Egg size, egg composition and reproductive success in the Oystercatcher *Haematopus ostralegus*

THEO D. JAGER[1,2*], JAN B. HULSCHER[1] & MARCEL KERSTEN[1,3]
[1]*Zoological Laboratory, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA, Haren, The Netherlands*
[2]*ARCADIS Heidemij Advies, PO Box 1018, 5200 BA, 's-Hertogenbosch, The Netherlands*
[3]*Centre d'Etudes Biologiques de Chizé (CNRS), 79360 Villiers-en-Bois, France*

We investigated the relationship between egg size and composition and their subsequent effects on hatching and fledging success in Eurasian Oystercatchers *Haematopus ostralegus* on the island of Schiermonnikoog (53°30′N, 06°10′E) in the Dutch Wadden Sea between 1986 and 1990. Egg size variation was considerable. The ratio in egg volume of the largest over the smallest egg was more than 1.5 in each of five years. Differences between females accounted for, on average, 61% of the total variance of egg volume. Individual females produced similarly sized eggs from one year to another. Nevertheless, average egg volume per clutch declined by 0.2 cm³ per year as females aged, but this explains little of the observed variation. Female size and food supplementation had no significant effect on egg volume. In absolute terms, large eggs contain more lean dry matter and lipid than small eggs, but the proportion of both constituents decreases with egg size. Consequently, the combustible energy content of eggs increases less than proportionally with egg size. Hatchability averaged 87% and was not correlated with egg volume. Hatchling weight increased with egg size, averaging 65% of fresh egg weight. Chick survival until fledging did not increase with egg volume. Consequently, within the size range observed, large and small eggs are of comparable quality. Since both the costs and benefits of large eggs compared with small eggs seem small at best, we propose that, within the size range encountered in this population, egg size can be considered an evolutionarily neutral trait.

In all bird species, egg size is highly variable (Williams 1994). Large eggs presumably contain more albumen and yolk than small eggs and should be more costly to produce. The additional food requirements for the production of larger than average eggs are sometimes assumed to entail a fitness cost (Cooke *et al.* 1995), but this has never been demonstrated.

Large eggs may have a higher hatchability (Thomas 1983) and result in larger hatchlings that may have better prospects of survival (Parsons 1970). It was generally assumed that there is a positive relation between egg size and chick survival (Amundsen & Stokland 1990, Clutton-Brock 1991), although this view has been criticized (Mueller 1990). A positive correlation between egg size and chick survival was reported in only 14 out of 34 studies reviewed by

Williams (1994). In several of these studies, the positive effect was not due to egg size itself, but could be attributed to parental properties (age, territory quality), which were positively associated with both egg size and chick survival. After controlling for these confounding factors, a residual effect of egg size on chick survival remained in only three seabird species. However, it is possible that this positive effect is due to relative rather than absolute egg size, caused by competitive asymmetry between chicks associated with intra-clutch egg size variation. A chick hatched from a 40-g egg may have a competitive advantage over siblings hatched from 30-g eggs, but is at a disadvantage when its siblings hatched from 50-g eggs.

The fact that considerable egg size variation is maintained within populations of virtually all bird species suggests that there is no directional selection towards a fixed optimal egg size, assuming that egg size is to a large extent genetically determined (Van Noordwijk *et al.* 1980, Larson & Forslund 1992). Heritable varia-

*Corresponding author at ARCADIS Heidemij Advies, PO Box 1018, 5200 BA, 's-Hertogenbosch, The Netherlands.
Email: t.d.jager@arcadis.nl

tion may be maintained if egg size is an evolutionarily neutral trait or when the balance between costs and benefits results in different solutions between individuals. This requires a quantification of these costs and benefits. The simple fact that no unequivocal evidence for the existence of costs and benefits associated with egg size variation has so far been reported suggests that these costs and benefits may be small and consequently difficult to quantify.

We report on egg size variation in the Eurasian Oystercatcher *Haematopus ostralegus* on the island of Schiermonnikoog in the Dutch Wadden Sea. We consider the factors affecting egg size, food and energy requirements for egg production as well as the effect of egg size on reproductive success.

METHODS

Study area and period

The study area is located on the western part of the salt marshes on Schiermonnikoog (53°30′N, 06°10′E), one of the Frisian isles which fringe the Dutch Wadden Sea. For a detailed description of the study area and the local breeding population see Ens *et al.* (1992). Data on egg size and hatching success were collected from 1986 to 1990. Egg composition and the effect of experimental food supplementation were investigated in 1987.

Every three days between late April and the end of June, the study area was thoroughly searched for new nests. Nest owners were identified as nearly all adults were marked with a unique combination of a colour ring and a 2.5-cm-high bar-code ring.

Egg measurements

All eggs were marked and their length and breadth measured to the nearest 0.1 mm using calipers.

Egg volume was measured in the laboratory by submerging the egg in water and measuring the resulting increase of the water level in a connected column to 0.2 cm³. According to Hoyt (1979), the volume of an egg (V in cm³) can be predicted from its linear dimensions using an equation of the form: $V = k_v (l \times b^2)$ where l and b represent length and breadth (cm), while k_v is a constant which depends on egg shape. We determined the volume of 245 eggs and the resulting regression equation: $V = 0.500 (l \times b^2)$ explained 93% of the variance. The standard error of k_v was 0.009.

