VARIATIONS IN BODY CONDITION AND EGG CHARACTERISTICS OF FEMALE KENTISH PLOVERS *CHARADRIUS ALEXANDRINUS*

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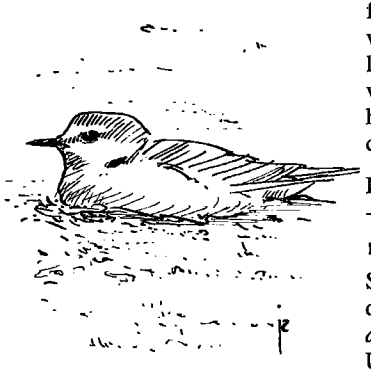
Offspring size is a very important life-history trait that may be affected by maternal effects and environmental conditions. We studied variation in egg size and within-clutch symmetry variation in egg volume in Kentish Plovers *Charadrius alexandrinus* in southern Spain over six years. Repeatability of egg volume among years was high. Repeatability of egg volume between clutches laid by individual females within a breeding season was also high. Repeatability of within-clutch egg size symmetry was low and not significant. Mean egg volume was correlated with indexes of both structural body size and body condition of females. The body masses of females showed consistency between years. Females in better condition were more able than females in lower body condition of laying not only larger eggs, but also eggs of more similar size. As we previously found that, within clutches, heavier chicks survived better than their lighter siblings, a higher body condition confers, through its effects on egg characteristics, a clear fitness advantage.



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INTRODUCTION

Directional selection should favour the production of larger eggs by females, because increased egg size may determine increased survival of offspring (e.g. Grant 1991; Blomqvist *et al.* 1997; Amat *et al.* 2000a). Nevertheless, in many organisms egg size experiences a high variability within clutches, what challenges the concept of an optimal egg size. Thus, it has been postulated that fitness is not egg size related, but rather that it is the phenotypic plasticity in egg size what would be the critical factor affecting fitness (Crump 1984; Hakkarainen & Korpimäki 1994; Bernardo 1996; Kaplan & King 1997). This may be particularly relevant for species inhabiting unpredictable environments, so that these plastic adjustments would give individuals an opportunity to optimise fitness at any stage in a fluctuating environment (Hakkarainen & Korpimäki 1994).

However, in some cases the variation in egg size within clutches may be the result of some constraints. Environmental effects, as mediated through feeding, may explain some of the variability in egg size of precocial birds (e.g. Redmon 1986; Galbraith 1988; Pehrsson 1991; Blomqvist & Johansson 1995). In shorebirds, nutrients and energy for egg formation may be acquired by females just before or during the egg laying period (Erckmann 1983), so that conditions encountered by females during this period could affect egg sizes. If so, intraclutch egg size variations should be more apparent when these species are subject to adverse conditions (Miller 1979; Grant

1991; Nol *et al.* 1997). In addition to environmental effects, maternal effects such as female size or female body condition may also affect egg size (Bernardo 1996). In this study we examined the relationship between female characteristics and egg size variations in the Kentish Plover *Charadrius alexandrinus*.

Shorebirds are ideal organisms on which to study the relationship between female characteristics and intra-clutch egg size variation because they lay clutches of constant size. The Kentish Plover is a small shorebird (42 g) with a modal and median clutch size of three eggs. Our study site is a seasonal lake with dramatic fluctuations in water levels, both within and between seasons (see below), and this may have an effect on food availability, and hence on individual body condition. In this lake, the nesting success of the plovers is low (Fraga & Amat 1996). After losing nests, the plovers may lay a replacement clutch, and up to 4-5 clutches have been recorded for the same individuals within a season (Warriner *et al.* 1986; Amat *et al.* 1999a).

Although egg size variation has been studied in some Kentish Plover populations (Rittinghaus 1956; Noszály & Székely 1993; Torre & Ballesteros 1994; Fraga & Amat 1996), most of these studies encompassed only a few years and/or when individual variation was considered, sample sizes were small. Furthermore, the emphasis of these studies was on variations between clutches, rather than within clutches. In this study we estimated repeatability's of egg characteristics in a small population of Kentish Plovers. Intraclutch egg size variation was analysed in relation to female characteristics (body size, body condition) over six breeding seasons, to test whether intraclutch variability in egg size should not be repeatable - as would be expected if egg size is constrained by conditions encountered during egg formation - and if females in better condition should be able to lay not only larger eggs, but also eggs of more similar size, i.e. clutches with lower intraclutch egg size variation than females in lower condition.

