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Brood survival of Kentish Plovers (Charadrius alexandrinus) in alkaline grasslands and drained fish-ponds

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We investigated the survival and growth of Kentish Plover *Charadrius alexandrinus* broods in alkaline grasslands and drained fish-ponds in southern Hungary between 1988 and 1990. Broods hatched in the bottom of drained fish-ponds survived better (0.985±0.024 (SD) day^{-1}) than the ones hatched in alkaline grasslands (0.851±0.247 day^{-1}). This difference remained significant when we controlled for potentially confounding factors such as brood age, date of hatching and parental care. We propose that fish-ponds were better brood raising habitats than grasslands because they provided more hiding places for the chicks. Growth of chicks, measured by weight gain and tarsus growth, did not differ between the two habitats. These results do not support the earlier suggestion that Kentish Plovers make a wrong decision when they lay their eggs in fish-ponds; offspring produced in fish-ponds have a higher chance of fledging than those produced in grasslands.

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1. Introduction

Selection of breeding habitat is an important decision in birds (Cody 1985, Rosenzweig 1987). Breeding habitats may influence egg size, clutch size, growth rate of the young and the reproductive success of parents (Pierotti 1982, Alatalo *et al.* 1985, Galbraith 1988, Peach *et al.* 1994, Nordahl *et al.* 1995). In this paper we investigate the reproductive success of Kentish Plovers (*Charadrius alexandrinus*) in two habitats: alkaline grasslands ('puszta') and the bottom of drained fish-ponds. In a previous study one of us showed that hatching success of Kentish Plover nests was lower in fish-ponds than in grasslands (Székely 1992). To explain this apparently non-adaptive behaviour Székely (1992) proposed the habitat mal-assessment hypothesis. According to the habitat mal-assessment hypothesis Kentish Plovers make a wrong decision by nesting in fish-ponds where their clutches suffer heavy predation. In this paper we investigate whether the habitat mal-assessment hypothesis remains a valid explanation when the survival of broods is taken into account.

Tab. 1. Number of Kentish Plover broods investigated in southern Hungary.

	Alkaline grasslands					Drained fish-ponds	
	Székalj	Makraszék	Fülöpszék	Libanevelő	Víztározó	Fertő	Csajtó
1988	5	3	4	1	0	1	0
1989	2	2	0	0	5	0	7
1990	8	2	0	0	0	1	0
All years	15	7	4	1	5	2	7

2. Methods

2.1 Field work

Kentish Plovers were studied in southern Hungary, near the towns of Szeged and Kistelek (46° 25'N, 20° 00'E). We investigated five alkaline grasslands and two fish-ponds between 1988 and 1990 (Tab. 1). Hatching dates of most broods were known and the ages of the broods found after hatching were estimated from the weights of the chicks (Székely & Lessells 1993). Broods were checked from a distance and the number of chicks (typically between 1-3) was counted at 2-4 day intervals. Evidence of complete predation of the whole brood is inherently less apparent than partial predation. If a brood was not found then a search was made to find the parent(s). If parents were seen without chicks or the search was unsuccessful after three consecutive dates, then the brood was considered predated. After observing broods we attempted to catch the chicks. Body mass and tarsus length of chicks were measured. Broods were identified either by the ring numbers of the chicks or by the colour rings of the attending adult(s). The same methods were followed in both habitats. 35-41 pairs of Kentish Plover bred in the study sites each year. Further details on the study sites and field methods are given elsewhere (Székely 1991, Székely & Lessells 1993).

