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Rearing conditions determine offspring survival independent of egg quality: a cross-foster experiment with Oystercatchers *Haematopus ostralegus*

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Variation in rearing conditions, due either to parental or to environmental quality, can result in offspring of different quality (e.g. body condition, immune function). However, evidence is accumulating that egg size and composition can also affect offspring quality. In Oystercatchers *Haematopus ostralegus*, high-quality rearing conditions result in a higher quantity as well as quality of offspring. This is thought to be caused by increased parental food provisioning to the chicks in high-quality environments. However, variation in egg quality between rearing conditions could also affect the quantity and quality of offspring. Determining the mechanism and ontogeny of quality differences is important in unravelling the causes of variation in reproductive success. To disentangle the effects of egg quality, and quality of the rearing conditions, on the future survival of offspring, we cross-fostered complete clutches between nests. When reared under conditions of similar environmental quality, chicks originating from eggs laid in low-quality environments survived as well as chicks originating from eggs laid in a high-quality environment. However, chicks reared in high-quality environments survived twice as long as chicks reared in low-quality environments, independent of the environmental quality in which the eggs were laid. This suggests that variation in the future survival of offspring is primarily caused by differences in environmental and/or parental quality, with no clear effect of egg quality (size).

Variation in rearing conditions, due either to parental or to environmental quality, can result in offspring of different quality. Offspring quality can be expressed as offspring mass, structural size and physiological condition. Quality differences, resulting from conditions experienced during early development, can have important long-term fitness consequences (Lindström 1999). Recently, evidence has accumulated that parents can also influence offspring quality by laying eggs of different quality. Egg size (Williams 1994, Hipfner 2000) and egg composition (nutritional, immunological and hormonal content) (Eising *et al.* 2001, Saino *et al.* 2003) can affect chick immune function, growth or survival. Furthermore, intraclutch variation in egg size and composition could result in hatching asynchrony or intraclutch variability in hatchling mass and as such could affect sibling competition and survival (Slagsvold *et al.* 1984). Determining the exact mechanism (quality of rearing conditions vs. egg quality) and understanding the ontogeny of quality differences are important in assessing the causal effects these life-history traits have on fitness.

In Oystercatchers *Haematopus ostralegus*, rearing conditions are thought to have a strong effect on both the quantity and the quality of offspring. Rearing conditions in Oystercatchers mainly vary as a result of the feeding ecology during the chick phase (Ens *et al.* 1992). Some parents (also called 'residents') can take their semi-precocial chicks to their adjacent feeding territory and feed them there (high-quality conditions). Other parents (also called 'leapfrogs') have to fly to their non-adjacent feeding territory and transport every food item back to their chicks (low-quality conditions). The quality of rearing conditions is therefore mainly thought to be determined by environmental quality (spatial organization of territory), possibly intercorrelated with parental quality. Pairs in high-quality environments consistently produce almost three times more fledglings per year than do pairs in low-quality environments. Furthermore, fledglings reared under high-quality conditions are

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on average 10% heavier than fledglings reared under low-quality conditions (Ens *et al.* 1992, Bruinzeel 2004). However, egg quality might also vary between environments of different quality, as a result either of differences in feeding areas or of differences in female quality. For example, under high-quality rearing conditions egg size is greater than under low-quality rearing conditions (Heg & van der Velde 2001). Amounts of fat, yolk, carotenoids or androgens deposited in the egg or the genetic quality of the egg might also differ between high- and low-quality rearing conditions, but this has not yet been investigated. Furthermore, intraclutch variation in egg size is larger under low-quality conditions than under high-quality conditions (Heg & van der Velde 2001).

Both egg size (and composition) and intraclutch variability could affect offspring quantity and quality. However, all these possible components of egg quality and the quality of offspring co-vary with the quality of rearing conditions. This makes it difficult to disentangle whether egg quality or the rearing condition is responsible for the observed differences in quantity and quality of offspring between high- and low-quality environments. Cross-foster experiments are necessary to disentangle any possible effects of egg quality and/or rearing conditions on the future prospects of offspring (e.g. Bolton 1991, Bize *et al.* 2002, and references therein). Here, we cross-fostered complete clutches of eggs originating from high- and low-quality rearing environments to nests in either high- or low-quality rearing environments and followed the growth and survival of the chicks.