STUDY AREA AND METHODS

Fieldwork was conducted at Fuente de Piedra lake in southern Spain (37°06'N, 4°45'W) during 1991-96. The lake is saline and shallow (usually < 60 cm deep), covering 1354 ha. The climate is Mediterranean, with an average annual rainfall of 466 mm. The lake usually dries up in early summer and floods again after autumn rains. However, yearly and monthly variations in the amount of rains modify the duration of flooding. Thus, the lake remained almost dry throughout the breeding season of 1995, but flooded in 1991 and 1996, whereas in the other years the lake dried up before the breeding season had finished. Although the lake was dry, its soil remained wet, even in the driest year (1995). There may be greater food availability for breeding plovers when water levels are lower, because large insect populations, which constitute the main food of Kentish Plovers (see below), start to develop at Fuente de Piedra when water levels are low (García & Niell 1991). Because partial nestpredation is rather frequent at Fuente de Piedra (Fraga & Amat 1996), even during the laying, we were not sure if clutches in nests containing less than three eggs were complete. Hence, in this study only clutches containing three eggs (the modal clutch size) were considered.

In this paper egg volume is used as a measure of egg size following methods published elsewhere (Fraga & Amat 1996; Amat *et al.* 2001). In short, egg length and width were measured with vernier calipers to the nearest 0.1 mm and egg volumes were estimated according to Douglas (1990). All egg measurements were made by the same observer. Within-clutch egg size symmetry, a measure of intraclutch egg size variation, was considered as the degree to which every egg was similar to the others in the clutch (Kilpi 1995; Catry & Furness 1997). To estimate this, eggs within clutches were ranked in order of size, and we calculated the relative size of every egg with respect to the others by dividing the volume of the smaller egg by the volume of the larger one. We performed these calculations for each pair of eggs in

the clutch, so that three values were obtained for each nest, which were then averaged.

Repeatabilities, or intra-class correlation coefficients (Sokal & Rohlf 1981; Lessells & Boag 1987) were estimated using mean values of egg characteristics from first clutches of individual females in different years, and also using mean values of egg characteristics of first and replacement clutches laid within a breeding season by individual females. Standard errors of repeatability estimates were calculated following Becker (1984).

Incubating adults were captured using walk-in traps. We ringed adults with numbered metal rings and provided each bird with a unique combination of colour rings. The body masses of adults were recorded with a Pesola spring balance to the nearest 1 g. Using vernier callipers we also measured bill (culmen) and tarsus lengths to the nearest 0.1 mm and with a rule measured wing length to the nearest mm. The same observer made all measurements. To derive a multivariate measure of structural body size, we used the first principal component scores of a principal component analysis of the three linear measurements of females. For an index of female condition, we used the residuals of a regression of body masses on tarsus lengths. Females were captured during different stages of incubation, so that any changes in body mass during incubation would affect the body condition index. However, at Fuente de Piedra there were no significant changes in body mass of Kentish Plover females during the incubation period (Amat *et al.* 2000).

Statistical tests were conducted using SYSTAT statistical software (Wilkinson 1990). When we used parametric statistical tests, data were inspected for normality and homoscedasticity (Sokal & Rohlf 1981). As within-clutch egg size symmetry was not normally distributed, it was arcsin-transformed to meet the assumptions of the tests. Egg characteristics were averaged for the entire clutch, so that sample sizes refer to clutches, not to eggs. Unless otherwise stated, mean values are presented ± 1 SD.