2.2. Statistical analyses

For each brood we used a maximum-likelihood estimate to calculate its survival probability. Suppose some arbitrary value s for the probability that a particular chick survives a single day. The probability that a particular chick survives n days is then s^n, and the probability that it fails to survive n days is $1\text{-}s^n$ (the assumption is that survival probability is independent of age). The probability that precisely N_2 out of N_1 chicks survive n_1 days is

$$\binom{N_1}{N_2} s^{n_1 N_2} \left(1 - s^{n_1}\right)^{N_1 - N_2} \qquad (1)$$

assuming that the survival of one chick is independent of survival of its sibs. Multiplying two such expressions together gives the probability that N_2 out of N_1 chicks survive n_1 days and then N_3 out of N_2 chicks survive a further n_2 days. For each brood the observations of brood size at different times gave the N's and n's, all successive pairs of observations contributing extra terms that were multiplied together to generate $P(s)$, the overall probability of getting the observed pattern of survival given a per-day survival of s. A range of values of s was tried (0 to 1 in steps of 0.0001) and the s giving the largest $P(s)$ is the maximum-likelihood estimate. A problem encountered in a very small proportion of the data is that broods grow in size, because of adoption; we then

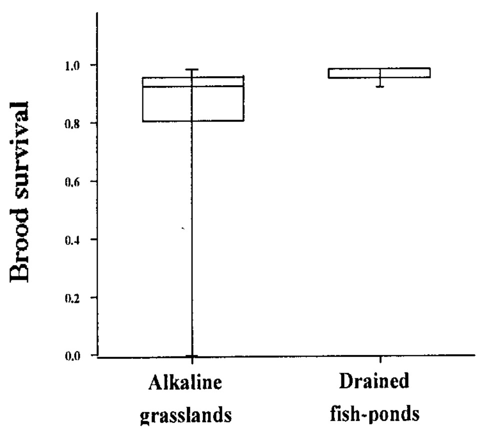

Fig. 1. Maximum-likelihood estimates of brood survival in Kentish Plover. Broods survived better in drained fish-ponds (n = 9) than in alkaline grasslands (n = 32). Mann-Whitney U test between grasslands and fish-ponds, z = 2.77, P < 0.01. Median and maximum values are equal in drained fish-ponds.

ignored just the pair of observations in which the increase occurred. The maximum-likelihood estimates of survival are bimodally distributed (in most broods at least some young survive very many days, but in a minority all the chicks died early and at the same time); accordingly we use non-parametric tests to compare maximum-likelihood estimates of brood survival between habitats.

In Kentish Plovers both parents incubate the clutch but one of the parents may desert the brood shortly after hatching (Székely & Lessells 1993). Timing of desertion was estimated as midway between the last observation of both parents with the brood and the first observation of the young with only one parent.

We calculated the growth of chicks as daily change in body mass and tarsus length. As another estimate of growth rate, we calculated residual weight and residual tarsus growth by taking the residuals of a linear regression of log (body mass or tarsus length) on brood age. Mean age and growth rate of chicks were used for each brood. Neither brood survival nor growth rate differed between years (survival: Kruskal-Wallis test, χ^2=1.59, P>0.4, n=41; weight gain: one-way ANOVA, $F_{(2,23)}$=0.99, P>0.3; tarsus growth: one-way ANOVA, $F_{(2,23)}$=0.38, P>0.6); thus we analysed the combined set of the three years.

Data were analysed by SPSS for the Macintosh 4.0. If the distribution of a variable violated the normality assumption of parametric tests we used non-parametric statistics. Mean ± SD and two-tailed probabilities are given.

3. Results

Daily survival of broods was higher in fish-ponds than in grasslands (Tab. 2, Fig. 1). This pattern could be an artefact

Tab. 2. Mean ± SD survival of Kentish Plover broods in grasslands and fish-ponds. Number of broods studied is given in brackets. Probabilities of Mann-Whitney U tests are given.

Year	Alkaline grasslands	Drained fish-ponds	P
1988	0.822 ± 0.276 (13)	1.0 ± 0.0 (1)	> 0.1
1989	0.909 ± 0.093 (9)	0.981 ± 0.026 (7)	> 0.09
1990	0.838 ± 0.309 (10)	1.0 ± 0.0 (1)	> 0.2
All	0.851 ± 0.247 (32)	0.985 ± 0.024 (9)	< 0.01