Reproductive success has declined strongly over the last two decades in this population (Bruinzeel 2004), and during the same period the average egg size decreased by 3% (M. van de Pol *et al.* unpubl. data). Investigating the causal effect of egg size on reproductive success by conducting a cross-foster experiment allows us to assess whether the decline in reproductive success is (at least partly) caused by a decline in egg size.

METHODS

Study area and nest searches

The study was conducted on the Dutch Wadden Sea island of Schiermonnikoog (32°29′N, 6°14′W), in the years 2002 and 2003. The study area consisted of a saltmarsh area where the colour-ringed Oystercatchers bred and intertidal mudflats where they fed. Following earlier studies, we designated territories with adjacent feeding and nesting areas as high-quality rearing conditions and territories with spatially separated feeding and nesting areas as low-quality rearing conditions (Ens *et al.* 1992, 1995). Nest searches were conducted from the end of April until the end of July, and territories were visited every other day to search for new nests and to check existing nests for new eggs. The identity of the parents was noted and the location of the nest was mapped. Oystercatchers lay 1–4 eggs with an interval of 28 h, resulting in a modal clutch size of three eggs (Strijkstra 1986). All newly found eggs were individually marked, weighed to the nearest 0.1 g using a balance, and egg width and length were measured to the nearest 0.1 mm using dial callipers. Egg size (volume, cm^3) was determined by $0.49 \times$ egg length [cm] $\times$ (egg width [cm])^2 (Jager *et al.* 2000). Intraclutch variation in egg size was calculated by the difference in egg size between the largest and the smallest egg in a clutch.

The clutch-completion date is the laying date of the last-laid egg in a clutch and coincides with the start of incubation. The clutch-completion date could be calculated by using two different methods. First, when a nest was newly discovered it usually contained only one or two eggs. During the next nest checks, new eggs were found and the day on which the last egg was laid was taken as the clutch-completion date. Secondly, in some cases we found nests in which no new eggs were laid during any later visits. In these cases, to determine the date of clutch completion, we made use of the fact that eggs lost weight at a constant rate through evaporation of water during incubation. Because Oystercatchers only started incubating after the last egg was laid, the number of days each egg in a clutch was already incubated could be determined from $199.0 - 183.5 \times$ (weight [g]/egg size [cm^3]) for a one- to three-egg clutch and from $191.1 - 176.2 \times$ (weight [g]/egg size [cm^3]) for a four-egg clutch. The clutch-completion date could then be determined by subtracting the number of days an egg had been incubated from the date the eggs were measured, taking the egg that had been incubated for the shortest period. This method is based on calibration from data from daily weighed eggs (Strijkstra 1986). Both methods gave a clutch-completion date with an error interval of 1 or 2 days.

Cross-foster experiment

We selected four nests for each experimental set, comprising two nests under high-quality rearing conditions and two nests under low-quality rearing

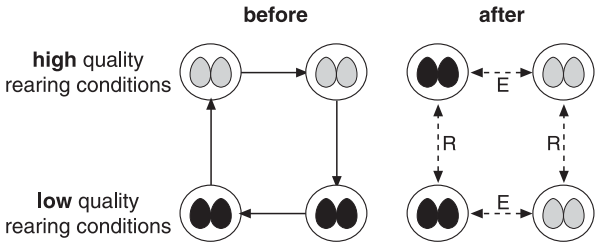

Figure 1. Schematic design of the cross-foster experiment. One swap set consisted of four nests (white circles), in which eggs from high-quality rearing environments (grey) and low-quality rearing environments (black) were swapped to other nests following the arrows in the left panel. As a result we created nests in high-quality rearing environments with eggs originating from either high- or low-quality environments and nests in low-quality rearing environments with eggs originating from either high- or low-quality environments (right panel). 'E' refers to the paired nests that enable testing of the effect of different egg origin; 'R' refers to the paired nests that enable testing of the effect of different rearing conditions. See text for further explanations.

conditions. We cross-fostered complete clutches as illustrated in Figure 1. We thus created clutches under high-quality rearing conditions with eggs originating from either high- or low-quality environments and we created clutches under low-quality rearing conditions with eggs originating from either high- or low-quality environments. Nests with eggs originating from either high- or low-quality environments and with the same quality of rearing conditions were considered statistically to be a paired unit (comparison 'E' in Fig. 1). Furthermore, nests with eggs originating from the same type of environmental quality but with different rearing conditions were also considered as a paired unit (comparison 'R' in Fig. 1).

