

Determination of clutch-size in the Kentish Plover *Charadrius alexandrinus*

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We studied the clutch-size distribution of Kentish Plover *Charadrius alexandrinus* in 1991 and 1992 and tested three hypotheses for determination of clutch-size: egg-formation ability of females, incubation ability of parents and nest predation. Variation in clutch-size was small: 71 out of 74 clutches had three eggs (coeff. var. = 7%). Females spent more time foraging ($51 \pm 6\%$) pre-laying and during egg-laying than their mates ($39 \pm 5\%$). However, we concluded that egg-formation was not constrained by food availability because 77% and 100% of clutches were initiated before the peaks of prey density and of prey mass, respectively. Furthermore, the number of clutches initiated and completed over time was unrelated to prey density. By experimentally reducing and enlarging clutches, we found that enlarged clutches of four eggs took longer to hatch (24.8 ± 0.9 days) than control clutches of three (21.6 ± 0.7 days). Eggs of enlarged clutches also lost weight more slowly during incubation in both years compared with control clutches. No difference was found in the incubation behaviour or weight loss of parents between reduced, control and enlarged clutches. We found no evidence to support the nest predation hypothesis, since neither the proportion of nests predated nor the number of chicks hatched was different between reduced, control and enlarged clutches. The results of this study are most consistent with the incubation ability hypothesis, although the parental ability hypothesis has remained untested.

Four hypotheses have been suggested to explain the determination of clutch-size in precocial birds (reviews: Klomp 1970, Winkler & Walters 1983, Walters 1984). Lack (1947a, 1954) proposed that the ability of a female to form eggs may be limited by the amount of food she is able to collect, that is by exogenous food availability. Lack (1947b, 1954) also suggested that clutch-size could be limited by the incubation ability of parents. According to this hypothesis, clutch-size is limited by the number of eggs that the incubating parent can cover and incubate effectively. Nest predation could also determine the maximum size of clutch (Perrins 1977). Large clutches take longer to lay, exposing both the eggs and the female to the risk of predation longer, and larger clutches may also be more attractive to predators (Walters 1984). Finally, Safriel (1975) and Walters (1984) argued that parental ability following hatching or during brood-rearing could set up an upper limit to clutch-size, since parents might be less able to protect large broods from being predated or to brood the chicks properly.

Shorebirds *Charadrii* are almost unique among birds in having small variation in clutch-size within populations (Lack 1947a, Maclean 1972), the distribution of clutch-sizes being truncated at the modal size (Winkler & Walters 1983). Al-

though shorebirds are considered to be indeterminate layers (Klomp 1970, Haywood 1993), their variation in clutch-size is typically smaller than that of determinate layers: e.g. Red-shank *Tringa totanus* and Lapwing *Vanellus vanellus* have coeff. var. of 8.1% and 13.0%, respectively (data from Cramp & Simmons 1983), while Turtle Dove *Streptopelia turtur* and Collared Dove *Columba palumbus* have coeff. var. of 16.3% and 20.1%, respectively (data from Cramp 1985).

Despite the limited variation in clutch-size of shorebirds, there have been few attempts to test the alternative hypotheses of clutch-size determination in this group (Safriel 1975, Walters 1982, Shipley 1984, Lank *et al.* 1985, Kálás & Løfaldli 1987, S. Hills, unpubl. MSc thesis, University of Washington; reviews: Winkler & Walters 1983, Walters 1984). Furthermore, although Winkler & Walters (1983) pointed out that the four hypotheses are not mutually exclusive, none of these studies has attempted to test more than a single hypothesis in the same species.

In this study, we first report on clutch-size distribution in the Kentish Plover *Charadrius alexandrinus* and secondly test three of the four hypotheses of clutch-size determination in this species by experimentally manipulating clutch-size. Specifically, we tested the following predictions: (1) if clutch-size is constrained by the egg-formation ability of the female, then females should spend a greater proportion of their time foraging before and during egg-laying than at other times,

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and a positive relationship should exist between clutch-size, clutch mass and prey abundance during the egg formation period, (2) if incubation ability affects clutch-size, then experimentally enlarged clutches should develop more slowly than reduced ones, they should have longer incubation periods, parents should spend more time incubating enlarged clutches and parents incubating enlarged clutches should lose more weight compared with parents incubating reduced clutches and (3) if the probability of nest predation determines clutch-size, then enlarged clutches should have higher mortality than reduced ones, and fewer chicks should hatch from enlarged clutches than from reduced ones.

