

**REPRODUCTION OF KENTISH PLOVER
CHARADRIUS ALEXANDRINUS
IN GRASSLANDS AND FISH-PONDS:
THE HABITAT MAL-ASSESSMENT HYPOTHESIS**

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Abstract

Reproduction of Kentish Plover (*Charadrius alexandrinus*) in grasslands and fish-ponds: the habitat assessment hypothesis

Kentish Plovers breed in two kinds of habitat in Hungary: in alkaline grasslands and in drained fish-ponds. Clutch size and size of eggs did not differ between the two habitats. However, hatching success was lower in fish-ponds than in grasslands and successful clutches tended to produce fewer young in the fish-ponds. The results of a field experiment confirmed that the survival of eggs was lower in fish-ponds because of greater predation than in grassland. Kentish Plovers move between two types of habitats during breeding session, so it is unclear why they breed in fishponds where hatching averages only 0.33 young per clutch compared to 0.64 young per clutch in grassland. I suggest that Kentish Plovers are attracted to fish-pond by the rich food supply and physiognomy of nest site (e. g bare ground), but are unable to assess properly the predation risk (mal-assessment hypothesis). Kentish Plovers only recently started to breed in fish-ponds, thus they may not have been enough time for avoidance of fish-ponds to have evolved. The malassessment hypothesis implies that although birds can readily exploit new man-made habitats for breeding, their reproductive success may be low there.

Introduction

Although plovers *Charadrii* usually inhabit open areas, they may breed on a variety of both natural and man-made habitats. For example Lapwings (*Vanellus vanellus*) may breed in either wetlands, dry grasslands or arable land (Cramp and Simmons 1983, Galbraith 1988a). Other waders, such as Little Ringed Plovers (*Charadrius dubius*) have been recorded breeding on dry river banks, dry beds, in gravel pits and on industrial wastelands (Cramp and Simmons, 1983). In contrast, Kentish Plovers (*Charadrius alexandrinus*) are mostly restricted to coastal sites (Rittinghaus, 1961), although in Hungary they breed either in alkaline grassland or in the drained bottoms of fish-ponds (Székely, 1991).

Two major groups of models have been put forward to explain habitat selection in birds (Brown 1969, Fretwell and Lucas 1970, review: Rosenzweig 1987). According to the despotic model, individuals are constrained in

habitat selection by the dominant individuals. As a result, part of the population is forced to breed in lower quality habitat and ultimately face lower reproductive success (O'Connor, 1985). Alternatively, the ideal free model proposes that the movement of individuals between habitat patches is unconstrained, so their expected reproductive success should be constant across habitats. Results of earlier bird studies have supported either the despotic model (Harris 1970, Holmes 1970, Galbraith 1988b) or the ideal free one (Pierotti 1982).

The aims of this study are (1) to compare clutch sizes, egg measurements and hatching success of Kentish Plovers between grassland and man-made fish-pond habitat, (2) to report the results of a field experiment designed to compare predation rates between these two habitats and (3) to discuss possible explanations for the observed pattern of habitat selection.

Study sites and methods

Breeding biology

Kentish Plovers were studied at five alkaline grasslands and two fish-ponds in southern Hungary (near the towns of Kistelek and Szeged). In the alkaline grasslands (puszta) the ground was mostly bare and the soil covered by salt. Halophytic plants such as *Camphorosma annua*, *Suaeda maritima*, *Puccinellia distans* and *Crypsis aculeatus* patchily covered the ground. Three out of five sites were grazed by either sheep or geese. Kentish Plovers bred only in two sites in all three years (Makraszék and Székely), while breeding in Fülöpszék occurred only in 1988–89, Libanevelő 1988 and Kistelek in 1989, because of the rapid succession of vegetation. The size of the grasslands varied between 4 and 32.5 ha (Marián 1980, Székely 1991).

Two fish-ponds were studied Fertő (1988–89) and Csaj-tó (1989–1990): Kentish Plovers bred on the bare dry mud of the bottom. Fishponds were only sporadically vegetated with *Polygonum amphibium*, *Chamomilla inodora* and *Phragmites communis*, and no grazing took place. The size of Fertő and Csaj-tó study sites was 10.8 and 145 ha, respectively. The total population of the seven study sites was 35–41 pairs during the study.