Eggs were weighed (± 1 g) within two days after clutch completion, that is before weight loss due to the

evaporation of water during incubation becomes a complicating factor.

Egg composition

In total, during the breeding season of 1987, 143 eggs constituting 41 whole clutches were collected for analysis of egg composition. Eggs were collected under licences 'Vogelvergunning F' number R696 to J.B. Hulscher and R813 to M. Kersten. The eggs were collected from a part of the saltmarsh just to the east of the main study area where all breeding attempts failed in 1985 and in 1986 due to predation by locally breeding Herring Gulls *Larus argentatus*. Eggs were collected every day and replaced with dummy eggs until further experimentation (see below).

Immediately after collection, fresh weight was determined in the laboratory to the nearest 0.1 g. Subsequently, the eggs were boiled for 20 minutes to facilitate the separation of shell, yolk and albumen. All components were dried to constant weight at 60°C before dry weight was determined to the nearest 0.01 g. Boiling resulted in some water loss but this did not affect the results as water content was determined from the weight difference between dry and initial fresh weight of the eggs. Fat content was determined for every yolk by extraction with petroleum ether in a Soxhlet apparatus. To check for the presence of fat in the albumen, fat content of the albumen was determined for ten eggs. The fat content of the albumen in these eggs was as low as 0.36% of the fresh weight of the albumen, so no further measurements were conducted. Nitrogen content of 14 samples of dry albumen and lean dry yolk was measured with the Kjendall–Lauro method. Measured nitrogen content was multiplied by 6.5 to determine protein content.

Replacement clutches and food supplementation

Eggs collected for composition analysis were replaced with dummy eggs, which were readily accepted. Dummy eggs were removed within a week after clutch completion to induce the production of a replacement clutch. The area was searched for replacement clutches every day. Replacement clutches were laid in new nests, usually within 10 m of the original nest.

To investigate the influence of food availability on egg volume, each day we provided 15 pairs, after removal of their first clutch, with 50 boiled mussels *Mytilus edulis* (average length 45.8 mm), placed 1–5 m from the original nest. Although Oystercatchers

defend an exclusive nesting territory, we did not know the exact boundaries between territories of these pairs. Therefore, we verified by visual observation that the mussels were consumed by the intended birds. Supplemented food was accepted by ten pairs, of which at least seven produced a replacement clutch. We cannot be sure that the other three pairs did not produce a replacement clutch, because several nests were predated before we were able to identify the owners. We compared average egg volume of initial and replacement clutches in food-supplemented ($n = 7$) and unsupplemented pairs ($n = 18$).

Hatchability and chick survival

Virtually all nests were discovered before clutch completion. Since incubation lasts on average 27 days, we were able to forecast the hatching date of the clutch. Hatchlings were marked with rhodamine or picric acid on the white underparts to allow easy identification in the field.

The age of each chick was thus known with an accuracy of one day. We checked at least once a week which chicks were still alive. Chicks were equipped with colour-rings prior to fledging, which occurred at 27 to 52 days of age (Kersten & Brenninkmeijer 1995). Chicks were considered to have fledged successfully when they accompanied their parents to feeding areas outside the breeding territory.

Data treatment and statistical analyses

The maximum clutch size of Eurasian Oystercatchers is four eggs but, because of heavy predation during egg laying, the modal nest contained only three eggs. Most nests with two or three eggs contain the remains of a four-egg clutch (Ens 1991), but others may be genuine three-egg clutches. Since we are not sure about the real clutch size of nests containing fewer than four eggs, we base our analyses on individual eggs and ignore a possible effect of clutch size.

Analyses of variance were performed with the statistical package SPSS PC+ Version 4.0.

RESULTS

Variation in egg size

The average dimensions of eggs showed little variation over years (Table 1), but within years the variation was considerable. Average egg volume varied only from 43.3 cm³ to 43.7 cm³ between years, whereas the coefficient of variation of egg volume within years was 7–8%. The variability of egg volume is probably best illustrated by the ratio of the largest egg to the smallest egg, which was more than 1.5 in every year (Fig. 1). Differences between females accounted on average for 61% of the total variance in egg volume (Table 2).

To verify whether individual females also produced similarly sized eggs from one year to another, we analysed the data from 15 females that produced a clutch of at least three eggs in each of five consecutive years. For each year we calculated the average volume of all eggs produced by each female (Fig. 2). A repeated-measurements ANOVA revealed that differences between females explained 87% of the variance in average egg volume, while year did not contribute significantly ($F = 2.270$, df $= 4, 14$, $P = 0.083$, Greenhouse–Geisser epsilon correction). However, average egg volume for these 15 females declined with 0.20 cm³/year between 1986 and 1990 and this trend was significant ($F = 10.335$, df $= 1, 14$, $P < 0.01$). This suggests that egg volume decreased slightly as females became older.

The persistent variation in egg volume between individual females may be related to variation in body size. In Oystercatchers, body size within sexes is best characterized by bill-length, and body weight is positively correlated with bill-length (Zwarts *et al.* 1996). Because body weight was determined during the incubation period, i.e. after the eggs were laid, we consider body weight to be an index of size rather than condition. Egg volume increased only slightly with female bill-length (mm), but the linear regression was far from significant ($Y = 0.08X + 37.3$; $r^2 = 0.001$, $n = 51$, $P > 0.1$). Similarly, female body weight (g) had no significant effect on egg volume ($Y = 0.01X + 36.6$; $r^2 = 0.03$, $n = 51$, $P > 0.1$).