RESULTS

The repeatability (R) of mean egg volume from first clutches of 94 individual females in different years was high ($R = 0.77 \pm 0.04$ (SE), $n_0 = 2.64$, $F_{93,154} = 9.99$, $P < 0.001$). The repeatability in mean egg size symmetry for first clutches of the same females was very low and not significant ($R = 0.06 \pm 0.07$, $n_0 = 2.64$, $F_{93,154} = 1.16$, $P = 0.206$). Similarly, the repeatability of mean egg size in first and replacement clutches laid within a breeding season by 63 individual females was also high ($R = 0.85 \pm 0.03$, $n_0 = 2.08$, $F_{62,70} = 13.14$, $P < 0.001$), but the repeatability in mean egg size symmetry was not significant and low ($R = 0.16 \pm 0.12$, $n_0 = 2.08$, $F_{62,70} = 1.38$, $P = 0.094$).

When considering first clutches, there were significant relationships between egg volume and female condition in all except one year (Table 1). The relationships between egg size symmetry and female condition were significant in only two years (Table 1). It is noteworthy that these significant correlations were of different sign, what may be due to a different individual composition of the population in those years. If females in better condition would be able of laying clutches with lower intraclutch egg size variation, the relationship

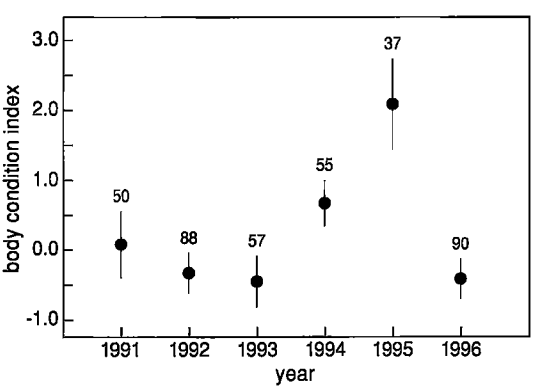

Fig. 1. Annual variations in the body condition index of female Kentish Plovers (mean ± 1 SE). The index of body condition was obtained as the residuals from a regression of body mass on tarsus length. Sample sizes are above the error bars.

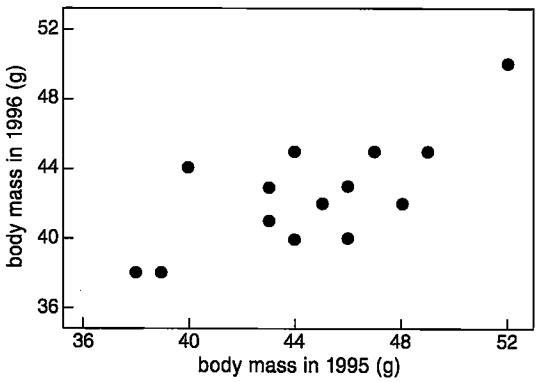

Fig. 2. Relationship between the body masses of 15 Kentish Plover females in 1995 and 1996.

between egg size symmetry and female condition should be analyzed on a per-individual basis. We compared data of individual females captured in both 1995 and 1996 to analyze whether body condition affected egg characteristics in similar ways in each of these years. These two years were chosen because those were the years with largest differences in the mean body condition indexes of females (Fig. 1). The body masses of these individual females were higher in 1995 than in 1996 (Table 2), but no significant differences between these years were found either in egg volume or within clutch egg size symmetry (Table 2). Those females that in 1995 were heavier, also were heavier in 1996 (r_{13} = 0.73, P = 0.002) (Fig. 2). Both egg volume (r_{13} = 0.52, P = 0.049) and within clutch egg size symmetry (r_{13} = 0.67, P =

Table 1. Pearson product moment correlations between the index of female condition and both mean egg volume and within clutch egg size symmetry in first clutches of Kentish Plovers. Numbers of clutches are in parentheses. Significant correlations are in bold.

Year (n)	Volume		Symmetry*	
	r	P	r	P
1991 (50)	0.29	0.045	0.12	n.s.
1992 (89)	0.29	0.005	–0.01	n.s.
1993 (57)	0.23	n.s.	0.19	n.s.
1994 (55)	0.40	0.002	–0.40	0.003
1995 (33)	0.34	0.050	0.43	0.012
1996 (90)	0.27	0.010	0.07	n.s.

*Within clutch egg size symmetry indicates the degree by which each egg is similar in volume to the others in the clutch.