Nests were located as early during incubation as possible, and were visited thereafter every other or every fourth day. Eggs were measured on the day incubation started. Clutches were judged successful either from capturing chicks at the nest or by finding 1–2 mm pieces of eggshell remains in the nest scrape. Small fragments of egg shell result from the process of pipping and thus are indicative of successful hatching. Failed clutches were identified from the tracks of mammalian predators or broken eggshell remains at the nests (Green *et al.*, 1987). Bird predators pierce a hole in the egg or remove the eggs out of nest scrape (Galbraith, 1988a). Eggshell fragments were occasionally found up to 300 m from nests.

Field experiment

To test whether predation risk in the two kinds of habitat differed, an experiment was performed in one grassland (Székálg) and one fish-pond (Csaj-tó) between 5 and 12 July 1990. Domestic chicken eggs and small pieces of flesh were as baits to measure the risk of predation. The null hypothesis was that no difference should exist between the two habitats in the survival chances of eggs or flesh. Neither the weight of the eggs (unpaired t-tests, $t = 0.17$, $p > 0.87$, $N = 10$) nor those of flesh pieces differed between the two habitats (unpaired t-test, $t = 1.62$, $p > 0.12$, $N = 10$).

The eggs and flesh pieces were arranged alternately in lines. In both sites, the minimum distance between eggs was 100 m, and between an egg and a piece of flesh 50 m. The experiment was set up on 5 July in both habitats, and field visits were made on three consecutive days (6, 7 and 8 July) and afterwards on 10 and 12 July. The sites were visited in consecutive hours. Checks were made from 5 m away, so that the eggs or pieces of flesh were not repeatedly handled unless having been preyed upon. Predation had occurred if parts of an egg or of a piece of flesh were eaten, or the whole item had been removed.

Statistical procedures

Length, breadth and weight of eggs were measured and for each clutch the means of egg measures were taken. The weight of fresh clutches are given only. A clutch was classified successful if at least one chick hatched. Mayfield's (1975) method was used to calculate hatching success for each study site in each year (success = 1 - no of nests failed/total nest days). Only complete clutches were included. Non-parametric statistics were used (Sokal and Rohlf, 1981). Statistical analyses were performed by SPSS (Norusis, 1988). Two-tailed probabilities, mean \pm SDs are given.

Results

There were no significant differences between the five sites of grassland in either clutch size (Kruskal-Wallis: $H = 3.82$, $p > 0.43$, $N = 65$), egg length ($H = 8.48$, $p > 0.07$, $N = 64$), egg breadth ($H = 4.40$, $p > 0.35$, $N = 64$), egg weight ($H = 1.52$, $p > 0.67$, $N = 28$) or hatching success (G-test: $G = 6.66$, $p > 0.1$, $N = 60$). There was also no difference between the two fish-pond sites (clutch size: $H = 0.74$, $p > 0.38$, $N = 34$, length: $H = 0.84$, $p > 0.35$, $N = 31$; breadth: $H = 0.57$, $p > 0.44$, $N = 31$; G-test with Yates correction of hatching success, $G = 0.002$, $p > 0.9$, $N = 33$). Thus sites with a habitat type were combined in all further analyses.

Movement of individually marked birds

Kentish Plovers moved widely between breeding sites before egg-laying. For example, in 1989 a colour ringed female was first seen in a fish-pond on 8. April (Fertő VI), on 17. April she was seen in a grassland (Fülöpszék, 28.8 km), and on 27. April in another grassland (Makraszék, 22.3 km). Her clutch was found on 20. May in a grassland (Kistelek, 10.9 km).

Failed breeders may also change breeding site. Three out of six individually marked grassland pairs changed to a new site after failure, in two cases to a fish-pond, and in one case to another grassland to lay a new clutch. The remaining three pairs laid repeat clutches in the same grassland. Only two failed fish-pond pairs were found to relay; both of them moved to grassland.

Size and weight of eggs

There was no significant difference in egg size between grassland vs. fish-pond habitats within any year (Table 1), or between years (*Kruskal–Wallis*, egg length: $H = 2.68$, $p > 0.26$, $N = 95$; egg breadth: $H = 0.08$, $p > 0.95$, $N = 95$) Although the fresh weight of alkaline grassland eggs was slightly larger than those of fish-ponds (Table 1) the sample size was small and egg weight was not significantly different when analysed in each year separately (Table 1). The egg weight was not significantly related to years (*Kruskal–Wallis*, $H = 4.34$, $p > 0.11$, $N = 33$).

Table 1. Egg-size, fresh egg weight and clutch size in grassland and fish-pond habitats in Hungary, mean \pm SD(N). Mann–Whitney U-test, * $p < 0,05$.