All nests in one experimental set were matched on the same clutch-completion date (± 1 day), as this date strongly affects fledging success and mass at fledging in Oystercatchers (Heg 1999). In addition, nests were matched on the number of eggs present on the day on which the eggs were experimentally swapped. In a few cases (14%) we induced artificial 'predation' to equalize the number of eggs, by removing one or two randomly selected eggs from clutches. Furthermore, the spatial distance between the four nests in one set was never more than 400 m, to reduce any possible effects of spatial heterogeneity on the outcome of the experiment. All clutches in an experimental set were swapped (more or less) simultaneously. Eggs were swapped 21 days after the start of incubation, about 7 days before hatching. Day 21 of the incubation was chosen for two reasons. First, we wanted to cross-foster the eggs as late as possible in the incubation cycle, because egg predation, which would eliminate nests from the experiment, is frequent in Oystercatchers (Verboven *et al.* 2001). Secondly, Oystercatcher chicks communicate through the eggshell with their parents for several days before hatching (our pers. obs.): a behaviour that might affect parental behaviour subsequently. We therefore cross-fostered eggs sufficiently early that auditory recognition by 'parents' could not yet have been established.

Chick growth and survival

Every day we checked nests to determine whether the cross-fostered eggs had hatched. Immediately after hatching, chicks were individually marked, by painting different combinations of the lower parts of breast, wing and rump feathers with dye (rhodamine red, picrine yellow or malachite green). After about 4 weeks, chicks were colour-ringed. In the period after hatching we searched for chicks every other day for a standardized period of 10 min (Oystercatcher chicks are semi-precocial and leave the nest cup 1 day after hatching). Furthermore, we recorded whether parents were still alarming (loud calls) as an indicator of the chicks being alive or not. If parents did not alarm during two consecutive visits, we assumed that any chicks were dead, as this is an extremely reliable indicator. Only rarely did we actually find a dead chick, as they are probably eaten by predators or scavengers. During nest checks, parental alarm signalled the chicks to hide in the vegetation and, as a result, chicks were sometimes hard to find. If chicks were not found for two consecutive checks, but parents were still alarming, we combined the searches with observations from a hide nearby until the chicks were found. We searched for chicks in each nest until 50 days after hatching, or until we were certain that all chicks were dead. When chicks were found alive they were weighed to the nearest 0.1 g, and wing length, tarsus-plus-toe and bill-plus-head were measured to the nearest 0.1 mm.

As we did not find all chicks during each nest check and because we sometimes had to rely on the alarming behaviour of parents as an indicator that at least one chick was still alive, we were not able to assess reliably the exact survival duration of each chick individually. However, if parents at some point stopped alarming, and we did not find the chicks, we were able to determine reliably for how long the longest-surviving chick from that brood had survived. Furthermore, we could also reliably

determine whether chicks had survived the entire period of 50 days, because chicks should have fledged by the end of this period and so were easy to observe by then.

Data analysis

In total, 25 sets of four nests were cross-fostered, but due to major flooding in both 2002 and 2003 only 12 of these sets were unaffected and could be used. Nine nests within these 12 sets were predated after cross-fostering but before hatching; these were also omitted from analyses, resulting in a total of 39 nests. As a result, we obtained 18 matched pairs of nests with different egg origins but equal rearing conditions (comparison 'E', Fig. 1). In 11 of these pairs both nests were in high-quality rearing conditions, while seven were in low-quality rearing conditions. We also obtained 15 pairs of matched nests differing in rearing quality but equal in egg origin (comparison 'R', Fig. 1). In eight of these matched pairs both clutches originated from high-quality environments, and in seven matched pairs both clutches originated from low-quality environments.

Chick survival and fledging success in 2002 and 2003 were very poor. Because most chicks died within their first 1 or 2 weeks, and only in five nests did a chick survive the entire period of 50 days and fledge, we could not use fledgling success or mass as fitness measures. The longest-surviving chicks of only a small subset of nests survived long enough to obtain sufficient measurements to estimate growth rates reliably (eight pairs of matched nests [comparison 'R'] had at least four measurements per individual). Therefore, we used the survival duration of the longest-surviving chick as a fitness measure. All durations of survival were log-transformed for use in statistical tests. All tests are two-tailed and means are given with standard errors (±se).

