)120[0384:COESFO]2.0.CO;2

Pinheiro, J. C., and Bates, D. M. (2000). 'Mixed-effects Models in S and S-Plus.' (Springer: New York.)

R Development Core Team (2011). 'R: A Language and Environment for Statistical Computing.' (R Foundation for Statistical Computing: Vienna.) Available at http://www.R–project.org [Verified 5 December 2011].

Robertson, G. J., and Cooke, F. (1993). Intraclutch egg-size variation and hatching success in the Common Eider. *Canadian Journal of Zoology* **71**, 544–549. doi:10.1139/z93-075

Robertson, G. J., Reed, A., and Gilchrist, H. G. (2001). Clutch, egg and body size variation among common eiders breeding in Hudson Bay, Canada. *Polar Research* **20**, 85–94. doi:10.1111/j.1751-8369.2001.tb00041.x

Rohwer, F. C. (1986). Composition of Blue-winged Teal eggs in relation to egg size, clutch size and the timing of laying. *Condor* **88**, 513–519. doi:10.2307/1368280

Rohwer, F. C. (1988). Inter- and intraspecific relationships between egg size and clutch size in waterfowl. *Auk* **105**, 161–176.

Rohwer, F. C., and Eisenhauer, D. I. (1989). Egg mass and clutch size relationships in geese, eiders, and swans. *Ornis Scandinavica* **20**, 43–48. doi:10.2307/3676706

Sjöberg, G., and Sjöberg, K. (1992). Geographical variation in reproductive investment in Canada Geese (*Branta canadensis*) in Sweden. *Journal für Ornithologie* **133**, 403–412. doi:10.1007/BF01640468

Stearns, S. C. (1992). 'The Evolution of Life Histories.' (Oxford University Press: New York.)

Swennen, C., and van der Meer, J. (1992). Variation in egg size of Common Eiders. *Ardea* **80**, 363–373.

Thomas, V. G., and Peach Brown, H. C. (1988). Relationships among egg size, energy reserves, growth rate, and fasting resistance of Canada Goose goslings from southern Ontario. *Canadian Journal of Zoology* **66**, 957–964. doi:10.1139/z88-142

Williams, T. D. (1994). Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews of the Cambridge Philosophical Society* **68**, 35–59. doi:10.1111/j.1469-185X.1994.tb01485.x

Yom-Tov, Y. (2001). An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. *Ibis* **143**, 133–143. doi:10.1111/j.1474-919X.2001.tb04177.x