1. táblázat. A tojásméretetek, a friss tojások tömege és a fészekalj nagyságok a szikes pusztán és halastómederben költő széki liléknél

	Length Hosszúság /mm/	Breadth Szélesség /mm/	Weight Tömeg /g/	Clutch size Fészekalj nagyság
1988				
Grasslands	31,6 \pm 0,8 (21)	23,1 \pm 0,5 (21)	8,6 \pm 0,9 (6)	2,9 \pm 0,4 (22)
Fish-ponds	32,0 \pm 0,4 (2) NS	23,3 \pm 0,1 (2) NS	–	3,0 \pm 0,0 (2) NS
1989				
Grasslands	32,0 \pm 1,0 (24)	23,1 \pm 0,5 (24)	9,1 \pm 0,3 (11)	3,0 \pm 0,2 (24)
Fish-ponds	31,5 \pm 1,1 (11) NS	23,0 \pm 0,4 (11) NS	–	3,0 \pm 0,0 (13) NS
1990				
Grasslands	32,4 \pm 1,1 (19)	23,2 \pm 0,2 (19)	8,8 \pm 0,4 (11)	3,0 \pm 0,0 (19)
Fish-ponds	31,8 \pm 0,9 (18) NS	23,1 \pm 0,5 (18) NS	8,4 \pm 0,4 (5) NS	2,9 \pm 0,3 (19) NS
All				
Grasslands	32,0 \pm 1,0 (64)	23,1 \pm 0,4 (64)	8,9 \pm 0,5 (28)	2,9 \pm 0,3 (65)
Fish-ponds	31,7 \pm 1,0 (31) NS	23,1 \pm 0,4 (31) NS	8,4 \pm 0,4 (5)*	2,9 \pm 0,2 (34) NS

Clutch size

Clutch size was invariable; among the 99 completed clutches 95 contained three eggs, and only three contained 2 eggs and one contained 1. The mean clutch size did not differ between grasslands and fish-ponds (Table 1), and was not different between years (*Kruskal-Wallis*, $H = 0.31$, $p > 0.85$, $N = 99$).

Hatching success

Hatching success was higher in alkaline grasslands than in fish-ponds (Table 2). In grasslands 43,3% of clutches hatched, while only 18,2% did in fish-ponds (X^2 -test with Yates correction on hatched vs. failed clutches, $X^2 = 4,90$, $p > 0.03$, $N = 93$). The main cause of failure was predation due to either mammals or birds (Table 2). Weasels (*Mustela nivalis*) Hedgehogs (*Erinaceus concolor*) foxes (*Vulpes vulpes*), stray dogs and cats were seen in both habitats, although no predation was witnessed. Potential bird predators, such as Marsh Harriers (*Circus aeruginosus*) Magpies (*Pica pica*) and Black-headed Gull (*Larus ridibundus*) were also observed in both types of habitat.

Table 2. Hatching success of Kentish Plovers in grasslands and fish-ponds (% of clutches). Other included failures due to trampling of sheep, flood and desertion
2. táblázat. A szikes pusztán és a halastómederben költő széki lilék költési sikere és a fészekalj-károsodások előidézői

	Predation by					N
	Successful Sikeres költés	Mammals Emlős	Birds Madár	Unidentified predator Nem ismert ragadozó	Other Egyéb	
1988						
Grasslands	47,1	17,6	5,9	0	29,4	17
Fish-ponds	50,0	50,0	0	0	0	2
1989						
Grasslands	33,3	16,7	20,8	0	29,2	24
Fish-ponds	30,8	15,4	7,7	46,1	0	13
1990						
Grasslands	52,6	10,5	5,3	15,8	15,8	19
Fish-ponds	5,6	22,2	55,5	0	16,7	18
All						
Grasslands	43,3	15,0	11,7	5,0	25,0	60
Fish-ponds	18,2	21,2	33,4	18,2	9,0	33

The predation rate of fish-pond clutches was higher than those of grassland clutches (G-test With *Yates* correction on predated vs. failed by other reason, $G = 6.786$, $p < 0.01$, $N = 61$). Survival rate of fish-pond nests tended to be lower in fish-ponds than in grassland, although the difference was not significant (Table 3). The survival of early clutches (laid before or on 31 May) was not different from that of the late ones (found after 31 May) either in grassland (early: 20 successful nests out of 44, late: 6 successful nests out of 16, X^2 -test with *Yates* correction, $X^2 = 0.06$, $p > 0.90$) or in fish-ponds (early: 1 successful nest out of 7; late: 5 successful nests out of 26, G-test with *Yates* correction, $G = 0.06$, $p > 0.90$).