RESULTS

The effect of growth on survival

Chick growth rates were a good predictor of survival duration. Differences in growth rates of body mass, measured over the same number of days and chick stage for two matched nests reared in the same conditions, were positively correlated with the differences in survival duration between those matched nests (Pearson's $r = 0.77$, $n = 8$ pairs, $P = 0.027$). Similar positive relationships were found between the growth rate of structural features (wing length, tarsus-plus-toe and bill-plus-head) and survival duration (all $P < 0.15$). Given the strong correlation between growth and survival time it is reasonable to assume that survival time is a reliable indicator of the fledging success and/or quality that birds would have achieved if environmental conditions had been better. For further analyses we only used survival duration, as we could not measure growth rates for the majority of cross-fostered clutches.

Egg origin vs. rearing conditions

In accordance with earlier results in this population (Heg & van der Velde 2001), eggs laid in low-quality environments were smaller (5%) than eggs laid in high-quality environments (40.8 ± 0.57 vs. 42.8 ± 0.63 cm^3, respectively; paired-$t = 2.20$, $df = 17$, $P = 0.042$), and tended to have larger intraclutch variation in egg size (although the latter was not significant in this sample; low: 3.3 ± 0.8 cm^3 vs. high: 2.5 ± 0.3 cm^3, paired-$t = 0.95$, $df = 17$, $P = 0.35$). Cross-fostered eggs laid in low-quality environments were from similarly sized clutches as eggs laid in high-quality environments (2.9 ± 0.2 vs. 3.0 ± 0.1 eggs, respectively; paired-$t = -0.37$, $df = 17$, $P = 0.72$).

Egg origin did not affect survival duration. When reared under similar conditions, the survival duration of chicks hatched from eggs laid in low-quality rearing conditions did not differ from that of chicks hatched in high-quality rearing conditions (Fig. 2a, paired-$t = 1.04$, $df = 17$, $P = 0.31$). However, rearing quality did strongly affect survival duration, being twice as long in high-quality rearing conditions as in low quality rearing conditions, when comparing eggs originating from the same quality environment (Fig. 2b, paired-$t = 2.81$, $df = 14$, $P = 0.014$).

Because clutches laid in low-quality environments contained smaller eggs and showed larger intraclutch variation in egg size than clutches laid in high-quality environments, we specifically tested whether the average egg size of a clutch as well as its intraclutch variation in egg size affected survival duration. Under the same quality rearing conditions, neither the egg size nor the intraclutch variation in egg size of foster clutches correlated with survival time (Table 1). The size of clutches from which the foster eggs originated did not affect the survival time (Table 1). Furthermore, the original egg size, the original intraclutch variation in egg size and the original clutch size of the adoption parents could indicate parental quality. However, none of these traits affected the survival

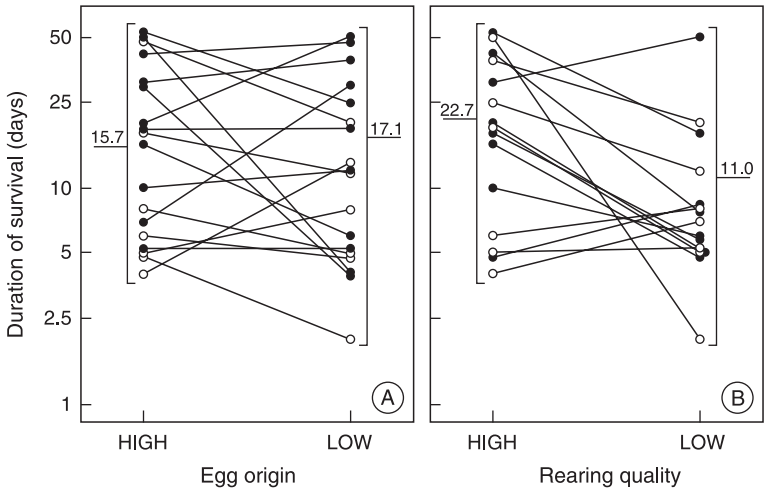

Figure 2. Survival duration of the longest-living chick in matched nests with (a) different egg origin, but same quality of rearing conditions (comparison 'E' in Fig. 1) and (b) different rearing conditions, but same egg origin (comparison 'R' in Fig. 1). Averages of groups are shown in numerals next to the brackets. In (a), closed dots refer to nests both reared in high-quality conditions, open dots refer to nests both reared in low-quality conditions. In (b), closed dots refer to clutches both originally laid in high-quality environments, open dots refer to clutches both originally laid in low-quality environments. Note the logarithmic *y*-axis.

Table 1. ANCOVA with survival duration of the longest-living chick as dependent variable (log-transformed). Swap-set was entered as a categorical variable into the model and never removed to account for the paired experimental design. Model selection was done by backward deletion of nonsignificant terms.