METHODS

Species and study site

Kentish Plovers are small shorebirds weighing about 42 g. Females typically lay clutches of three, and previous studies have found little deviation from this clutch-size (one out of 290 clutches and two out of 389 clutches had four eggs at two sites cited by Glutz *et al.* [1975]). Both parents take part in incubation, although one of the parents deserts the brood after hatching and may subsequently remate (Lessells 1984, Székely & Lessells 1993). Kentish Plovers are insectivorous, inland populations feeding chiefly on flies (Diptera), spring-tails (Collembola) and beetles (Coleoptera) (Cramp & Simmons 1983, Sterbetz 1988, T. Székely, I. Karsai & T.D. Williams, pers. obs.).

Field work was carried out in an alkaline grassland of about 2000 ha in central Hungary (Miklapuszta) (46°40'N, 19°10'E) in 1991 and 1992. Kentish Plovers breed on bare ground, interspersed with patches of *Lepidium cartilagineum* and *Puccinellia distans*. In 1991 and 1992, 66 and 50 nests were studied, respectively, and females were colour ringed in 47% and 68% of nests. Potential nest predators were common in the study site including Foxes *Vulpes vulpes*, Hedgehogs *Erinaceus europaeus*, Weasels *Mustela nivalis*, Badgers *Meles meles*, Marsh Harriers *Circus aeruginosus*, Montagu's Harriers *C. pygargus* and Hooded Crows *Corvus corone cornix*.

Prey sampling

Ten traps were used in 1991 to estimate prey availability. Each trap consisted of a 10- × 10-cm glass plate wrapped in plastic film. The upper surface of film was covered by Hyvis, an adhesive liquid. The traps were placed horizontally on the ground, and their edges were smoothed to the ground level. Five traps were arranged in two lines each. The distance between the traps was 50 m in a line, and the two lines were approximately 800 m apart. The traps were exposed on the third or fourth day of each 8-day period, and they were collected 48 h later. Arthropods were identified under a stereomicroscope without removing them from the plastic film. The length of each arthropod was measured to

the nearest 0.1 mm (<3 mm) or to the nearest 1 mm (≥3 mm), depending on size. The average number of arthropods on ten traps was used as an index of prey density. Dry mass was estimated from the length of arthropods, using the equation provided in Rogers *et al.* (1976). Dry masses of arthropods were weighted by the number of arthropods per trap, and the weighted means were used as the index of prey mass (mg/100 cm²). Kentish Plovers fed and bred within the sampling areas, e.g. eight nests were within 300 m of the traps in 1991.

Behavioural observations

The behaviour of pre-laying, laying and incubating pairs was observed from a hide each day for 1 h. Each pair was observed once before or during egg-laying. One member of each pair was observed for 30 min, then the behaviour of the other member was recorded for 30 min. We randomized whether the male or the female was observed first. Behaviour was categorized as foraging, standing, preening, sitting, running, flying, displaying, scraping and copulating. Duration and category of behaviour were recorded if the behaviour lasted for at least 5 seconds. The proportion of time spent in each behaviour was then calculated for the male and the female of each pair. Pairs were identified from colour ring combinations or from the location of their nest scrape. The plumages of males and females are sufficiently different to allow identification of sexes. The number of pecks was also estimated several times over 1-min periods when the focal bird foraged, and the mean pecking rate was calculated for both the male and the female. We aimed to observe incubating birds every other day either between 0600h and 1300h or between 1400h and 2100h. At 1-min intervals, we recorded whether or not the clutch was incubated and if incubated, by which parent. The time of observation was randomized within morning and afternoon sessions. The behaviour of females attending their broods was observed (active attendance) as was that of females away from their broods (non-active attendance).