Table 2. Comparison of some characteristics (mean ± SD) of 15 individual breeding Kentish Plover females in 1995 and 1996. Within clutch egg size symmetry indicates the degree by which each egg is similar in volume to the others in the clutch.

	1995	1996	Paired t-test	P
Body mass (g)	44.47 ± 3.78	42.47 ± 3.11	2.96	0.010
Egg volume (cm^3)	9.10 ± 0.87	8.86 ± 0.94	1.57	n.s.
Egg symmetry	0.96 ± 0.04	0.96 ± 0.02	0.64	n.s.

0.007) were affected by the condition of females, but only in 1995, when females were heavier. Also, only in 1995 there was a significant relationship between egg volume and egg size symmetry (r_{13} = 0.64, P = 0.011). However, when controlling for the effect of body condition, the relationship between mean egg volume and within clutch egg size symmetry in 1995 was no longer significant (partial r_{13} = 0.46, P = 0.087). When considering all first clutches, after controlling for female condition, there was a significant relationship between egg volume and the index of structural body size (partial r = 0.25, n = 232 individual females, $P < 0.001$). The relationship between egg size symmetries and female size was not significant (r = –0.02, n = 236 individual females, P = 0.765).

DISCUSSION

As has been found for other shorebirds, repeatability of egg size of Kentish Plovers among years was high (Nol *et al.* 1984, 1997; Thompson & Hale 1991). Replacement clutches also exhibited a high degree of repeatability with first clutches, as has also been found between first and second clutches of polyandrous Kentish Plovers (Amat *et al.* 1999b) and in other shorebirds (Thompson & Hale 1991). By contrast, repeatability of within clutch egg size symmetry between first and replacement clutches of Kentish Plovers was low. Similarly, egg size symmetries within clutches between years were very low and not significantly repeatable, as for skuas (Catry & Furness 1997). Even if variations in the size of eggs within clutches are small, they may be important in accounting for fitness of laying females, since within clutches, heavier chicks, which hatched from larger eggs, survived better than their lighter siblings (Amat *et al.* 2001). Given the relationship between egg size and individual fitness, the low repeatability of within clutch egg size symmetry was not unexpected (Price & Schluter 1991). This suggests that most of the variation in egg size symmetry was due to intra-individual variation in response to environmental conditions, or non-additive genetic variance. We found some evidence for the first possibility (see below).

Egg volumes of Kentish Plovers at Fuente de Piedra were not affected by laying date in four of six years (Amat *et al.* 2001). Egg size was related to female body size. Positive correlations between egg size and female size have also been found in other species, both altricial and precocial, laying clutches of constant size (Väisänen *et al.* 1972; Murton *et al.* 1974; Miller 1979; Redmond 1986; Weidinger 1996; Nol *et al.* 1997). However, as egg size also showed a positive relationship with the body condition of Kentish Plover females, this means that there may be some phenotypic variation in egg size that is not genotypically controlled.

At our study site the availability of the main prey of breeding Kentish Plovers (*Bledius* Staphylinid beetles, M. Castro, A. Pérez-Hurtado & J. A. Amat, unpublished data) is very high (> 2500 individuals m^{-2} García & Niell 1991). This high availability of food suggests that laying females may not be food limited at our study site, even in the year in which water levels were higher (1996) and the availability of *Bledius* lowest (pers. obs.). Although in 1996 the body condition of females was lower than in the other years, this did not result in decreased egg sizes, which suggests that the condition of females in 1996 was not low enough to negatively affect egg volumes. On the contrary, when the body condition of females was highest (1995), there was a slight, albeit not significant, increase in mean egg volume. At least in the more favourable year the body condition of individual females affected both egg size and within-clutch egg size symmetry. These last two variables were in turn positively related in 1995, however, the relationship was no longer significant after controlling for body condition. Thus, under very favourable conditions, females of better quality were more able than females of lower quality of laying not only slightly larger eggs, but also eggs of more similar size.