Explanatory variable	β	s.e. (β)	*F*	*df*	*P*
error				26	
corrected model ($R^2 = 0.34$)			2.63	12	0.019
intercept			378	1	< 0.001
In final model					
swap set			1.89	11	0.089
rearing quality	0.36	0.11	9.93	1	0.004
Removed from final model					
rearing quality * egg origin	0.15	0.23	0.44	1	0.52
egg origin	−0.08	0.13	0.40	1	0.53
foster egg size	−0.03	0.03	0.80	1	0.38
foster intra-clutch egg size differences	0.01	0.04	0.02	1	0.88
foster clutch size	0.16	0.15	1.10	1	0.31
original egg size	−0.02	0.02	0.78	1	0.39
original intra-clutch egg size differences	0.02	0.03	0.03	1	0.62
original clutch size	−0.18	0.12	2.51	1	0.13

duration. Only the quality of the rearing conditions was significantly related to the survival duration (Table 1).

DISCUSSION

In this study, egg quality, defined by the environmental quality in which the eggs were laid, did not affect the survival of chicks (in agreement with Reid & Boersma 1990, Meathrel *et al.* 1993, Smith *et al.* 1995, Blomqvist *et al.* 1997, Styrsky *et al.* 1999, Bize *et al.* 2002). However, rearing conditions strongly affected the duration of chick survival. We therefore conclude that although parents in high-quality environments laid larger eggs, this did not improve chick survival subsequently. Egg size appears to be a neutral trait, under no selection pressure (in accordance with Jager *et al.* 2000). Furthermore, the original egg size and clutch size of the foster parents, possible

correlates of parental quality, also did not affect chick survival, in contrast to that for some other species (Reid & Boersma 1990, Bolton 1991, Smith *et al.* 1995, Blomqvist *et al.* 1997, Hipfner 2000, Bize *et al.* 2002).

It is somewhat puzzling why an initial advantage of hatching from a larger egg does not constitute a head start for the chick to increase its survival probability. This is especially surprising, given that egg size is strongly correlated with both hatchling mass (hatchling mass [g] = 1.84 + 0.68 × egg size [cm^3], $R^2 = 0.68$, $n = 702$, $P < 0.001$, Jager *et al.* 2000) and fledgling mass (fledgling mass [g] = 141.8 + 3.62 × egg size [cm^3], $R^2 = 0.05$, $n = 204$, $P = 0.002$, M. van de Pol unpubl. data) in this population. It has been argued that some studies have been unable to detect effects of egg size or egg quality on future survival of offspring because of the absence of adverse conditions and substantial chick mortality (Smith *et al.* 1995, Bize *et al.* 2002). Although we did not investigate directly whether starvation or predation was the principal cause of chick mortality in this experiment, we have strong circumstantial evidence that starvation was the more important. First, the availability of the two primary prey species (measured as the combined ash-free dry mass of Baltic Tellin *Macoma balthica* and Ragworm *Nereis diversicolor*) was extremely low in the study area during the experiment (2002: 4.8 g/m^2; 2003: 5.4 g/m^2) compared with other years (1985–2001: 9.9 ± 0.9 g/m^2). Secondly, the five chicks that fledged in the experiment were 13% lighter than fledglings reared under the same environmental conditions from 1985 to 2001 (Δbody mass = –42 ± 21 g; measured at day 30). However, even under these extremely adverse conditions we did not find any relationship between egg size and future survival.

An alternative explanation for the absence of a relationship between egg size and survival is that the survival duration of the longest-living chick is not an appropriate fitness measure. However, differences in survival duration were strongly related to differences in growth rate, and we found differences in duration of chick survival between adoption parents in high- and low-quality environments. Because we consider that survival duration is an appropriate indirect fitness measure, we conclude that egg size did not affect survival time. Consequently, this suggests that the observed decline in reproductive output in this population is unlikely to be caused by a decrease in egg size over the same period.