Clutch-size manipulation

Only clutches found during egg-laying or at the start of incubation were used in manipulation experiments. The start of incubation was defined as the point when the clutch was continuously incubated and when at least one egg of a clutch sank to the bottom of water, the apex of the egg not rising up by more than 45 degrees. This 'flotation' stage corresponds to day 3.4 (s.d. ±0.6) of incubation (based on daily flotation of the third egg in four clutches for which the laying date was known, T. Székely, I. Karsai & T.D. Williams [unpubl. data]). Three groups of experimental clutches were created: reduced-enlarged, control-1-control-1 and control-2-control-2. In the first group, one egg was removed from a clutch (reduced) and added to another clutch (enlarged). In the second group, one egg was exchanged be-

tween two clutches (control-1), and in the third group, the clutches were left unmanipulated (control-2). Clutches in the first group were randomized as to whether they became reduced or enlarged unless one of them contained less than three eggs. In this case, the clutch with less than three eggs was always enlarged. All eggs moved between clutches were chosen at random. The allocation of clutches to the three groups was intended to achieve an equal number of clutches in each treatment. The eggs from one clutch of two were distributed to two other clutches in both 1991 and 1992. The weight of distributed eggs (8.7 ± 0.2 g, $n = 4$) was not different from the eggs which were removed and added to create enlarged clutches (8.6 ± 0.1 g, $n = 21$) (Mann-Whitney U -test, $z = 0.63$, n.s.). One control-1 clutch was not completed in 1991, and one enlarged and two reduced clutches were lost to predators in 1991 and 1992, respectively, before incubation had started. One female laid a fourth egg after we removed one of her eggs. The latter clutch was excluded from clutch-size distribution, but it was included in analyses as a control-2 clutch once incubation began. Nests were checked initially at 2- or 4-day intervals after incubation had started and then every day before hatching. Successful hatching was identified by eggshell remains in the nest scrape or by the presence of chick(s). Predation was recognized by the remnants of eggs around nests. Eggs that disappeared were assumed to have been removed by predators. Length of survival was calculated between the start of incubation and the hatching date or, if the nest failed, then between the start of incubation and the date of discovery.

We attempted to capture parent birds every fourth day by funnel trapping, starting 8 days after the onset of incubation. Three enlarged clutches were abandoned in 1991, and one reduced clutch was abandoned in 1992 shortly after one of the parents was caught (out of 27 and 18 clutches, respectively, where at least one of the parents was caught on the nest). Abandoned clutches were excluded from the analyses of clutch survival and predation rate.

Data processing and statistical testing

Only clutches which were found before the start of incubation or which had not been incubated more than 13 days on the day of finding were included in the correlation between number of initiated or completed clutches in each 8-day period and food supply. Date of clutch initiation was estimated to take place 11 days before laying the last egg, since the egg-laying interval is 1.9 days (s.d. ± 1.0) and the period of egg formation is about 7 days (Székely & Lessells 1993). Mean prey density and prey mass on the first and last days of egg-formation or laying were used to estimate food availability before and during egg-laying, respectively. The correlation between clutch mass and food supply included only fresh clutches, i.e. clutches found before or at the start of incubation.

In all analyses, comparisons were made between the years 1991 and 1992 and between control-1 and control-2 clutch-

es. Control-1 and control-2 clutches were not significantly different in any analyses ($P > 0.05$). If years were different ($P < 0.05$), then they were analysed separately. Non-parametric statistics, including Spearman rank correlation, were used except for the changes in egg density during incubation, which were compared by analyses of covariance. For analyses of covariance, probabilities of interaction term (treatment*incubation time) and degrees of freedom (interaction, residual) are given. None of the variables used in analyses of covariance deviated from normality (Kolmogorov-Smirnov test). For all analyses, the conventions given in Sokal & Rohlf (1981) were followed, and data were analysed using SPSS-PC+. Two-tailed probabilities and mean \pm s.e. are given unless s.d. is indicated.

RESULTS

Clutch-size manipulation

Three variables may confound the results of clutch-size manipulations: different timing of manipulation between treatment groups, different developmental stage of eggs at the start of incubation or different clutch mass before the manipulation. However, neither timing of manipulation (Kruskal-Wallis test, 1991: $\chi^2_3 = 0.13$, n.s.; 1992: $\chi^2_3 = 2.47$, n.s.; Table 1) nor the flotation stage of eggs differed at the start of incubation between reduced, control and enlarged clutches (G-test, control-1 and control-2, and both years combined, $\chi^2_2 = 2.38$, n.s.). Similarly, clutch masses were not different between treatment groups before manipulation (Kruskal-Wallis test, 1991: $\chi^2_3 = 0.98$, n.s.; 1992: $\chi^2_3 = 4.07$, n.s.), though they differed after manipulation (Kruskal-Wallis test, 1991: $\chi^2_3 = 35.2$, $P < 0.001$; 1992: $\chi^2_3 = 26.5$, $P < 0.001$; Table 1).

