

## Trade-offs in nest site selection in coastal populations of Lapwings *Vanellus vanellus*

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In coastal populations of Lapwings *Vanellus vanellus* in southwestern Sweden, arable fields predominated as foraging habitat before laying. Females caught more large prey items on arable fields and shores than on pastures. Close to egg laying, females foraged mainly near their future nest sites. Arable land and pastures were used to a similar extent for nesting. We found no difference in nest predation between habitats. Egg volume varied among females and was correlated with wing-length, body mass and condition. Mean egg volume also was positively correlated with feeding time on arable land before laying. Pairs nesting on arable fields therefore generally produced larger eggs than those on pastures. The distances between nests and chick foraging areas, however, were significantly longer for birds nesting on arable land than for those on pastures. Moreover, in 2 of 3 years, the proportion of hatched chicks that survived until fledging was negatively correlated with this distance. There was no difference in chick survival between broods hatched on arable fields and pastures. We suggest that nest site selection and offspring production involve a trade-off between the benefits of nesting close to rich feeding grounds for adults and the costs of moving long distances between nest sites and chick-rearing areas.

Most waders (Charadrii) have precocial, mobile and self-feeding chicks (e.g. Walters 1984). These chicks must hatch at an advanced developmental stage and retain sufficient yolk reserves to sustain them during the first days after hatching, requirements that depend on high female energy investment in eggs (Galbraith 1988b, Grant 1991). In both altricial and precocial birds, chicks hatched from large eggs are heavier and larger than those from small eggs (e.g. Parsons 1970, Ricklefs 1984, Galbraith 1988b, Grant 1991). Moreover, several studies have shown that chicks from large eggs grow faster and/or survive better than those from small ones (e.g. Parsons 1970, Galbraith 1988b, Grant 1991 and references therein). Lapwings *Vanellus vanellus*, as well as most of the northerly breeding waders, have a clutch size limited to four eggs (e.g. Walters 1984), and production of larger and more nutrient-rich eggs when food is abundant may be one way of increasing reproductive output (Miller 1979). Thus, in these species natural selection should favour individuals that are able to produce large eggs (but see Redmond 1986, Galbraith 1988b).

The Lapwing is a widespread Eurasian plover (Charadriidae) which breeds in open habitats such as wetlands, pastures, moors and arable land (Cramp & Simmons 1983). Vegetation height and structure, concealment of nests and adults, and distance to chick foraging areas as well as to potential predator refuges such as trees and bushes may

influence nest site selection (e.g. Klomp 1954, Redfern 1982, Elliot 1985, Galbraith 1989). Lapwings defend territories around their nest sites (e.g. Cramp & Simmons 1983); foraging habitats and food supply in the vicinity of the nest therefore may also influence nest site choice (Berg 1993).

Nesting and chick rearing may require different habitats, and Lapwings sometimes nest in places unsuitable for feeding chicks (Redfern 1982, Galbraith 1989). Here we analyse costs and benefits of nesting in different habitats. We examine distribution of nests, nest predation risk and chick survival. Variation in egg size is analysed in relation to female traits and foraging location. Finally, we discuss trade-offs in nest site selection and feeding areas in the Lapwing.

## METHODS

### Study areas

The main part of the study was carried out from 1987 to 1990 at three sites on the coast of southwestern Sweden: Ödsmåls kile (57°56'N, 11°47'E), Vallda Sandö (57°29'N, 11°56'E) and Torkelstorp (57°26'N, 12°7'E). Additional data (capture of adults) were collected in 1991 at two of the localities. All sites consisted of shallow marine bays surrounded by arable land and old, unimproved pastures. The arable land was situated on more elevated parts, adjacent

to the slightly sloping pastures that bordered the seashore. The pastures were irregularly flooded by sea water (mostly during autumn and winter).

### Observations of foraging females before laying

Selection of foraging habitats during pre-laying was studied in 1989–1990 by time budgets of individual female Lapwings. We defined the pre-laying period as the time from first arrival to the start of incubation. We studied 16 females from mid-March to mid-April. Thirteen of the 16 females were individually colour-ringed (see below), and the remaining ones were identified by plumage characteristics (differences in amount of white on throat and breast).