Table 1. Average dimensions of Eurasian Oystercatcher eggs during the study period. Results are mean ± sd.

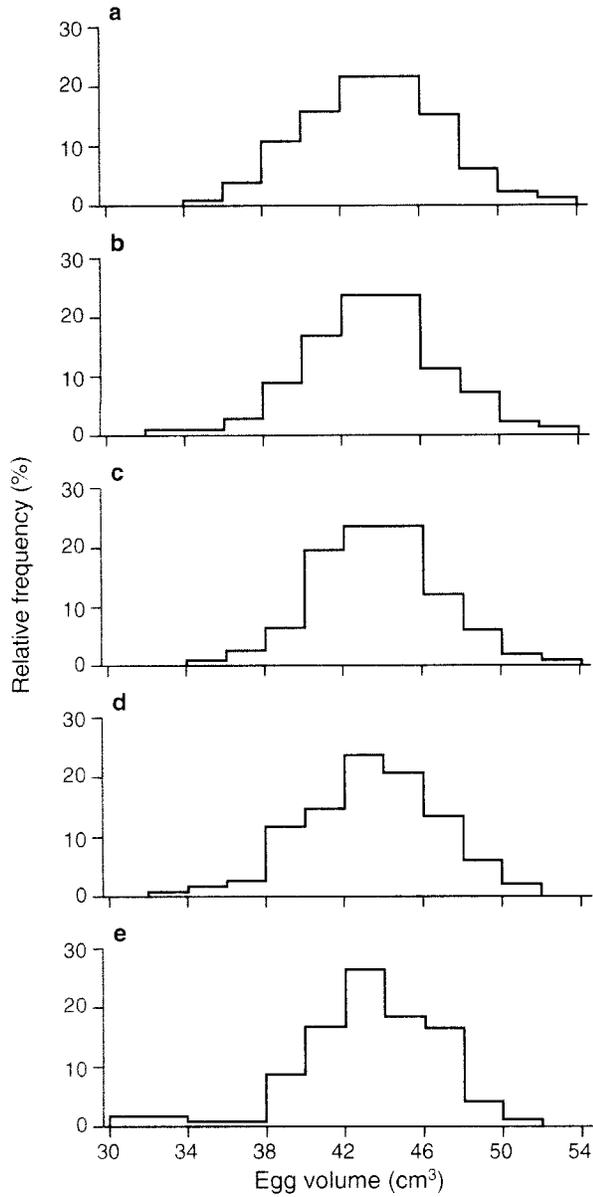| Year	Length (mm)	Breadth (mm)	Volume (cm³)	Weight (g)	n
1986	55.71 ± 2.31	39.53 ± 1.07	43.57 ± 3.10	45.87 ± 3.26	291
1987	55.44 ± 2.42	39.59 ± 1.05	43.50 ± 3.25	45.96 ± 3.52	379
1988	55.96 ± 2.44	39.52 ± 1.04	43.74 ± 3.08	45.98 ± 3.01	113
1989	55.34 ± 2.41	39.56 ± 0.99	43.37 ± 3.25	45.90 ± 3.65	137
1990	55.51 ± 2.75	39.49 ± 1.10	43.33 ± 3.37	46.02 ± 2.85	174

Figure 1. Annual frequency distribution of Oystercatcher egg volumes on Schiermonnikoog, the Netherlands, from 1986 to 1990. (a) 1986, *n* = 291; (b) 1987, *n* = 379; (c) 1988, *n* = 113; (d) 1989, *n* = 137; (e) 1990, *n* = 174.
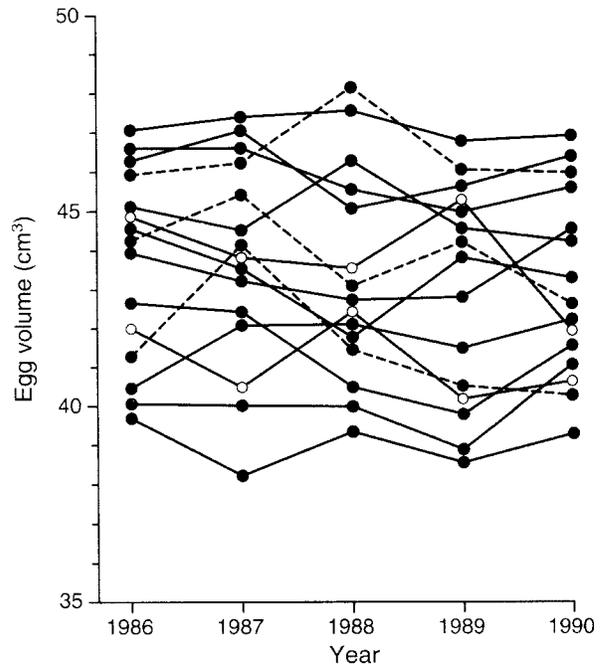

Figure 2. Average egg volume of 15 individual females during five consecutive years. Egg volume was calculated for three-egg and four-egg clutches. Different lines and symbols only serve to lead the eye and have no special meaning.

Average egg volume in replacement clutches did not differ from that in the preceding clutches, regardless of whether the initial clutches disappeared because of natural causes or due to experimental removal (Fig. 3). In addition, food supplementation after clutch removal did not result in an increase of the average egg volume typical for that particular female.