Variation in clutch-size and mass

Two out of 42 and one out of 32 freshly laid clutches contained two eggs in 1991 and 1992, respectively. All other clutches had three eggs. The coeff. var. of clutch-size were 7.3% and 6.0% in 1991 and 1992, respectively, and 6.7% for both years pooled. Mass of fresh clutches was 26.0 ± 0.4 g ($n = 42$) in 1991 and 25.4 ± 0.4 g ($n = 32$) in 1992. Variation in mass of fresh clutches was also small: coeff. of var. were 9.0% and 8.6% in 1991 and 1992, respectively, and 8.8% for both years.

Egg production and food supply

Density and mass of prey varied highly significantly during the breeding season (Kruskal-Wallis test, density: $\chi^2_{11} = 70.1$, $P < 0.001$; biomass: $\chi^2_{11} = 97.0$, $P < 0.001$; Fig. 1). Peak prey density occurred between 20 and 22 May, while the highest prey mass occurred between 13 and 15 June. The most numerous prey items recorded ($n = 14,063$) were springtails (Collembola, 63.6%), flies (Diptera, 26.9%), plant bugs (Homoptera, 5.1%) and ants and wasps (Hymenoptera,

Table 1. Clutch mass before and after manipulation (mean \pm s.d.) in Kentish Plover. Only clutches of three were manipulated. One egg was removed (reduced clutches), swapped (control-1 clutches) or added to clutches (enlarged clutches). Control-2 clutches were unmanipulated. Timing of manipulation is the number of days between start of incubation and 1 March (mean \pm s.d.). Probabilities of Mann-Whitney U-test are given (1) between reduced and combined control-1 and control-2, (2) between control-1 and control-2, (3) between combined control-1 and control-2 and enlarged, (4) between reduced and enlarged clutches. *** = $P < 0.001$; n.s. = not significant

	Reduced	(1)	Control-1	(2)	Control-2	(3)	Enlarged	(4)
Clutch mass (g)								
Before manipulation								
1991	26.1 \pm 0.4	n.s.	26.3 \pm 0.6	n.s.	26.8 \pm 0.4	n.s.	26.4 \pm 0.5	n.s.
1992	25.2 \pm 0.5	n.s.	26.1 \pm 0.7	n.s.	25.6 \pm 1.0	n.s.	25.8 \pm 0.3	n.s.
After manipulation								
1991	17.3 \pm 0.3	***	26.4 \pm 0.6	n.s.	26.7 \pm 0.4	***	35.3 \pm 0.4	***
1992	16.8 \pm 0.4	***	26.1 \pm 0.6	n.s.	25.6 \pm 1.0	***	34.2 \pm 0.3	***
Timing of manipulation (days)								
1991	75 \pm 21	n.s.	77 \pm 26	n.s.	4 \pm 19	n.s.	73 \pm 19	n.s.
1992	64 \pm 23	n.s.	64 \pm 17	n.s.	68 \pm 24	n.s.	77 \pm 23	n.s.
No. of clutches								
1991	11		9		8		13	
1992	7		6		7		11	

3.0%), which have been shown to be the main items in the diet in other studies (Cramp & Simmons 1983). Frequency of Collembola was higher before 2 June ($n = 7119$) than after 2 June ($n = 1820$), while frequency of Diptera was lower before 2 June ($n = 660$) than after 2 June ($n = 3119$) (chi-square test, $\chi^2_1 = 4323$, $P < 0.001$) (no. of arthropods = 8210 and 5853 before and after 2 June, respectively).