Although nocturnal foraging may occur, Lapwings feed mostly by day (Cramp & Simmons 1983). We divided the daylight hours (0600–2100h) into five 3-h periods. Females were watched continuously for up to 30 min, and birds included in the analysis were studied during at least three periods (spread over most of pre-laying). Total observation time was 32 h, and females were observed on average for  $2.0 \pm 0.4$  (s.d.) h. The observation sequence during a day was randomized among focal birds in the area.

We recorded feeding time in different habitats for each female and period. The mean proportion of time spent by a female in each habitat was then calculated. Foraging areas were classified into three major habitats:

(1) Arable land: mostly ploughed cereal fields (spring cereals) but also some stubble fields, autumn cereals and leys (arable land temporarily used for hay).

(2) Coastal pastures: moderate–intensively grazed grasslands with temporary pools.

(3) Shore: more or less exposed mudflats in the bays. We scored the water level at sea (influenced by weather conditions; variation due to tide is negligible) using three categories: (I) low: several extensive mudflats exposed in the bay, (II) medium: some minor exposed mudflats and (III) high: no or very small mudflats visible. These levels corresponded roughly to 50–100%, 5–50% and 0–5%, respectively, of the maximum area of exposed mudflats.

At each visit to a study area, we plotted the positions of feeding females on maps; thus we could study the distance between feeding areas and future nest sites for each female. If a female was observed at several feeding sites during 1 day, we calculated the mean distance for that day.

During time-budget studies, we also measured feeding rates of individual females by recording the number of prey items caught per feeding time. We included only successful feeding efforts, i.e. when we saw a bird swallow a prey item. Prey items were classified as “large” (item visible) or “small” (item not visible). For each habitat, we pooled data on feeding rates since we found no significant differences between years ( $z_{14} < 0.6$ , n.s., Wilcoxon rank sum test) or among localities ( $\chi^2_2 < 4.5$ , n.s., Kruskal-Wallis one-way analysis of variance). Unless otherwise stated, means  $\pm$  s.e. are given.

### Nest site selection, nest survival and trapping of adults

Lapwing nests were found by locating incubating birds from distant viewpoints. For each nest, we recorded habitat (the three categories described above) and clutch size. We also measured the available area of nest site habitats (arable land and pastures) from maps (scale 1:10,000). In this analysis, we excluded areas unsuitable for nesting (tall grass vegetation and areas with trees or bushes).

By assuming 5 days for clutch completion and an incubation period of 27 days (Ettrup & Bak 1985, D. Blomqvist & O.C. Johansson, pers. obs.), the start of egg laying was calculated by back-dating from (1) observed laying, (2) observed hatching or (3) estimated incubation stage (by floating the eggs in water; van Paassen *et al.* 1984). Nests usually were revisited two or three times during incubation and were checked at the estimated hatching date. They were recorded as hatched if chicks were found in or near the nest or, if no chicks were observed, if the nest lining contained small fragments of egg shells. Empty nests or nests containing large pieces of egg shells were classified as destroyed by predators (Green *et al.* 1987, Galbraith 1988a, Baines 1990). Since the nests were found at different stages of incubation, daily survival and predation rates were estimated by the methods of Mayfield (1961, 1975) and Johnson (1979). Most nests on arable fields survived spring cultivation because farmers agreed to avoid them, so we could analyse daily nest survival and predation rate in this habitat also.

In 1988–1991, incubating birds were caught using walk-in-traps; in total, 43 adults (41 females and two males) were individually colour-ringed. Birds were trapped on average 16 days ( $\pm 7$  s.d.,  $n = 36$ ) after start of incubation. For each adult, we measured body mass (g) and lengths (mm) of wing (straightened and flattened wing, from carpal joint to tip), bill, bill + head and tarsus + toe. Female body condition was estimated from the residuals in a log-log regression of mass on bill + head-length (condition index; see Ormerod & Tyler 1990).

### Egg size

Length and breadth of the eggs were measured with vernier calipers to the nearest 0.1 mm. Egg volumes ( $V$ ) in  $\text{cm}^3$  were calculated as  $V = k_v \times \text{length} \times \text{breadth}^2/1000$  (e.g. Hoyt 1979). We used 0.457 as estimate of the constant  $k_v$  (Galbraith 1988b).