Egg composition

Egg mass (g) correlated well with volume (cm^3) according to the relation: $M = 2.674 + 0.994V$ ($r^2 = 0.93$, $n = 819$). Fresh weight of shell, albumen and yolk increased with fresh egg weight (Fig. 4). The proportion of albumen increased slightly with fresh egg

Table 2. One-way analyses of variance to separate within-female and between-female components in the total variance of egg volume. The within-female component comprises both within-clutch variance as well as between-clutch variance of eggs in initial and replacement clutches produced by the same female during a particular year.

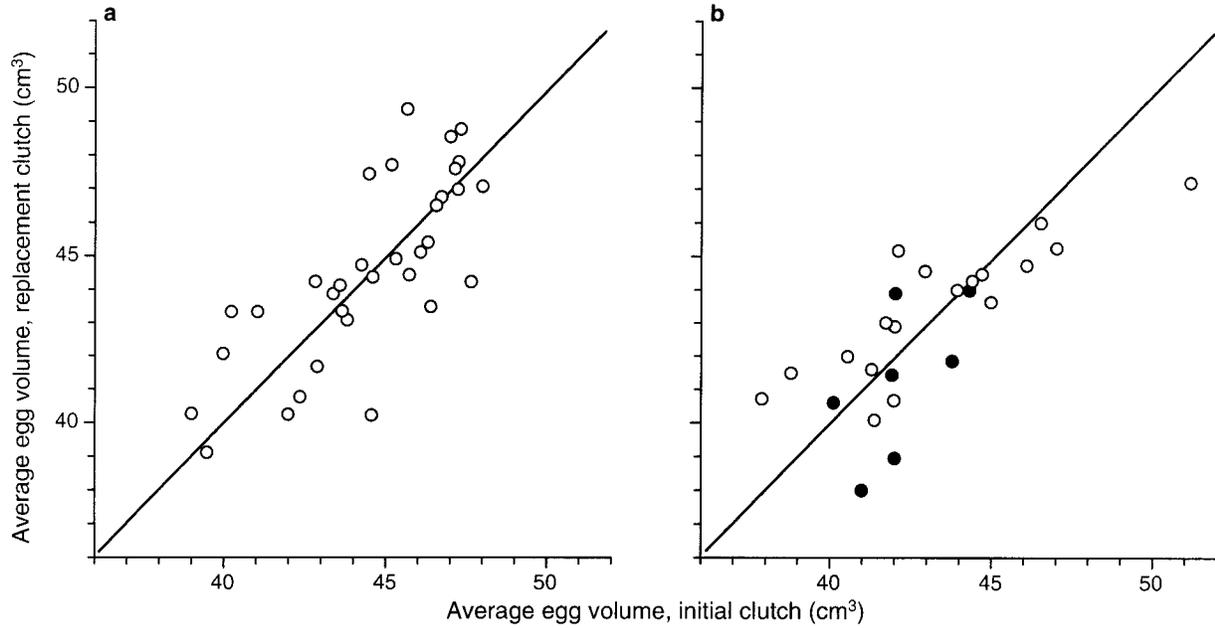| Year	Within-female variance (df)		Between-female variance (df)		F	P	Proportion within
1986	3.3566	(168)	6.0458	(59)	7.72	< 0.001	0.643
1987	3.9892	(405)	6.5793	(107)	8.82	< 0.001	0.623
1988	3.8442	(176)	6.2525	(67)	6.85	< 0.001	0.619
1989	4.4804	(180)	4.9989	(71)	4.90	< 0.001	0.527
1990	5.2139	(128)	8.9841	(49)	7.12	< 0.001	0.633

Figure 3. Average egg volume of initial and replacement clutches produced by the same female. (a) Natural replacements (data 1986–90, n = 33); (b) replacements after experimental removal in 1987; data are separated for pairs supplied with additional food (●, n = 7) and controls (○, n = 18).

weight (exponent: 95% CI 1.007–1.165), while the proportion of yolk decreased slightly (exponent: 95% CI 0.646–0.972).

Albumen contained on average 13.2% dry matter and hardly any fat (0.36%). The proportion of dry mat-

ter did not depend on fresh weight of the albumen (r^2 = 0.00). Dry albumen contained 11.9% nitrogen, equivalent to a protein content of 77%.