caused by several confounding variables; but nevertheless we argue that this is unlikely. First, one alternative explanation for the observed difference in survival between habitats is that survival rate changes with age and one age range was more intensely sampled in one habitat than in the other. We examined this by first interpolating (when possible) the number of chicks alive in each brood at a series of ages and then calculating the proportion of the total number of chicks alive at one age that survived 5 further days. Sample size is too small to be reliable for fish-ponds but in the grassland habitat survival shows a strong increase with age (P=0.011). (It does not matter whether this was because each chick became less prone to die as it aged, or because the more susceptible chicks died off early so that the chicks beyond a certain age were those less prone to mortality.) We then examined the intervals between observations, dividing them into two categories (2 days or less, and over 2 days) and related them to when the observations were made (10 days of age or before, and after 10 days of age). There was no significant difference between habitats in the proportion of short intervals at early versus late ages, nor in the proportion of long intervals at early versus late ages (χ^2=2.83, n=2, P=0.24). In fact the only suggestive trend is for relatively more short intervals at early ages in the fish-pond habitat; the effect of this would be to bias survival downwards in fish ponds, whereas the trend we have found is for survival to be higher in fish-ponds.

The second confounding effect is possible if brood survival decreased over the breeding season; thus broods would survive better in fish-ponds than in grasslands because they hatched earlier in fish-ponds. However, brood survival was unrelated to the date of hatching (Spearman rank correlation, r_s=-0.19, n=41, P>0.1), and clutches hatched 16 days *later* in fish-ponds (18 June ± 21 days, n=9) than in grasslands (2 June ± 17 days, n=32, Mann-Whitney U test, z=2.17, P<0.03).

Third, parental care may influence the survival of young. If both parents attend the broods for longer in fish-ponds and biparental care improves brood survival, then broods would survive better in fish-ponds than in grasslands. Although broods were attended longer by both parents in fish-ponds (6.2 ± 8.1 day) than in grasslands (5.9 ± 5.9 day), the difference was not significant (Mann-Whitney U test, P>0.7; Székely & Lessells 1993).

Fourth, the reliability of resighting broods may be different between fish-ponds and grasslands. The fish-ponds were larger in area than the grasslands (Székely 1991) and their vegetation was taller (see below); thus chicks were more likely to be missed in fish-ponds than

Tab. 3. Growth of Kentish Plover broods in drained fish-ponds and alkaline grasslands, mean ± SD. Number of broods are given in brackets. Residual weight and tarsus length were calculated by taking the residuals from the regression of log size (body mass or tarsus length) on brood age. Probabilities of t-tests are given.

	Alkaline grasslands	Drained fish-ponds	P
Weight change (g day^{-1})	0.780 ± 0.352 (20)	0.940 ± 0.552 (6)	> 0.3
Residual weight	0.002 ± 0.011 (20)	-0.005 ± 0.012 (6)	> 0.2
Tarsus growth (mm day^{-1})	0.357 ± 0.164 (20)	0.295 ± 0.114 (6)	> 0.3
Residual tarsus length	0.000 ± 0.003 (20)	-0.001 ± 0.002 (6)	> 0.3

grasslands. This bias, however, would produce a difference in the opposite direction to that which we report here.

Growth rate of chicks, as measured by daily increase in body mass and tarsus length, did not differ between broods in grasslands and fish-ponds (Tab. 3). This was also true for the residual gain in body mass and tarsus length (Tab. 3).

4. Discussion

Kentish Plovers achieved higher brood survival in fish-ponds than in grasslands; nevertheless, we consider this result preliminary. We studied a small number of broods, particularly in fish-ponds, and these samples were distributed over seven sites and three years. Thus a few broods which survived particularly well may have distorted the distribution of brood survival in fish-ponds.

With this reservation in mind we suggest that fish-ponds could be better habitats than grasslands, because they may provide more hiding places for the young than grasslands. First, the vegetation was taller in fish-ponds than in grasslands (11.8 ± 5.2 cm versus 4.2 ± 3.2 cm, estimated around 18 and 51 nests, respectively (Mann-Whitney U test, $z=5.10$, $P<0.001$, Székely unpubl. data). Second, the bottom of drained fish-ponds were divided by deep crevices which were favourite hiding sites of Kentish Plover chicks. These crevices were scarce in grasslands.