Especially for low quality females it may be costly to increase the size of all eggs in the clutch

and simultaneously laying eggs of similar size. By laying clutches with larger mean egg volume, the time that females took to complete a clutch increased, and this may be important for a species that is subject to high levels of clutch failure, like the Kentish Plover at Fuente de Piedra, and that frequently replace lost nests (Amat *et al.* 1999a, 2001). As we have suggested, the fitness benefits of increasing fecundity (i. e., number of clutches), should outweigh the benefits of increasing chick survival prospects through increased egg size (Amat *et al.* 2001).

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REFERENCES

Amat J.A., R.M. Fraga & G.M. Arroyo 1999a. Replacement clutches by Kentish Plovers. Condor 101: 746-751.

Amat J.A., R.M. Fraga & G.M. Arroyo 1999b. Brood desertion and polygamous breeding in the Kentish Plover *Charadrius alexandrinus*. Ibis 141: 596-607.

Amat J.A., R.M. Fraga & G.M. Arroyo 2001. Intraclutch egg-size variation and offspring survival in the Kentish Plover *Charadrius alexandrinus*. Ibis 143: 17-27.

Amat J.A.., G.H. Visser, A. Pérez-Hurtado & G.M. Arroyo 2000. Brood desertion by female shorebirds: a test of the differential parental capacity hypothesis on Kentish Plovers. Proc. R. Soc. Lond. B 267: 2171-2176.

Becker W.A. 1984. Manual of Quantitative Genetics, 4th ed. Academic Enterprises, Pullman, Washington.

Bernardo J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. Amer. Zool. 36: 216-236.

Blomqvist D. & O.C. Johansson 1995. Trade-offs in nest site selection in coastal populations of Lapwings *Vanellus vanellus*. Ibis 137: 550-558.

Blomqvist D., O.C. Johansson & F. Götmark 1997. Parental quality and egg size affect chick survival in a precocial bird, the Lapwing *Vanellus vanellus*. Oecologia 110: 18-24.

Catry P. & R.W. Furness 1997. Egg volume and within-clutch asymmetry in Great Skuas: are they related to adult quality? Colon. Waterbirds 20: 399-405.

Crump M.L. 1984. Intraclutch egg-size variability in *Hyla crucifer* (Anura:Hylidae). Copeia 1984: 302-308.

Douglas R.M. 1990. Volume determination of reptilian and avian eggs with practical applications. S. Afric. J. Wildl. Res. 20: 111-117.

Erckmann W. 1983. The evolution of polyandry in shorebirds: an evaluation of hypotheses. In: Waser S.K. (ed.) Social Behavior of Female Vertebrates: 113-168. Academic Press, New York.

Fraga R.M. & J.A. Amat 1996. Breeding biology of a Kentish Plover (*Charadrius alexandrinus*) population in an inland saline lake. Ardeola 43: 69-85.

Galbraith H. 1988. Effects of egg-size and composition on the size, quality and survival of Lapwing *Vanellus vanellus* chicks. J. Zool. (Lond.) 214: 383-393.

García C.M. & F.X. Niell 1991. Burrowing beetles of the genus *Bledius* (Staphylinidae) as agents of bioturbation in the emergent areas and shores of an athalassic inland lake (Fuente de Piedra, southern of Spain). Hydrobiologia 215: 163-173.

Grant M.C. 1991. Relationship between egg-size, chick size at hatching, and chick survival in the Whimbrel *Numenius phaeopus*. Ibis 133: 127-133.

Hakkarainen H. & E. Korpimäki 1994. Environmental, parental and adaptive variation in egg-size of Tengmalm's owls under fluctuating food conditions. Oecologia 98: 362-368.

Kaplan R.H. & E.G. King 1997. Egg-size is a developmentally plastic trait: evidence from long term studies in the frog *Bombina orientalis*. Herpetologica 53: 149-165.

Kilpi M. 1995. Egg-size asymmetry within Herring Gull clutches predicts fledging success. Colon. Waterbirds 18: 41-46.