Although the amounts of fat and lean dry matter in yolk increased with fresh weight of the yolk (Fig. 5),
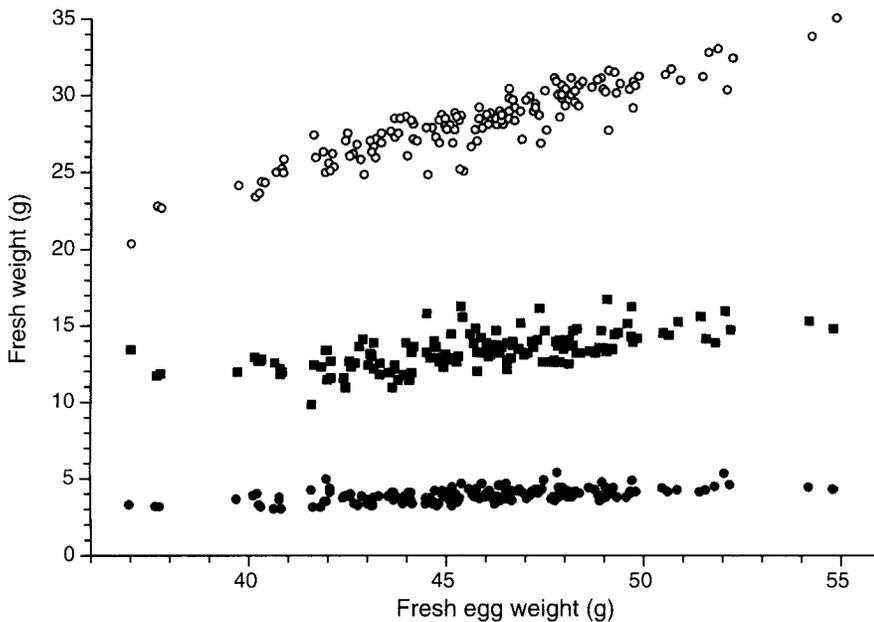

Figure 4. Fresh weight of shell (●), albumen (○) and yolk (■) in relation to the total fresh weight of the entire egg directly upon laying (n = 143 eggs). The weight of each component increased with fresh egg weight according to the following allometric equations: shell: $Y = 0.082X^{1.018}$; r^2 = 0.37; albumen: $Y = 0.446X^{1.086}$; r^2 = 0.84; yolk: $Y = 0.609X^{0.809}$; r^2 = 0.40.
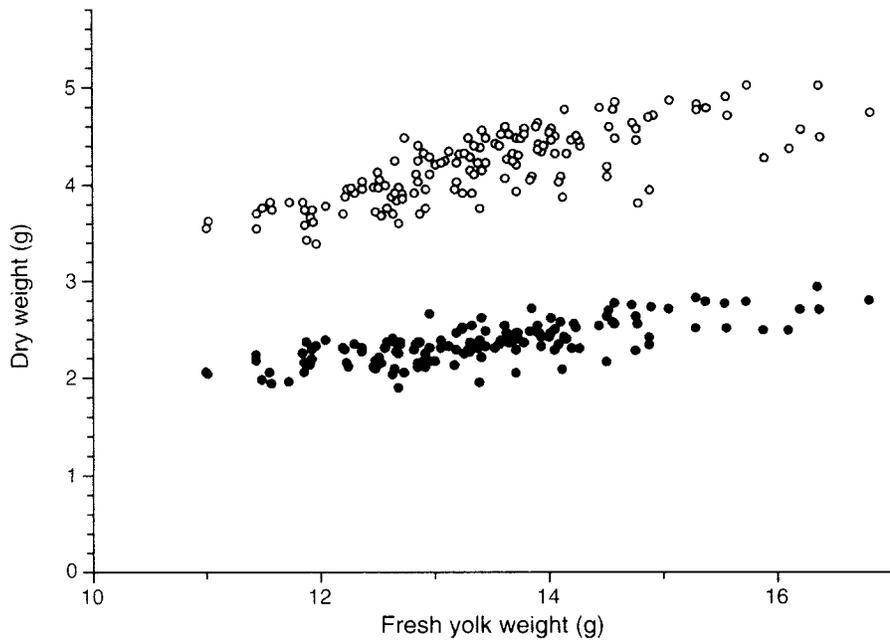
Figure 5. Relation between yolk contents (○, lipids; ●, lean matter) and yolk size (n = 143 eggs). The weight of each component increased with fresh yolk weight according to the following allometric equations: lean dry: $Y = 0.311X^{0.783}$; r^2 = 0.56; fat: $Y = 0.543X^{0.789}$; r^2 = 0.62.

the proportions of both components decreased (95% CI of exponents: fat, 0.685–0893; lean dry matter, 0.669–0.897). Lean dry yolk contained 11.8% nitrogen, equivalent to a protein content of 77%.

Because the principal constituents do not scale isometrically with fresh egg weight, the composition of large eggs differs slightly from that of small eggs. In absolute terms, large eggs contain more lean dry matter and lipids than small eggs, but the proportion of both constituents decreases with egg size (Table 3). However, this departure from direct proportionality is quantitatively rather modest. For example, a 25%

increase in egg volume from 40 cm³ to 50 cm³ is accompanied by a 17% increase in the combustible energy content.

Egg volume and chick survival

The hatching probability of eggs which did not disappear due to flooding or predation averaged 87% and was not correlated with egg volume ($P > 0.1$, Fig. 6). The body weight of chicks at hatching increased linearly with egg weight according to the relation $Y = 0.634X + 2.16$ (r^2 = 0.65, n = 189, t = 18.64,

Table 3. Composition and energy content of Oystercatcher eggs in relation to egg volume, calculated from the allometric relations in Figures 4 and 5.

| Volume (cm³) | Fresh weight | | | | Lean dry matter | | Fat | | Energy[a] (kJ) |
	Egg (g)	Shell (g)	Yolk (g)	Albumen (g)	(g)	(%)[b]	(g)	(%)[b]	
30	32.5	2.8	10.2	19.6	4.5	13.8	3.4	10.4	216
35	37.5	3.3	11.4	22.8	5.1	13.6	3.7	9.9	240
40	42.4	3.7	12.6	26.1	5.7	13.5	4.0	9.5	263
45	47.4	4.2	13.8	29.5	6.3	13.3	4.3	9.1	286
50	52.4	4.6	15.0	32.8	6.9	13.2	4.6	8.8	308
55	57.3	5.0	16.1	36.2	7.5	13.1	4.9	8.5	330