Successful clutches in grassland tended to produce more chicks than the successful fish-pond clutches (Table 3), although the difference was not significant in either year. Using the typical incubation time of 26 days (*Rittinghaus, 1961*), a grassland clutch was expected to produce 0.64 young, while a fish-pond clutch only 0.33.

Table 3. Mayfield's estimate of hatching success, and productivity of successful clutches in two habitats, mean \pm SD(N). Mann-Whitney U-test, NS $p > 0,05$

3. táblázat. A költési siker és a produktivitás becslése a két élőhelyen
Mayfield módszere alapján

	Nest survival per days	Chick produced per egg csibe/tojás	Chicks produced per clutch csibe/fészekalj
1988			
Grasslands	0,96 \pm 0,02 (4)	0,96 \pm 0,12 (8)	2,62 \pm 0,74 (8)
Fish-ponds	0,93 \pm 0,0 (1)NS	1,00 \pm 0,00 (1)NS	3,00 \pm 0,0 (1)NS
1989			
Grasslands	0,92 \pm 0,05 (4)	0,83 \pm 0,25 (8)	2,50 \pm 0,76 (8)
Fish-ponds	0,93 \pm 0,02 (2)NS	0,67 \pm 0,38 (4)NS	2,00 \pm 1,15 (4)NS
1990			
Grasslands	0,97 \pm 0,02 (2)	0,93 \pm 0,14 (10)	2,80 \pm 0,42 (10)
Fish-ponds	0,93 \pm 0,0 (1)NS	0,67 \pm 0,00 (1)NS	2,00 \pm 0,0 (1)NS
All			
Grasslands	0,95 \pm 0,04 (10)	0,91 \pm 0,18 (26)	2,65 \pm 0,63 (26)
Fish-ponds	0,93 \pm 0,01 (4)NS	0,72 \pm 0,33 (6)NS	2,17 \pm 0,98 (6)NS

Field experiment

The results of the experiment confirmed the findings of the field study. Both the chicken eggs and pieces of flesh tended to disappear sooner in the fish-pond than in the alkaline grassland (Table 4). The daily loss of both eggs and pieces of flesh was high; in fish-pond habitat all pieces of flesh disappeared or were partially eaten after only one day of exposure (Table 4).

Table 4. Predation on experimental baits (mean \pm SD). Chicken eggs and pieces of flesh were arranged in two breeding sites, and they were checked for 1–2 days afterwards. X^2 -tests were used to compare the number of predated items, while Mann-Whitney U-test for the day of predation

4. táblázat. A ragadozók hatásának szimulált vizsgálata a költési időszakban tyúktojások és húsdarabok felhasználásával

	Grassland Szikes puszta	Fish-pond Halastómeder	Significance Sznifikancia
No. of eggs – Tojások száma	10	10	
No taken by predators	9	8	$p > 0,9$
Day of predation	$3,6 \pm 1,1$	$1,5 \pm 1,6$	$p < 0,007$
Daily survival	0,77	0,69	
No. of flesh pieces – Húsdarabok száma	10	10	
No taken by predators	7	10	$p > 0,75$
Day of predation	$1,7 \pm 1,6$	$0,9 \pm 0,3$	$p > 0,14$
Daily survival	0,79	0,0	

Discussion

Egg size and clutch size

This study found that neither clutch size nor egg-size of Kentish Plovers differed between fish-pond and grassland habitats. The lack of relation may be caused by two factors: either the local food resources of laying females were not significantly different, or laying females visited off-breeding sites for feeding. Unfortunately, we do not have data on invertebrate densities of the two habitats, although the drained fish-ponds attracted more birds for feeding than dry grasslands (pers. obs.). The wide movement of Kentish Plovers within a single breeding season suggests that laying females are not restricted to local resources.