In this study, relayings could be determined only for colour-ringed females. Of ten such clutches, seven were laid in May. Laying dates (i.e. laying of the first egg) for 201 clutches varied between 30 March and 29 May with 15 April as median laying date. About 75% of the clutches were laid before 1 May; most later clutches probably were replacements and are treated as such in the analysis.

Mean egg volumes were approximately normally distrib-

uted ( $W = 0.99$ , n.s.,  $n = 216$  clutches, Shapiro-Wilks statistic); therefore differences in egg size were tested with ANOVA and  $t$ -test. Except for first clutches in 1988 ( $F_{1,36} = 7.5$ ,  $P < 0.05$ ), i.e. in one of six comparisons of first and replacement clutches, we found no significant differences in egg volume among sites ( $F = 2.6$ , n.s., one-way ANOVA). In 1988, however, there was no significant difference in mean egg volume between nest site habitats ( $t_{36} = 0.3$ , n.s.); therefore we pooled egg size data from all study areas.

### Brood movements and survival

At each visit to the study areas in 1988–1990, the positions of foraging broods were plotted on maps. Broods were identified by colour-ringed adults and/or chicks (a unique combination for each brood). For broods with known nest location and hatching date, we recorded movements from nests to the first feeding areas. Broods were considered to have reached feeding areas at a maximum of 3 days after hatching (cf. Redfern 1982). Brood movement data were subdivided since distance between nest sites and chick foraging areas was significantly shorter in 1990 ( $68 \pm 17$  m,  $n = 18$ ) than in 1988 and 1989 (1988:  $160 \pm 47$ ,  $n = 4$ ; 1989:  $192 \pm 53$ ,  $n = 6$ ;  $\chi^2_2 = 6.7$ ,  $P < 0.05$ , Kruskal-Wallis analysis).

Brood survival was defined as the proportion of hatched young surviving until fledging (including broods that did not survive, see below). Lapwing chicks are able to move considerable distances (Galbraith 1988a, D. Blomqvist & O.C. Johansson, pers. obs.). To reduce the possibility that some broods had left the study areas, they were considered dead only if the adults were seen without chicks and with no obvious parental behaviour or adults and chicks could not be found and chicks were younger than 3 weeks at the last sighting (chick mortality was low after this age; O.C. Johansson & D. Blomqvist, unpubl.). Data on brood survival were pooled since we found no significant differences among years ( $\chi^2_2 = 1.3$ , n.s.,  $n = 41$ ) or sites ( $\chi^2_2 = 3.6$ , n.s.,  $n = 41$ , Kruskal-Wallis analysis).

In the analyses of brood movements and survival, all replacement clutches were excluded due to small sample sizes. To avoid pseudo-replication, colour-ringed adults tending a brood in more than 1 year were included only once in the analysis (randomly chosen year).

## RESULTS

### Foraging habitats and feeding success of females before laying

Lapwings usually arrived at the study areas in early March. At first, the birds foraged in flocks at communal foraging sites, i.e. areas with no territories (the shore and some arable fields). Within 2–3 weeks after arrival, territory occupation began, and the flocks gradually dissolved. The distance between feeding areas and future nest sites decreased towards

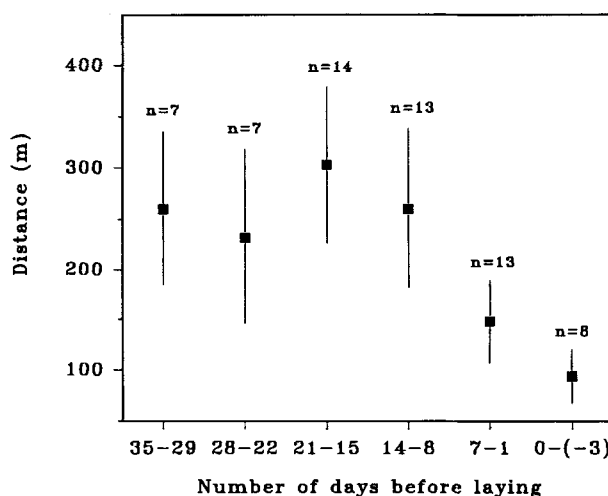


Figure 1. Mean distance ( $\pm$  s.e.) between foraging areas and nest sites at different periods before egg-laying in Lapwings ( $n$  = number of females).

egg laying (Fig. 1). Females foraged significantly closer to nest sites during the week before laying ( $170 \pm 58$  m) than they did prior to this period ( $321 \pm 100$  m,  $T = 1$ ,  $P < 0.05$ ,  $n = 8$  females, Wilcoxon matched-pairs signed-ranks test).