[a]Lean dry matter contains 77% protein and 23% ash (this study); energy equivalent of protein and fat 23.62 kJ/g and 39.71 kJ/g respectively (Ricklefs 1974). [b]Relative to fresh egg weight.
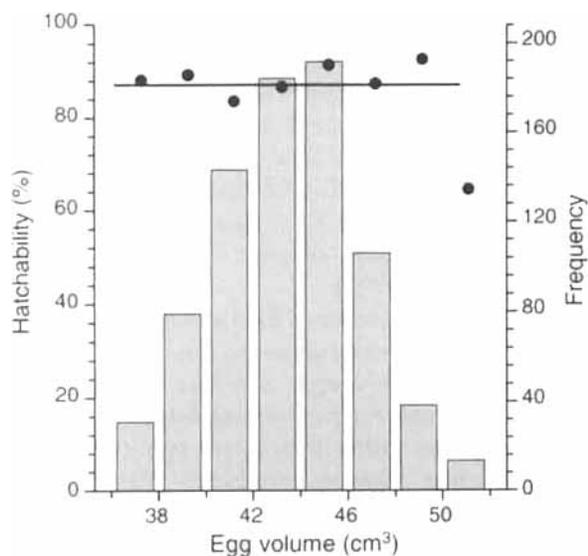
from a large egg may constitute an advantage during these early days. However, the data show that, even at this young age, chicks hatching from small eggs were not at a disadvantage compared with those hatching from large eggs (Fig. 7). Only 30% of the hatchlings managed to fledge successfully irrespective of the volume of the egg from which they hatched (χ^2 = 0.305, df = 2, $P > 0.1$).

DISCUSSION

Determinants of egg size

The size of Oystercatcher eggs is highly variable and most of this variation is due to consistent differences between females. The within-female component of egg size variation within a year amounted to 61%, while 87% of the variance in average egg volume per clutch from one year to another was explained by female identity. High consistency in the egg sizes of individual females has previously been reported in many other bird species, including the closely related American Oystercatcher *Haematopus palliatus* (Nol *et al.* 1984) and several other wader species (Väisänen *et al.* 1972, Miller 1979, Redmond 1986, Grant 1991, Nol *et al.* 1997). Heritability of egg size, based on mother–daughter correlations, has not yet been determined in any wader species. Heritability coefficients in Great Tit *Parus major* (Ojanen *et al.* 1979, Van Noordwijk *et al.* 1980), Red Grouse *Lagopus lagopus scoticus* (Moss & Watson 1982) and Barnacle Goose *Branta leucopsis* (Larson & Forslund 1992) were invariably higher than 60%. If similarly high values apply to waders, this would mean that most of the phenotypic variation in egg size observed in our Oystercatcher population is genetically determined.

The average volume of eggs produced by the same females decreased slightly over the five-year study period. A significant effect of age on egg size has been reported in several other bird species, but usually egg size increases with age (Davis 1975, Brooke 1978, Lloyd 1979, Mills 1979, Thomas 1983, Weimerskirch 1990, 1992, Hamer & Furness 1991, Croxall *et al.* 1992, Sydeman & Emslie 1992). Evidence that egg size may decline again as individuals become older is less abundant and often anecdotal, referring explicitly to very old individuals (Andersen 1951, Richdale 1955, Davis 1975, Hamer & Furness 1991). Croxall *et al.* (1992) could not detect any reduction of egg size in Wandering Albatrosses *Diomedea exulans* up to an age of at least 35–40 years. Although we do not know the precise age of the 15 female Oystercatchers in our

Figure 6. Hatchability of Oystercatcher eggs (●) in relation to their volume. The histogram shows the frequency distribution of egg volumes over which hatchability was calculated.

$P < 0.01$). Consequently, chicks hatch with a body weight close to 65% of the fresh weight of their egg. Chick survival between hatching and fledging did not improve with egg volume (Fig. 7). Most chick mortality occurred shortly after hatching. Only 44% of all hatchlings survived until an age of 12 days (Kersten & Brenninkmeijer 1995). Since small chicks are more vulnerable to environmental perturbations, hatching
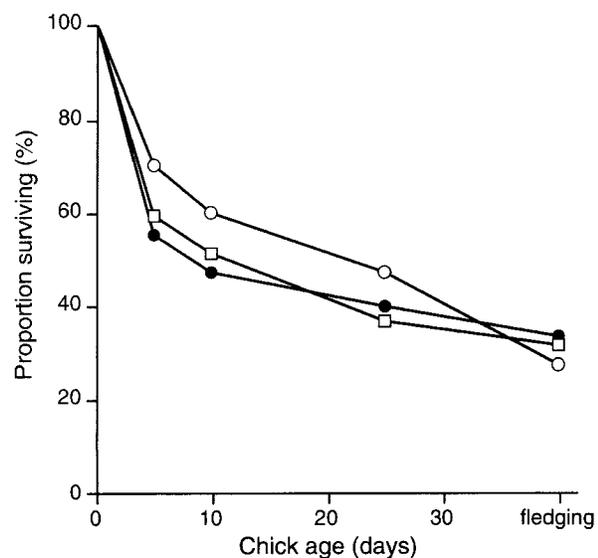

Figure 7. Survival of chicks in relation to the volume of the egg from which they hatched. (○) Small eggs 36–42 cm³ (*n* = 30); (●) medium eggs 43–46 cm³ (*n* = 78); (□) large eggs 47–52 cm³ (*n* = 41).

sample, the data suggest an age-related decline in egg volume. It seems unlikely that this decline was due to deteriorating environmental conditions over the study period, because the average volume of all the eggs in the population hardly changed (Table 1).