The mal-assessment hypothesis

Despite the lack of egg and clutch size differences, hatching success was found to be lower in fish-ponds than in grasslands. Lower nest survival was due almost entirely to predation. Why, then, do Kentish Plovers breed in fish-ponds where the expected reproductive success is low? The ideal-free model predicts roughly equal levels of reproductive success across the two habitats, and clearly this was not observed. The despotic model of habitat selection may not be relevant either, since it assumes dominant individuals exclude others from using the superior quality habitat. However, Kentish

Plovers are not territorial during most of the breeding season (Page *et al.*, 1985). The breeding density of Kentish Plovers is 0.2–1.2 nests/ha in Hungary (Székely *unpubl. data*), while Rittinghaus (1961) found much higher density (100 nests/0.7 ha) in Germany, suggesting that birds are not forced into fish-ponds because of unavailable grassland breeding areas. Moreover, according to this model fish-ponds should be settled only after birds are excluded from grassland areas. This was not the case, since both grasslands and fish-ponds were occupied as soon as they became available for breeding (Tajti *L. pers. comm.*)

I suggest a third explanation, the mal-assessment hypothesis. This hypothesis proposes that Kentish Plovers may make a wrong decision when they settle in fish-ponds. Drained fish-ponds are sparsely vegetated, and they offer extensive areas of bare mud-surface available for nesting. Adjacent water puddles may also offer rich food supply. These two proximate factors may attract Kentish Plovers to settle. However, Kentish Plovers may be unable to assess properly the risk of predation when settling. The assessment of predation may be more difficult than those of food supply and nest-site characteristics, since predators may infrequently appear during egg-laying. Also, the nest-hunting behaviour of predators may be affected by the presence of clutches themselves, so the predators may concentrate their effort in a habitat only if some of their hunts were successful. Although waders have camouflaged eggs, a specialized predator can be very successful. Oring and Lank (1986) report that a single mink caused widespread breeding failure in the Spotted Sandpiper (*Actitis macularia*). Such a risk of predation would be difficult to foresee during egg-laying.

Recently waders have begun to inhabit man-made habitats. Hale (1980) reports that the Curlew (*Numenius arquata*) extended its range both in Europe and England from its original marshland habitat into agricultural land. Kentish Plovers started to breed in fish-ponds only recently, the first confirmed record being in 1973. (Bod *P. unpubl. data*). In Hungary Collared Pratincoles (*Glareola pratincola*) have also started to breed in sunflower fields (Kovács 1990., Széll *unpubl. data*) and Stone Curlews (*Burhinus oedicnemus*) have been found to nest in vineyards (Szenek *Z. pers. comm.*). The mal-assessment hypothesis suggests that these birds invade new type of habitats by using simple proximate habitat-selection clues, although they may suffer from low reproductive success.

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**A predációs veszély
és a költési siker a szikes pusztákon
és a halastavak medrében fészkelő széki liléknél
(*Charadrius alexandrinus*)**

Dr. Székely Tamás

A széki lilék két élőhelytípusban fészkelnek a Dél-alföldön; szikespusztákon és lecsapolt halastómedrekben. A fészkealj nagyság és tojásméret nem különbözik a két élőhelytípusban. A halastavi fészkek kelési sikere azonban kisebb mint a szikes pusztaiaké, és a sikeres fészkealjából is kevesebb fióka kel a halastavon. A terepkísérlet eredménye alátámasztja, hogy a tojások túlélési esélye alacsonyabb a halastavon, mivel ott a predáció intenzívebb. Mivel a széki lilék mozognak a két élőhelytípus között egyetlen fészkelési időszakon belül, nehéz megérteni, miért fészkelnek mégis a halastóban, ahol átlagosan csupán 0.33 fióka kel egy fészkekből, míg egy szikes pusztai fészkekből 0.64. A szerző feltételezi, hogy a széki liléket a gazdag táplálék és a fészkelőhely megjelenési jellegzetessége (pl. kopár felszín) vonzza a lecsapolt halastavakhoz, de nem képesek helyesen felmérni a predációs veszélyt (mal-assessment hipotézis). A széki lilék csupán az utóbbi évtizedben kezdtek el költeni halastavakon, így valószínűleg még nem tudtak alkalmazkodni az új élőhely elkerülésére. A mal-assessment hipotézis szerint habár a partimadarak képesek fészkelésre használni az új mesterséges élőhelyeket (pl. székicsér a mezőgazdasági táblákat, az ugartyúk a szőlőskerteket), fészkelési sikerük mégis sokkal kisebb lehet, mint a természetes élőhelyeken. Így természetvédelmi szempontból a természetes élőhelyek értéke lényegesen nagyobb, mint a mesterséges élőhelyeké, holott a fészkelő párok száma alapján a mesterséges élőhelyek tűnhetnek jelentősebbnek.