Of 53 clutches, 77% and 53% of clutches were initiated or completed before the peak in density of arthropods, respectively, and 100% and 89% of clutches were initiated and completed before the peak in mass of prey (Fig. 1). Number of clutches initiated or completed was not related to prey

density (initiation: $r_{14} = -0.24$, n.s.; completion: $r_{14} = 0.30$, n.s.), although number of clutches initiated related inversely to prey mass (initiation: $r_{14} = -0.68$, $P < 0.003$; completion: $r_{14} = -0.13$, n.s.). The mass of fresh clutches also related inversely to prey density during pre-laying ($r_{42} = -0.27$, $P < 0.02$) but not during laying ($r_{42} = -0.17$, n.s.). Similarly, clutch mass related inversely to prey mass during both pre-laying ($r_{42} = -0.34$, $P < 0.02$) and laying ($r_{42} = -0.28$, $P = 0.038$). There was no difference in prey density and prey biomass during the laying periods of clutches of two ($n = 2$) and of three ($n = 40$) (Mann-Whitney U-test, prey density: $z = 0.42$, n.s.).

Foraging was the most time-consuming activity of females before and during egg-laying (Table 2). Although females spent more time foraging than did their mates ($39.4 \pm 5.2\%$), 43.5% of females' time was spent in non-feeding activities (standing, preening or sitting; Table 2). Females spent sig-

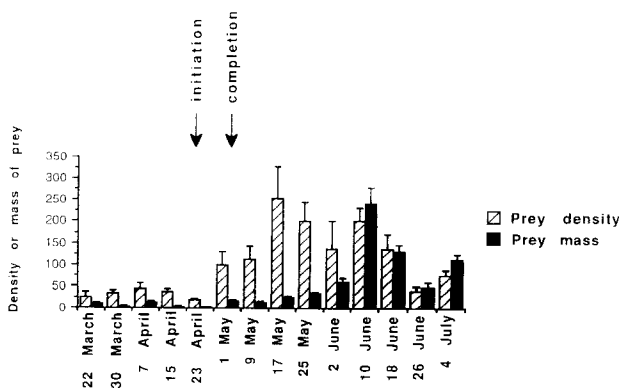


Figure 1. Relative density (number of arthropods/100 cm²) and dry mass (mg/100 cm²) of prey of Kentish Plover in 1991 (mean \pm s.e.). Ten traps were exposed on the third or fourth day of each 8-day period for 2 days (± 2 h). The first days of each 8-day period are shown. Mean initiation and completion dates of clutches are shown by the arrows ($n = 53$ clutches).

Table 2. Behaviour of female Kentish Plover before and during egg-laying and behaviour of their mates (mean \pm s.e.)

Behaviour	Female	Male	P^*	n^\dagger
Foraging (%)	51.0 \pm 6.3	39.4 \pm 5.2	0.023	27
Standing (%)	28.8 \pm 5.6	18.1 \pm 3.1	0.086	27
Preening (%)	8.4 \pm 2.0	13.7 \pm 2.3	0.15	27
Sitting (%)	6.3 \pm 3.2	10.5 \pm 4.4	0.48	27
Pecking rate (pecks/min)	18.7 \pm 1.5	19.3 \pm 2.2	0.90	21

* Probability of Wilcoxon matched-pairs test between males and females.

† Number of pairs.

Table 3. Length of incubation in Kentish Plover and slope of linear equation between egg density (g/cm^3 , dependent variable) and incubation time (d, independent variable) (mean \pm s.e.). Mean density of eggs for each clutch was used. n is the number of measurements. Length of incubation was tested by Mann-Whitney U-test, and slopes were compared by analyses of covariance. Slopes were different between 1991 and 1992 (ANCOVA, $F_{1,298} = 4.98$, $P = 0.026$). Probabilities of the respective tests are shown (1) between reduced and control, (2) between control and enlarged and (3) between reduced and enlarged clutches; ** = $P < 0.01$; * = $P < 0.05$; n.s. = $P > 0.05$. Slopes were significant in each equation (t-test, $P < 0.001$)

	Reduced	(1)	Control	(2)	Enlarged	(3)
Length of incubation (days)	22.8 \pm 0.9	n.s.	21.6 \pm 0.7	*	24.8 \pm 0.9	n.s.
Egg density (g/cm^3)						
1991						
Slopes	-0.058 \pm 0.006	n.s.	-0.063 \pm 0.003	**	-0.051 \pm 0.004	n.s.
n	35		65		54	
1992						
Slopes	-0.069 \pm 0.004	n.s.	-0.069 \pm 0.005	*	-0.056 \pm 0.003	*
n	44		55		49	

nificantly more time foraging before or during egg-laying than during chick-rearing when actively attending chicks ($10.0 \pm 4.5\%$, $n = 12$, Mann-Whitney U-test, $z = 3.35$, $P < 0.001$), although the difference between females during pre-laying or laying and during non-active chick attendance is not significant ($39.5 \pm 12.7\%$, $n = 6$ females, Mann-Whitney U-test, $z = 0.75$, n.s.).