Arable land was the main foraging habitat during the pre-laying period. On average,  $62 \pm 6\%$  of the feeding time was spent in this habitat, while foraging on pastures and shore was less common ( $23 \pm 6\%$  and  $15 \pm 5\%$ , respectively,  $n = 16$  females). Proportion of feeding time on the shore was  $38 \pm 11\%$  and  $0.4 \pm 0.4\%$  at low ( $\leq$  level II) and high (level III) water levels, respectively ( $T = 0$ ,  $P < 0.05$ ,  $n = 6$ , Wilcoxon matched-pairs test).

We found no significant difference between habitats in feeding rate of small prey items, but birds foraging on arable fields and on the shore caught on average more large prey items (mainly earthworms and polychaetes, respectively) than did those on pastures (Fig. 2). Pairwise comparisons of all three habitats showed that feeding rates (large prey and total) were significantly higher on the shore than on pastures ( $P < 0.05$ ), but the other differences were nonsignificant (multiple comparisons test, Siegel & Castellan 1988). When we compared only the future nest site habitats, however, females caught significantly more large prey items on arable land than on pastures ( $z_{12} = -2.1$ ,  $P < 0.05$ , Wilcoxon test). Since females foraging on pastures did not increase their intake rate of small prey items, feeding on pastures was less profitable than on the other habitats (assuming no nutritive differences in food items selected in each habitat).

### Nest site selection and nest survival

Over the 4 years 1987–1990, 252 nests were found. Of these, 56% were on coastal pastures and 43% on arable land (al-

most entirely on spring cereals, only four nests on autumn cereals and leys). Four nests also were found on mudflats but were flooded when the water level rose. We compared the proportion of available area of arable land and pastures with the proportion of nests in these habitats in different years. Except for replacement clutches in 1990, there were no significant differences between these proportions (Table 1), suggesting the birds did not prefer one habitat type over the other.

Of 211 nests visited at least twice, 70% hatched. Nest losses (30%) were caused mainly by predation (16%) and farming operations on arable land (6%). A few nests were flooded (4%), deserted (3%) or destroyed by grazing cattle (1%). There was no significant difference in predation rate between nests placed on arable land and on pastures (Table 2).

### Variation in egg size

Egg dimensions were based on measurements of 787 eggs from 216 clutches. In all years, variation in egg volume was significantly larger between than within clutches ( $P < 0.001$ , except  $P < 0.05$  for replacement clutches in 1987, one-way ANOVA). Thus, individual females tended to lay eggs of similar size, but there were significant differences among females. Two-way ANOVA of eggs from colour-ringed females (with identified replacement clutches) confirmed that differences among females explained most of the variation in egg volume ( $F_{8,47} = 16.8$ ,  $P < 0.001$ ). Differences between years ( $F_{1,50} = 0.2$ , n.s.) and between first and replacement clutches ( $F_{1,47} = 2.3$ , n.s.) did not significantly influence egg size ( $n = 65$  eggs from nine females).

Eggs generally were larger in nests on arable land than on coastal pastures (first clutches: on average 3% larger,  $n = 61$  and 101 clutches, respectively; relayings: 4% larger,  $n = 13$  and 37 clutches), but the difference was significant only for replacement clutches in 1989 and first clutches in 1990 (Table 3). Time budgets showed that females nesting on pastures also foraged on arable land ( $15 \pm 9\%$ ,  $n = 8$ ). This behaviour may reduce the difference in egg size between nest site habitats. If nests on pastures close to arable land (within 100 m; cf. Fig. 1) were excluded, mean egg volume was larger on arable land than on pastures also for first clutches in 1988 (Table 3).