Lessells C.M. & P.T. Boag 1987. Unrepeatable repeatabilities: a common mistake. Auk 104: 116-121.
Miller E.H. 1979. Egg-size in the Least Sandpiper *Calidris minutilla* on Sable Island, Nova Scotia, Canada. Ornis Scand. 10: 10-16.
Murton R.K., N.J. Westwood & A.J. Isaacson. 1974. Factors affecting egg-weight, body-weight, and moult of the Woodpigeon *Columba palumbus*. Ibis 116: 52-73.
Nol E., A.J. Baker & M.D. Cadman 1984. Clutch initiation dates, clutch size, and egg-size of the American Oystercatcher in Virginia. Auk 101: 855-867.
Nol E., M. Sullivan Blanken & L. Flynn 1997. Sources of variation in clutch size, egg-size and clutch completion dates of Semipalmated Plovers in Churchill, Manitoba. Condor 99: 389-396.
Noszály G. & T. Székely 1993. Clutch and egg-size variation in the Kentish Plover (*Charadrius alexandrinus*) during the breeding season. Aquila 100: 161-179. (In Hungarian, English summary.)
Pehrsson O. 1991. Egg and clutch size in the Mallard as related to food quality. Can. J. Zool. 69: 156-162.
Price T. & D. Schluter. 1991. On the low heritability of life-history traits. Evolution 45: 853-861.
Redmond R.L. 1986. Egg-size and laying date of Long-billed Curlews *Numenius americanus*: implications for female reproductive tactics. Oikos 46: 330-338.
Rittinghaus H. 1956. Untersuchungen am Seeregenpfeifer (*Charadrius alexandrinus* L.) auf der Insel Oldeoog. J. Ornithol. 97: 117-155.
Sokal R.R. & F.J. Rohlf 1981. Biometry, 2nd edition. W.H. Freeman, San Francisco.
Thompson P.S. & W.G. Hale 1991. Age-related reproductive variation in the Redshank *Tringa totanus*. Ornis Scand. 22: 353-359.
Torre I. & T. Ballesteros 1994. Variabilidad en el tamaño del huevo de Chorlitejo Patinegro *Charadrius alexandrinus* en el Delta del Llobregat. Butll. Grup Català Anellament 11: 89-92.
Väisänen R.A., O. Hildén, M. Soikkeli & S. Vuolanto 1972. Egg dimension variation in five wader species: the role of heredity. Ornis Fenn. 49: 25-44.
Warriner J.S., J.C. Warriner, G.W. Page & L.E. Stenzel. 1986. Mating system and reproductive success of a small population of polygamous Snowy Plovers. Wilson Bull. 98: 15-37.
Weidinger K. 1996. Egg variability and hatching success in the Cape Petrel *Daption capense* at Nelson Island, South Shetland Islands, Antarctica. J. Zool. (Lond.) 239: 755-768.
Wilkinson L. 1990. SYSTAT: The System for Statistics. SYSTAT, Inc., Evanston, Illinois.

SAMENVATTING

Zoals bij veel nestvliedende vogelsoorten komen ook bij Strandplevieren *Charadrius alexandrinus* de zwaarste kuikens uit de grootste eieren. Bovendien hebben zware eendagskuikens de grootste overlevingskansen. Aan de hand van resultaten van zes jaar onderzoek aan een populatie Strandplevieren die rond een (soms droogvallend) meer in Zuid-Spanje broeden, wordt besproken in hoeverre eigrootte en de mate waarin eieren binnen een legsel onderling in grootte verschillen, afhangen van de grootte en conditie van het vrouwtje of van omgevingsfactoren. Er was zowel binnen een jaar als tussen jaren een grote mate van herhaalbaarheid in de grootte van de eieren in legsels die door een vrouwtje. Dit was niet het geval voor variatie in eigrootte. De gemiddelde eigrootte hing af van de lichaamsgrootte van het vrouwtje (gemeten aan snavel-, tarsus- en vleugellengte) en van de conditie van het vrouwtje (lichaamsgewicht statistisch gecorrigeerd voor lichaamsgrootte). Vrouwtjes met de beste conditie legden niet alleen grotere eieren, maar ook eieren waarvan de grootte onderling minder van elkaar verschilde. Omdat uit grotere eieren kuikens met betere overlevingskansen komen, is het voor Strandplevierenvrouwtjes van wezenlijk belang om tijdens de eileg in een zo goed mogelijke conditie te verkeren. (TP)

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