Pecking rate did not differ between pre-laying or laying females and their mates (Table 2). Females were able to lay a replacement clutch shortly after their first clutch failed. Two females out of 17 in 1991 and four out of 11 in 1992 laid second clutches after their first clutches were lost to predators, the first egg of the replacement clutch being laid 8.5 ± 1.1 days ($n = 6$) after clutch failure.

Incubation ability

Manipulation of clutch-size had no significant effect on the length of incubation (Kruskal-Wallis test, $\chi^2_2 = 5.43$, n.s.). Enlarged clutches took longer to hatch than control clutches,

although there was no difference between reduced and control clutches in the length of incubation (Table 3). Manipulation affected weight loss of eggs during incubation (analyses of covariance, 1991: $F_{2,148} = 3.31$, $P < 0.05$; 1992: $F_{2,142} = 3.59$, $P < 0.03$; Table 3). Enlarged clutches lost weight at a slower rate than control clutches in both years, and weight loss of enlarged clutches was significantly slower than the weight loss of reduced clutches in 1992 (Table 3).

Incubation behaviour of parent birds did not differ between reduced, control and enlarged clutches (Table 4): neither the percentages of total incubation time (Kruskal-Wallis test, 1991: $\chi^2_2 = 0.73$, n.s.; 1992: $\chi^2_2 = 1.06$, n.s.) nor the percentages of time nests were incubated by females were different between treatment groups (Kruskal-Wallis test, 1991: $\chi^2_2 = 0.53$, n.s.; 1992: $\chi^2_2 = 1.66$, n.s.). The manipulation of clutch-size did not affect either weight change of parents during incubation (Kruskal-Wallis test, females: $\chi^2_2 = 0.83$, n.s.; males: $\chi^2_2 = 1.63$, n.s.; Table 5) or condition of parents at late incubation (Kruskal-Wallis test, females: $\chi^2_2 = 2.54$, n.s.; males: $\chi^2_2 = 3.47$, n.s.; Table 5).

Table 4. Incubating behaviour of Kentish Plover. Percentage of time that the clutch is incubated by either parent and the female share of incubation time (mean \pm s.e.). Mann-Whitney U-test (1) between reduced and control clutches, (2) between enlarged and control clutches and (3) between reduced and enlarged clutches. Percent incubation was different between 1991 and 1992 (Mann-Whitney U-test, $z = 2.36$, $P < 0.02$, $n = 47$). n.s. = $P > 0.05$

Incubation	Reduced	(1)	Control	(2)	Enlarged	(3)
1991						
% incubated	93.3 \pm 1.9	n.s.	91.7 \pm 2.1	n.s.	93.2 \pm 1.4	n.s.
% incubation by female	63.7 \pm 17.7	n.s.	73.0 \pm 12.2	n.s.	56.0 \pm 13.8	n.s.
No. of nests	7		8		8	
1992						
% incubated	94.7 \pm 1.4	n.s.	96.4 \pm 1.6	n.s.	95.1 \pm 2.0	n.s.
% incubation by female	66.4 \pm 9.1	n.s.	71.5 \pm 12.9	n.s.	66.6 \pm 11.3	n.s.
No. of nests	6		10		8	

Table 5. Weight change (g/day) of incubating Kentish Plover parents and condition after the 18th day of incubation (100-weight [g]/wing [mm]) (mean \pm s.e.). *n* is the number of individuals. Mann-Whitney U-test (1) between reduced and control clutches, (2) between enlarged and control clutches and (3) between reduced and enlarged clutches. n.s. = $P > 0.05$