### Factors causing variation in egg size

Mean egg volume was positively correlated with female mass ( $r^2 = 0.29$ ,  $P < 0.001$ ), condition index ( $r^2 = 0.21$ ,  $P < 0.01$ ) and wing-length ( $r^2 = 0.15$ ,  $P < 0.05$ ). Other female traits were not significantly correlated with egg volume ( $r^2 \leq 0.09$ , linear regression analysis). A multiple regression analysis, with wing-length and mass or condition as independent variables, did not substantially improve the relationship with egg size ( $r^2 = 0.34$  and 0.30, respectively). There was no

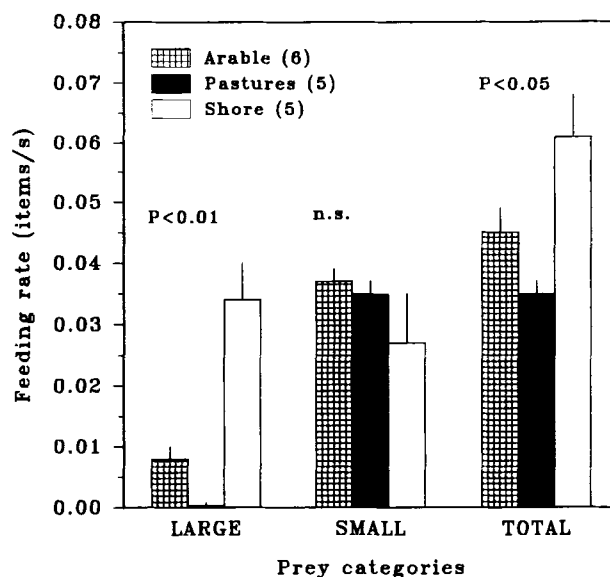


Figure 2. Mean feeding rate ( $\pm$  s.e.) of female Lapwings in different habitats. Number of females within parentheses. Differences were tested with Kruskal-Wallis one-way analysis of variance.

correlation between incubation stage and female mass or condition (mass:  $r_s = -0.09$ , condition index:  $r_s = -0.17$ , n.s.,  $n = 36$ ).

Females nesting on arable land had longer wings ( $220.6 \pm 0.9$  mm) than did those on pastures ( $217.6 \pm 1.0$  mm,  $t_{39} = 2.3$ ,  $P < 0.05$ ) but did not differ in other measurements ( $0.3 < t_{39} < 1.5$ , n.s.). Females nesting on arable fields, however, were trapped later in the incubation period (mean  $\pm$  s.d.:  $21 \pm 7$  days,  $n = 7$ ) than were those on pastures ( $15 \pm 7$  days,  $n = 29$ ), which possibly influenced mass and condition. Variation in wing- and bill + head-length was larger for females nesting on pastures ( $F_{32,7} = 5.2$  and  $F_{32,7} = 7.0$ , respectively,  $P < 0.05$ ).

We found a significant positive correlation between egg volume and proportion of feeding time on arable land before laying (Fig. 3). As expected, females that foraged mostly on coastal pastures laid smaller eggs ( $r_s = -0.56$ ,  $P < 0.05$ ). There was no correlation between egg size and proportion of feeding time on the shore ( $r_s = 0.15$ , n.s.,  $n = 13$ ).

Interactions among egg size, feeding time on arable land and female size were analyzed by partial correlations. We used wing- and bill + head-length since these variables gave the best relationship with egg size (mass was not measured in the same year as time budgets). When female size was controlled for, we found approximately the same relationship between egg size and proportion of feeding time on arable land (Table 4, cf. Fig. 3). There was no correlation between egg size and female size when controlling for feeding time on arable land. Female foraging location before laying was therefore an important determinant of variation in egg size.



**Table 1.** Proportion (%) of Lapwing nests found on arable land and coastal pastures and available area (%) of each habitat (within parentheses). Differences were tested with  $\chi^2$ -test (d.f. = 1). Nests found in 1987 were excluded due to small sample sizes

Year		Nest site habitat			Number of nests
		Arable land	Pastures		
1988	First clutches	60 (49)	40 (51)	n.s.	40
	Replacements	62 (49)	38 (51)	n.s.	21
1989	First clutches	40 (40)	60 (60)	n.s.	57
	Replacements	44 (40)	56 (60)	n.s.	18
1990	First clutches	33 (40)	67 (60)	n.s.	75
	Replacements	18 (40)	82 (60)	$P < 0.05$	22

### Brood movements and survival

Shortly after hatching, nests were abandoned and parents led the chicks to their foraging areas. Distances between nest sites and chick-rearing areas varied between 9 and 332 m. In 1988–1989 (but not in 1990), when broods on average moved a longer distance to reach feeding areas than they did in 1990, brood survival was negatively correlated with this distance (Fig. 4).