Differences in rearing conditions could be a result of environmental quality, parental quality or a combination of both as high-quality parents might select high-quality environments (Verhulst *et al.* 1997, Heg 1999). If environmental quality were the principal determinant of reproductive performance, we should expect that individuals that move from low- to high-quality environments would improve their reproductive performance to the level of pairs already in high-quality environments. However, a female's average egg size does not change if she switches between environments of different quality (Fig. 3a, paired-$t = -0.53$, $df = 46$, $P = 0.59$): it is constant within females (61% repeatability, Jager *et al.* 2000). Differences in egg size in our study system therefore seem to be to a large extent determined by female 'quality', and environmental conditions seem to play a lesser role. By contrast, fledging success is probably, to a greater extent, determined by environmental quality, as females that switched between environments changed the fledging success of their chicks accordingly (Fig. 3b, paired-$t = -2.57$, $df = 46$, $P = 0.012$), although we cannot exclude the possibility that

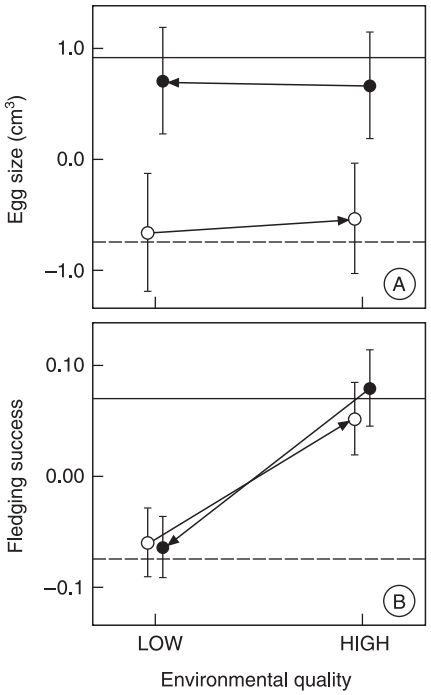

Figure 3. Changes in egg size (a) and fledging success (b) for females switching from low- to high-quality environments (white dots, $n = 25$) and for females switching from high- to low-quality environments (black dots, $n = 22$). The averages of all individuals breeding in high-quality environments and low-quality environments are given by the continuous and dashed line, respectively. Values are corrected for differences between years (1985–2003) and population averages are set to zero.

individuals move to a high-quality environment as a result of an increase in individual quality.

Williams (1994) showed that 42% of studies that investigated the relationship between egg size and chick survival reported a positive correlation. Most cross-foster experiments (that control for the confounding effects of parental and environmental quality) have provided no evidence for a causal relationship between egg size and offspring survival (this study, Reid & Boersma 1990, Meathrel *et al*. 1993, Smith *et al*. 1995, Blomqvist *et al*. 1997, Styrsky *et al*. 1999, Bize *et al*. 2002). Only a few studies have found that egg size affects survival (Bolton 1991, Risch & Rohwer 2000), but effects on growth have been reported more often (e.g. Amundsen & Stokland 1990, Hipfner & Gaston 1999, Hipfner 2000). In the non-experimental studies that reported a positive correlation between egg size and chick survival, egg size only explained a minor part of the variation in chick survival between nests. Therefore, egg size is probably not a key life-history trait that explains much of the variation in reproductive performance between nests. However, the situation might differ completely for within-nest variation in performance, as sibling competition can be manipulated by intraclutch asymmetries in egg size (Heg & van der Velde 2001). Furthermore, egg quality is a multidimensional trait, in which many other features besides egg size might be important determinants for between- (and within-) nest variation in reproductive performance.

If egg size is a neutral trait in this Oystercatcher population, this does not explain why egg size is consistently higher in a high-quality environment. One explanation might be that females in high-quality environments lay larger eggs because they are themselves larger. Other important unmeasured 'female quality' characteristics (e.g. motivation, size of the reproductive tract), which might be associated with egg size, might also differ between females breeding in high- and low-quality environments. In contrast to the American Oystercatcher *Haematopus palliatus* (Nol *et al*. 1984) egg size is not related either to body size or to mass in this population (Jager *et al*. 2000), nor does female body size or mass differ between environments of different quality (Ens *et al*. 1995). Another explanation might be that females in low-quality environments lay smaller eggs to obtain the observed larger intraclutch variation in egg size. This argument would hold if females cannot increase the size of their largest egg but can only decrease the size of the smallest egg to increase the intraclutch variation in egg size. However, both the largest (42.1 ± 0.1 cm^3) and the smallest eggs (39.1 ± 0.1 cm^3) laid in clutches in low-quality environments are smaller than the largest (43.3 ± 0.1 cm^3) and smallest (41.4 ± 0.1 cm^3) eggs laid in clutches in high-quality environments (M. van de Pol unpubl. data). At this moment we must conclude that we do not understand why consistent differences in egg size exist: the puzzle remains.

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