	Reduced	(1)	Control	(2)	Enlarged	(3)
Weight change						
Female	-0.12 ± 0.11	n.s.	-0.13 ± 0.10	n.s.	-0.08 ± 0.26	n.s.
<i>n</i>	6		7		4	
Male	-0.15 ± 0.08	n.s.	-0.47 ± 0.45	n.s.	$+0.04 \pm 0.11$	n.s.
<i>n</i>	3		4		2	
Condition						
Female	42.1 ± 1.6	n.s.	38.8 ± 0.6	n.s.	40.0 ± 1.2	n.s.
<i>n</i>	2		5		5	
Male	41.1 ± 0.5	n.s.	39.5 ± 0.6	n.s.	40.3 ± 0.1	n.s.
<i>n</i>	5		5		4	

Nest predation

Predation was the major cause of nest failure: 76% of reduced clutches, 73% of control clutches and 81% of enlarged clutches were lost to predators, including two, four and five nests, respectively, which were trampled by sheep (Table 6).

Rates of predation of nests were independent of clutch-size: no difference was found between reduced and control clutches (G-test, $\chi^2_1 = 0.06$, n.s.) or between enlarged and control clutches (G-test, $\chi^2_1 = 0.40$, n.s.). Clutch survival, number of chicks hatched per nest and number of chicks hatched per egg were not different between reduced, control and enlarged clutches (Kruskal-Wallis test, clutch survival: $\chi^2_2 = 0.04$, n.s.; no. of chicks per nest: $\chi^2_2 = 0.22$, n.s.; no. of chicks per egg: $\chi^2_2 = 0.34$, n.s.).

DISCUSSION

Of the three hypotheses for clutch-size determination that we tested, the results of this study are most consistent with the incubation ability hypothesis (Lack 1947b, 1954). We

found no data to support the hypothesis that clutch-size in the Kentish Plover is limited by food supply. First, most clutches were initiated prior to the beginning of the marked seasonal increase in prey biomass and density. Egg formation therefore occurred during a period of relatively low food availability (this gave rise to the overall negative relationship between number of clutches initiated and prey biomass). Both clutch-size and clutch mass decrease throughout the season in Kentish Plover (T. Székely & G. Noszaly, unpubl. data), despite the seasonal increase in food availability further contributing to the inverse relationship observed. Second, although egg formation occurred largely during the period of relatively low food availability, pre-laying females spent greater than 40% of their time in non-foraging activities (with most of this time spent simply standing or sitting, i.e. not in other 'essential' activities). Third, females which lost first clutches started laying replacement clutches only 9 days after nest failure. This period is equivalent to the minimum time required for egg formation, showing that females are able to resume egg production very rapidly after cessation of laying of the first three-egg clutch. Lank *et al.* (1985) also failed to find any relationship between egg size,

Table 6. Clutch survival of Kentish Plover. Clutches that hatched at least one chick are included as hatched clutches. Predation included disappeared nests and the ones trampled by sheep. Survival time is mean \pm s.e. day between start of incubation and date of hatching or date of failure. Mann-Whitney U-test (1) between reduced and control clutches, (2) between enlarged and control clutches and (3) between reduced and enlarged clutches. n.s. = $P > 0.05$

	Reduced	(1)	Control	(2)	Enlarged	(3)
Number of nests	17		30		21	
Hatched (%)	24		27		19	
Predated (%)	76		73		81	
Survival time (days)	13.1 ± 1.9	n.s.	13.0 ± 1.4	n.s.	12.8 ± 1.9	n.s.
No. chicks produced per nest	0.41 ± 0.19	n.s.	0.56 ± 0.19	n.s.	0.57 ± 0.27	n.s.
No. chicks produced per egg	0.21 ± 0.10	n.s.	0.19 ± 0.06	n.s.	0.14 ± 0.07	n.s.

number of eggs laid and prey density (in 8 of 9 weeks) in the Spotted Sandpiper *Actitis macularia*. However, they showed that the pre-laying period was shorter at higher prey densities, an effect also demonstrated by Högstedt (1974) in Lapwing. The duration of egg formation (and thus the pre-laying period) may also vary in relation to food supply in the Snowy Plover *Charadrius alexandrinus nivosus*; e.g. Warriner *et al.* (1986) showed that both the length of the pre-laying period and the laying interval declined throughout the breeding season, inversely to the presumed pattern of food availability.