As females nesting on arable fields generally laid larger eggs than did those on pastures, it might be expected that higher fledging rates occurred on arable land. Distances between nests and chick foraging areas, however, were significantly longer for broods hatched on arable fields ( $215 \pm 38$  m) than for those hatched on pastures ( $65 \pm 13$  m,  $z_{26} = 2.9$ ,  $P < 0.01$ , Wilcoxon test). Overall, we found no significant difference in survival between broods hatched on arable fields ( $24 \pm 8\%$ ) and on pastures ( $29 \pm 6\%$ ,  $z_{33} = -0.7$ , n.s., Wilcoxon test).

### DISCUSSION

Female Lapwings foraged mostly on arable fields where the intake rate of large prey items (earthworms, Lumbricidae) was comparatively high. Marine mudflats also provided large

prey (polychaete worms), but use of this habitat was constrained by variation in sea water level. Galbraith (1989) and Baines (1990) also found that Lapwings in the U.K. in the pre-breeding season foraged mainly in habitats where prey abundance and feeding success were high. Earthworms and leatherjackets (Tipulidae) probably constituted important prey items at that time of the year (Högestedt 1974, Thompson 1983, Galbraith 1989, Baines 1990).

Nests were distributed in proportion to the available area of each habitat, implying no preference difference between arable fields and pastures. Galbraith (1989) suggested that, due to background colouration and structure, incubating adults and nests are more cryptic and difficult to locate for visually hunting predators on arable fields and proposed that a preference for nesting on arable fields was due to lower predation risk. Some studies (Galbraith 1988a, Baines 1990, Shrubbs 1990) have reported lower nest predation on arable land than in grassland habitats, although with variation between years. We found no difference in predation rate, and the proportion of nests destroyed by predators (16%) was fairly low and comparable with the value (17%) reported by Shrubbs (1990). In our study areas, therefore, nest predation risk was unlikely to influence nest site choice between arable fields and pastures.

Most broods hatched on arable land left the nest site hab-

**Table 2.** Proportion (%) of Lapwing first clutches hatched or destroyed by predators on arable land and coastal pastures. Daily predation rate (DPR) and its standard error are also given. Nests found in 1987, and replacement clutches in other years, were excluded due to small sample sizes. There was no significant difference in daily predation rate between habitats

Year	Arable					Pastures				
	Hatched	Destroyed	DPR	n	s.e. ( $\times 10^{-3}$ )	Hatched	Destroyed	DPR	n	s.e. ( $\times 10^{-3}$ )
1988	72	28	0.02	18	7.8	81	19	0.01	16	5.7
1989	79	21	0.01	14	7.4	74	26	0.02	31	5.7
1990	100	0	0	7	0	96	4	0.002	46	1.5

**Table 3.** Mean Lapwing egg volume in  $\text{cm}^3$  ( $\pm \text{s.e.}$ ) in nests on arable land and coastal pastures. Replacement clutches in 1987 and 1990 were excluded due to small sample sizes. Probability values refer to differences in egg volume between arable land and the other habitats (t-test)

Year		Nest site habitat		
		Arable land (n)	Pastures (n)	Distant pastures* (n)
1987	First clutches	23.2 $\pm$ 0.6 (6)	22.0 $\pm$ 0.5 (3) n.s.	21.0 (1) not tested
1988	First clutches	23.3 $\pm$ 0.3 (22)	23.2 $\pm$ 0.4 (16) n.s.	21.8 $\pm$ 1.3 (3) $P < 0.05$
	Replacements	22.9 $\pm$ 0.3 (3)	23.1 $\pm$ 0.6 (8) n.s.	22.9 $\pm$ 0.7 (6) n.s.
1989	First clutches	23.2 $\pm$ 0.3 (16)	22.7 $\pm$ 0.2 (34) n.s.	22.5 $\pm$ 0.2 (25) n.s.
	Replacements	24.2 $\pm$ 0.4 (4)	22.7 $\pm$ 0.3 (10) $P < 0.05$	22.7 $\pm$ 0.4 (8) $P < 0.05$
1990	First clutches	24.1 $\pm$ 0.3 (17)	23.1 $\pm$ 0.2 (48) $P < 0.01$	22.9 $\pm$ 0.2 (28) $P < 0.01$