Although a significant effect of age on egg size has been documented in several species, age accounted for only 5–10% of the overall variation in egg size (Weimerskirch 1990, 1992, Croxall *et al.* 1992). The age-related reduction of egg volume in the Oyster-catcher is also small (0.2 cm³/year), and by no means sufficient to explain a large part of the observed variation in the population. A reproductive career of 20 years would result in a 4 cm³ decrease in egg volume. This represents only 20% of the observed range in egg volumes in any year. In addition, age as an important factor in the variation of egg volumes is not consistent with the observed symmetrical frequency distribution of egg volumes (Fig. 1). Given a 95% annual adult survival rate (Ens *et al.* 1995), only 36% of the recruits into the population would still be alive after 20 years. This means that young birds out-number old birds by a factor of three, which would result in a strongly skewed frequency distribution of egg volumes. The observed frequency distribution is, in fact, almost symmetrical (Fig. 1) with eggs of inter-mediate size outnumbering both small and large eggs. Therefore we conclude that, although female age has a small effect on egg volume, most of the observed variation in egg volumes must be due to persistent differences between individual females.

We found no indication that egg volume increased with female bill-length or body weight. By contrast, egg volume increased significantly with both female body weight and with the geometric mean of eight external measurements in the American Oystercatcher (Nol *et al.* 1984). Other studies have also yielded conflicting results, even within such well studied species as the Great Tit and Pied Flycatcher *Ficedula hypoleuca*. In general, a positive effect of female size on egg size is either absent (De Steven 1978, Ojanen *et al.* 1979, Birkhead & Nettleship 1981, Järvinen & Väisänen 1983, Grant 1991, Smith *et al.* 1993) or small (Väisänen *et al.* 1972, Miller 1979, Ojanen *et al.* 1979, Otto 1979, Järvinen & Pryl 1989, Reid & Boerma 1990, Blomqvist & Johansson 1995).

A number of authors have shown that differences in egg size may result from differences in food supply. Most of these studies apply to gulls: Herring Gull *Larus argentatus* (Van Klinken 1992, Pons 1992), Glaucous-winged Gull *Larus glaucescens* (Reid 1987), Red-billed Gull *Larus novaehollandiae scopulinus*

(Mills 1979), California Gull *Larus californicus* (Winkler & Walters 1983) and Lesser Black-backed Gull *Larus fuscus* (Houston *et al.* 1983, Bolton *et al.* 1992). In these studies, individuals that could benefit from a more favourable food supply, either natural or experimentally induced, produced larger eggs. How-ever, in the Arctic Tern *Sterna paradisaea* egg size was not affected by good or poor breeding conditions (Monaghan *et al.* 1992).

In our study, we increased food availability to certain females. This did not result in the production of larger eggs. Although the sample size was small (*n* = 7), the tendency was for food-supplemented females to produce smaller rather than larger eggs (–0.9 ± 1.8 cm³), whereas controls produced slightly larger replacement eggs (+0.2 ± 1.8 cm³). We conclude that egg size was not constrained by food availability. Similarly, Nol (1989) concluded that food availability did not affect egg size in the American Oystercatcher.

Högstedt (1981) showed that Magpies *Pica pica* provided with supplemental food produced eggs which were 0.33 g (3%) heavier than before. Although we cannot exclude a similar small effect of food avail-ability on egg size, regarding the small number of food-supplemented females in our study, food avail-ability is not likely to account for the 50% higher volume of large eggs compared with small eggs. This conclusion is supported by data on annual differences in food intake rate and average egg volume. Kersten and Visser (1997) showed that food intake rate during the incubation period was significantly higher in 1987 than in 1989 (0.98 versus 0.59 g/min, fresh weight). This difference was not reflected by a decline in average egg volume, which remained remarkably con-stant over the entire study period (Table 1).

Egg composition

Egg composition in birds is related to the position in the precocial–altricial spectrum (Carey *et al.* 1980). The eggs of precocial species contain 30–35% yolk and 50–60% albumen. Fat is concentrated in the yolk, usually 30–35%, while protein is distributed over yolk and albumen. Dry protein accounts for 11–12% of fresh egg weight and slightly more than 50% of this occurs in the albumen (Ricklefs 1974). The Eurasian Oystercatcher fits well into this pattern: yolk accounts for 28–31% of fresh egg weight and contains 30–33% fat. Albumen accounts for 60–63% of fresh egg weight. Dry protein represents 13–14% of fresh egg weight and 58–64% of all protein is stored in the albumen.