We similarly found no evidence that clutch-size was related to the risk of nest predation in Kentish Plovers. Although predation was the main cause of egg loss, experimentally enlarged clutches had similar rates of nest predation and mean survival times compared with control clutches. Shipley (1984) also found no difference in predation rates of control and enlarged clutches in the American Avocet *Recurvirostra americana*, supporting the conclusion that shorebirds are able to adequately protect clutches larger than the modal clutch-size laid. We did not test the parental ability hypothesis in this study, and it remains possible that the levels of parental investment and predation risk post-hatching limit clutch-size in the Kentish Plover. Safriel (1975) showed that experimentally enlarged broods of Semipalmated Sandpipers *Calidris pusilla* were less successful than control broods of the modal clutch size. However, he did not determine whether higher mortality in enlarged broods was due to predation or because chicks were brooded less effectively.

In the Kentish Plover, enlarged clutches of four eggs took longer to incubate and showed slower rates of egg (embryo) development compared with modal three-egg clutches. This is consistent with the incubation ability hypothesis. S. Hills (unpubl. MSc thesis, University of Washington) similarly showed that experimentally enlarged clutches of Dunlin *Calidris alpina* took longer to hatch and that egg temperatures were lower in enlarged clutches of Spotted Sandpiper. Consistent with this latter observation, we found no evidence that Kentish Plover 'compensated' for enlarged clutches by increasing their incubation effort: there was no difference in the time spent incubating or in weight loss of incubating birds between enlarged, control or reduced clutch-sizes. In contrast, Kálás & Løfaldli (1987) found that the condition of incubating Dotterel *Eudromias morinellus* deteriorated more rapidly in three-egg clutches after these were experimentally enlarged, suggesting that birds did increase their incubation effort. This species difference may reflect the fact that Dotterel show uniparental care during incubation compared with biparental care in other species (such as the Kentish Plover).

If incubation ability determines clutch size in Kentish Plover, as in other shorebirds, why does this species produce only a three-egg clutch rather than the four-egg clutch seen in most other species? Waders typically develop two, smaller, individual and lateral brood patches rather than a single,

large brood patch as occurs in other precocial species (such as ducks and geese, which have much larger clutch sizes; Drent [1973]). In shorebird species laying four-egg clutches, the 'area' of the clutch corresponds closely to the brood patch area; enlarging the clutch area in these species results in eggs not fitting the brood patch properly, with consequent uneven development of eggs and increased hatching asynchrony (S. Hills, unpubl. MSc thesis, University of Washington). Other avian species laying three-egg clutches (e.g. Laridae) develop three individual brood patches, and this may also be the case in Kentish Plover. Why this species should have evolved such a pattern of brood patch development (in contrast to other shorebird species) is not clear. However, as Winkler & Walters (1983) pointed out, it is likely that incubation ability (brood patch area) has coevolved with clutch-size. Although Kentish Plover lay small clutches compared with most other shorebirds, the total clutch mass produced is similar to congeners of the same body size, and Kentish Plover therefore lay fewer but relatively larger eggs. For example, Little Ringed Plover *Charadrius dubius* (38–39 g) lay four eggs averaging 7.7 g compared with three eggs of 9 g in Kentish Plover. This suggests that there may be some particular advantage to large egg size in the latter species, which selects for females to allocate nutrients to fewer, larger eggs. Egg size correlates with chick size at hatching in several shorebird species (Ricklefs 1984), and there is some evidence for increased survival and more rapid growth at least over the initial period after hatching (Galbraith 1988, Grant 1991). Larger chicks may be more successful in obtaining food, they may have better thermoregulatory abilities or they may be better able to escape predators. Females producing larger eggs and thus better developed young may be able to desert their mates sooner and increase their reproductive success by subsequently remating. Female desertion is rare or it occurs only when chicks are at least half-grown in species which lay four-egg clutches, such as Little Ringed Plover and Ringed Plover *Charadrius hiaticula* (Cramp & Simmons 1983). In shorebirds laying three-egg clutches, desertion by females is typical after egg-laying (e.g. Dotterel, Kálás & Løfaldli 1987; Wilson's Plover *Charadrius wilsonia*, Bergstrom 1981) or shortly after hatching (e.g. Kentish Plover, Lessells 1984, Warriner *et al.* 1986, Székely & Lessells 1993). These aspects of chick development, in relation to clutch- and egg size, warrant further consideration in the Kentish Plover.

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