\* Nests on pastures, more than 100 m to nearest arable field (see text).

it at soon after hatching. Parents moved their chicks to the shore or to the wet and intensively grazed parts of the pastures. The distance between nest sites and chick-rearing areas was on average about three times longer for birds nesting on arable land than for those on pastures. Moreover, in 1988–1989, there was a significant negative relationship between this distance and brood survival. In 1990, when journey distances were significantly shorter, we found no correlation between brood movements and survival. Chicks may be vulnerable to predation during movements between nests and foraging areas. Extensive movements probably are energetically costly for newly hatched young and may result in increased mortality, either directly through starvation or indirectly through increased food demands, thus exposing chicks to predators. Galbraith (1988a) also found that Lapwing chicks with close access to feeding areas tended to have lower mortality rates than those that undertook longer journeys. The distance between nest site areas and suitable chick foraging areas is probably an important factor in nest site choice.

Given that we found no significant difference in nest predation between the two alternative habitats, selection for minimizing journey time and distance would favour nesting on pastures. Since no such preference was observed, nesting on arable land is likely to entail some other advantage. We found that birds foraging on arable fields had a high intake rate of large prey, and females that used mostly this habitat during pre-laying laid larger eggs. Moreover, eggs generally were larger in nests on arable land. For Lapwings nesting on arable fields, we propose that the cost of long distances to chick foraging areas is balanced by the potential of producing larger eggs. This was supported by similar survival of broods hatched in the two habitats. Galbraith (1989) and Baines (1990) suggested that, since adults forage on "neutral" or communal foraging areas outside territories, food supply in the vicinity of nests is not very important for nest site choice. In a study of Lapwings breeding on mixed farmland in central Sweden, however, Berg (1993) found that foraging outside territories occurred in less than 9% of the observation time, and he concluded that Lapwings choose

**Table 4.** Spearman partial correlation coefficients for relationships between Lapwing mean egg volume (dependent variable) and mean proportion of feeding time on arable land during pre-laying, wing-length and bill + head-length ( $n = 11$  females)

Independent variable	Controlling for	$r_s$	$P$
Feeding time	Wing-length	0.66	$< 0.05$
Feeding time	Bill + head-length	0.71	$< 0.05$
Feeding time	Wing-length, bill + head-length	0.71	$< 0.05$
Wing-length	Feeding time	0.15	n.s.
Bill + head-length	Feeding time	-0.29	n.s.

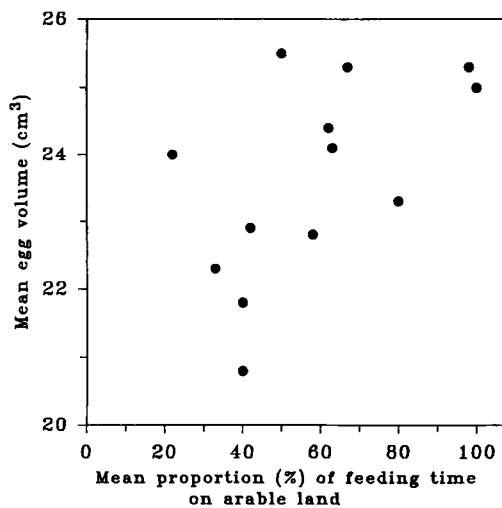


Figure 3. Relationship between egg size and feeding time of Lapwings on arable land during pre-laying ( $r_s = 0.61$ ,  $P < 0.05$ ,  $n = 13$  females, Spearman rank correlation test).

nesting areas with suitable foraging habitats for adults nearby. We found that females close to egg laying foraged near their future nest sites. In waders, females acquire energy and nutrients for egg laying mainly during or close to the laying period (Erckmann 1983 and references therein). Rich foraging areas in the vicinity of the nest should be important also during incubation, which like pre-laying is a period of high energy demands on adults (e.g. Norton 1972, Kálás & Løfaldli 1987). Since both parents defend the nest against predators (e.g. Cramp & Simmons 1983, D. Blomqvist & O.C. Johansson, pers. obs.), long distances to feeding areas during incubation probably would also increase the risk of nest predation (also see Berg [1992] for Curlew *Numenius arquata*).