Several studies on precocial species show that the

proportion of yolk increases with egg size, while the proportion of albumen decreases: Leach's Storm-petrel *Oceanodroma leucorhoa* (Montevecchi *et al.* 1983), Mallard *Anas platyrhynchos* (Birkhead 1985), Blue-winged Teal *Anas discors* (Rohwer 1986) and Wood Duck *Aix sponsa* (Hepp *et al.* 1987). A similar positive association was not apparent in our study. Oystercatchers do not store disproportionately large quantities of fat and protein in large eggs. In fact, the proportion of yolk decreased significantly with egg size. Although the absolute amounts of fat and protein increased with egg size, the proportion of each of these constituents also decreased.

Assuming a 77% efficiency of egg production (Brody 1945), the total amount of energy involved in the production of a four-egg clutch consisting of 40 cm^3 eggs equals 1368 kJ ($4 \times (100/77) \times 263$), whereas the production of a similar clutch with 50 cm^3 eggs requires 1600 kJ ($4 \times (100/77) \times 308$). The additional energy requirements during a 12.5-day period of clutch formation (Kersten 1997) are on average 109 kJ/day (1368/12.5) for eggs of 40 cm^3 and 128 kJ/day (1600/12.5) for eggs of 50 cm^3. These represent 19% and 22% respectively of the daily energy expenditure of free-living females after clutch completion, which averaged 570 kJ/day (Kersten 1997). Consequently, although a female's energy requirements increase considerably during clutch formation, the energetic consequences of producing either small or large eggs appear marginal. Considering that rates of energy acquisition are likely to differ by much more than 3% from one year to another, we interpret the remarkable consistency of the average egg size (Table 1) as an indication that egg size is not constrained by food availability. From this we deduce that females that produce large eggs can afford the marginally higher energy and nutrient requirements.

Hatching and fledging success

Hatchability (the percentage of eggs surviving to the end of incubation that hatch) of Oystercatcher eggs is independent of egg volume and averaged 87%. This is close to the average value of 89.5% for carnivorous birds (Koenig 1982).

A positive correlation between egg size and hatchability has been reported in Common Wood Pigeon *Columba palumbus* (Murton *et al.* 1974, Murton & Westwood 1977), Kittiwake *Rissa tridactyla* (Thomas 1983) and Wandering Albatross *Diomedea exulans* (Croxall *et al.* 1992). Williams (1994) noted that such a positive association may result from differences

between parents (for example age) rather than from differences in egg size itself. In line with our results, most studies could not detect a positive association between egg size and hatchability (De Steven 1978, Tullet & Burton 1982, Lloyd 1979, Reid & Boersma 1990, Williams 1990, Bolton 1991, Hakkarainen & Korpimaki 1991, Williams *et al.* 1993).

Obviously, there is a lower limit to egg size in any bird species. We suspect that hatchability increases rapidly when egg size exceeds this minimum viable egg size, but at a decelerating rate. In the Oystercatcher, hatchability does not increase any further when egg size surpasses 36 cm^3 (>99% of eggs found) (Fig. 6). This implies that the minimum viable egg size in Oystercatchers is probably quite a bit smaller than 36 cm^3. Within the size range of eggs produced in our study population, the viability of small eggs is not impaired compared to that of large eggs.

Larger eggs give rise to heavier hatchlings and these may have a better prospect of survival until fledging. A recent review (Williams 1994) reported that, in 42% of 34 studies, chick survival was positively related to egg size. However, in several of these studies this positive effect was not due to egg size *per se*. Confounding factors, such as egg-size-related competitive asymmetry between chicks within a brood, or parental attributes like age or territory quality, turned out to be responsible for the positive effects of egg size.

In this study, we found no evidence that chicks hatching from large eggs were more likely to survive until fledging. If egg size has any positive effect on chick survival, its contribution seems completely overridden by other factors. The most important factor determining fledging success in the study population is territory quality. Parents have to transport food over short distances (1–50 m) in high-quality resident territories and over long distances (200–1000 m) in low-quality leapfrog territories. Consequently, the rate of food provisioning is higher in resident territories than in leapfrog territories, although food is collected at a faster rate in leapfrog territories (Ens *et al.* 1992). Fledging success is generally low (Kersten & Brenninkmeijer 1995), but chicks raised in a resident territory are 3.5-times more likely to survive until fledging than chicks raised in a leapfrog territory (Ens *et al.* 1995). Williams (1994) rightly pointed out that a positive correlation between egg size and fledging success may be due to the confounding effects of parental or territory quality. Likewise, the absence of a correlation between egg size and fledging success may also be related to parental attributes other than egg size. In theory, a positive correlation between egg size

and fledging success may be masked by an association of large eggs with low quality territories and of small eggs with high quality territories. The reverse seems to be true. Eggs are slightly larger in resident territories (average: 44.5 cm³; 95% CI: 44.0–45.0, n = 117) than in leapfrog territories (average: 43.5 cm³; 95% CI: 42.9–44.1, n = 126). Therefore, we see no evidence that larger eggs breed better birds.

In conclusion, the absence of a positive correlation between egg size and fledging success indicates that small and large eggs are of comparable quality. Further, the energy requirements of females producing large eggs are only marginally higher than those of females producing small eggs, while egg size is probably not constrained by food availability (see above). Since both the costs and benefits of large eggs compared with small eggs seem small at best, we propose that, within the size range encountered in the study population, egg size is effectively an evolutionarily neutral trait. This may explain why a considerable, probably heritable, variation of egg sizes is maintained in the population. Since egg size variation in many other bird species is of a similar magnitude and differences between females usually explain a large part of this variation, this conclusion may have a general application.

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