Differences among females were the main source of variation in egg size. This seems to be a common pattern in waders (e.g. Ricklefs 1984, Galbraith 1988b, Grant 1991). High consistency (between years and clutches) in egg size of individual females may imply high heritability (e.g. Grant 1991). There is, however, experimental evidence that food supply affects egg size in precocial birds, such as the Lesser Black-backed Gull *Larus fuscus* (Hiom *et al.* 1991) and the Mallard *Anas platyrhynchos* (Pehrsson 1991). Since clutch size is fixed in waders, environmental influence on egg size could be important in these birds (Miller 1979, Grant 1991).

Female body size, mass and condition explained part of the observed variation in egg volume (up to 34%). Similar results were found in several studies of waders (e.g. Miller 1979, Ricklefs 1984, Redmond 1986, Galbraith 1988b, Grant 1991). The partial correlation analysis suggested, however, that type of foraging habitat used during pre-laying was the main factor. It is also possible that older and/or more experienced females lay larger eggs. Age-dependent variation in egg size has been documented in two waders (Gratto *et*

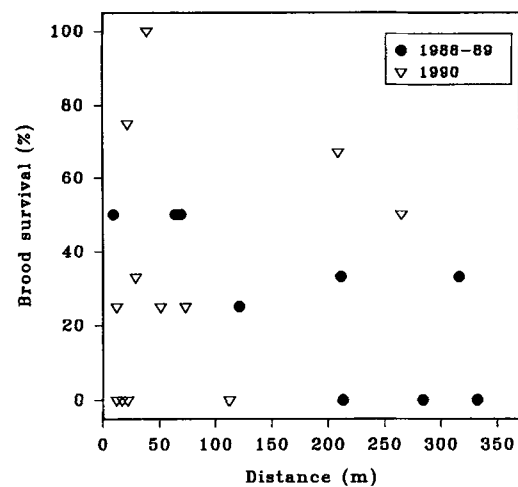


Figure 4. Relationship between brood survival and distance between nests and chick foraging areas for Lapwings in 1988–1989 ( $r_s = -0.79$ ,  $P < 0.05$ ,  $n = 9$ ) and 1990 ( $r_s = 0.35$ , n.s.,  $n = 12$ , Spearman rank correlation test).

*al.* 1983, Thompson & Hale 1991), but our data on age variation in egg size are too few.

On arable land, nest losses due to farming operations can be extensive (e.g. Galbraith 1988a, Shrubb 1990, Berg *et al.* 1992). Low breeding success and population declines have been found in several studies of Lapwings breeding on arable land in Europe (Beser & Helden-Sarnowski 1982, Matter 1982, Kooiker 1984, Ettrup & Bak 1985, Galbraith 1988a). There are several possible reasons why Lapwings continue to breed on farmland. First, due to changes in management, arable fields may only recently have become unsuitable as nesting habitats, and Lapwings have not yet responded to these changes (Galbraith 1988a). Second, extensive losses of first clutches might be compensated for by high hatching success of replacement clutches (Berg *et al.* 1992). Third, there may be no high-quality breeding habitats, such as wet grasslands, available. In Denmark, Lapwings breed in higher densities and produce more fledged chicks on coastal pastures than on arable land (Ettrup & Bak 1985). Since the area of wet grassland is decreasing in Europe (e.g. Hötker 1991), Lapwings may be forced to nest in habitats that are sub-optimal. Finally, even if better habitats are available, Lapwings may still breed on arable land if the choice between arable land and pastures is not genetically fixed but is flexible enough for offspring to settle in habitats different from that in which they were hatched. As long as arable fields provide some basic requirements (e.g. short vegetation height, rich food supply and access to nearby wet areas), recruits may continue to colonize this habitat.

To sum up, the choice of nest site involves conflicting selection pressures. In this study, pairs nesting on arable fields produced larger eggs and raised equal numbers of fledglings as those nesting on pastures, although their young had to move longer distances to reach chick foraging areas.

We propose that nest site choice in the Lapwing, besides being related to antipredator advantages such as semicolonial nesting and avoidance of predator refuges (Elliot 1985, Galbraith 1989, Berg *et al.* 1992), may involve a trade-off between the benefits of nesting in habitats with rich food supply for adults and the costs of larger distance between nest sites and chick-rearing areas.

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