The higher fledging success of Kentish Plover broods in fish-ponds contradicts the habitat mal-assessment hypothesis. Even if one takes into account that the daily survival of nests is higher in grasslands than in fish-ponds (0.947 versus 0.930, Székely 1992), this difference over the 26 days of incubation (0.243 versus 0.151) does not compensate for the difference in brood survival reported here over the 28 days of the fledging period (0.011 versus 0.655). Thus <1% and 10% of eggs are expected to produce fledged young in alkaline grasslands and fish-ponds, respectively. Such contrasts between nesting and brood rearing successes were also found in Curlews *Numenius arquata* in Sweden (Berg 1992). Curlew nests had higher risk of failures in tillage than in grassland, but once the chicks hatched they enjoyed higher survival in tillage than in grassland.

The implication of this study is, therefore, that one needs to investigate several aspects of the reproductive success before evaluating the importance of a habitat for reproduction. Thus we need to investigate not only the hatching success of nests and fledging success of young, but the recruitment rate of young, survival of parents, and ultimately the life-time reproductive success of parents in both habitats. This may be a difficult task, because Kentish Plovers often change breeding sites (Székely 1992).

In each year of this study there was a clear conflict of interests between fish-farms and conservation. The harvesting technique of fish-ponds requires the draining of some fish-pond units during the breeding season. 2-4 weeks after draining the units are ploughed and tilled, and may be refilled with water shortly afterwards. However, the bare ground of fish-ponds attracted shorebirds such as Avocets *Recurvirostra avosetta*, Lapwings

Vanellus vanellus, Little Ringed Plovers *Charadrius dubius* and Kentish Plovers for nesting. The interest of conservation is to protect these nests and thus to prevent or restrict the activity of fish-farms during the breeding season. A practical conclusion of this study is that fish-ponds may not be inferior habitat to the semi-natural grasslands. Thus conservation authorities should attempt to safeguard the nests on fish-ponds as well as the ones in grasslands. Perhaps fish-ponds managed chiefly for conservation purposes would be a significant development to resolve the conflict between conservation and economics over the use of drained fish-ponds.

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Összefoglalás

Széki lile *Charadrius alexandrinus* fiókák túlélése szikespusztai és lecsapolt halastavi élőhelyen

A dél-alföldi szikespusztákon és a lecsapolt halastavak medrében költő széki lilék fiókáinak túlélését és növekedését hasonlítottuk össze. Kilenc fiókás családot vizsgáltunk a halastavakon, míg 32 család sorsát követtük nyomon a szikespusztai élőhelyen 1988 és 1990 között. Kimutattuk, hogy a fiókák napi túlélése magasabb a halastómederben (0.985 ± 0.024 (átlag ± szórás)) mint a szikespusztán (0.851 ± 0.247). Ezen különbség nem magyarázható a fiókák életkorával, a fiókatúlélés szezonális változásával, sem pedig a fiókát kísérő szülők gondozásának változásával. Véleményünk szerint a fiókák nagyobb halastavi túlélését az okozza, hogy a halastó medre több búvóhelyet biztosít, mint a szikespuszták, pl. a fiókák jobban elrejtőzködhetnek a kiszáradt tómeder repedéseiben. Nem találtunk eltérést a halastavi és szikespusztai fiókák növekedésében.

A vizsgálatunk rámutat, hogy a madarak szaporodási sikerének becsléséhez nem elegendő a fészkek kelési sikerének megállapítása, hanem a reproduktív sikeresség további összetevőinek az ismerete is szükséges, pl. a fiókák felnövekvési esélyének és a szülők élettartamának a vizsgálata is. Ugyanakkor vizsgálatunknak vannak természetvédelmi vonzatai is, mivel felhívja a figyelmet arra, hogy a májusban és júniusban lecsapolt halastavak tómedrei az 1970-es évek elejétől egyre fontosabb fészkelőhelye számos ritka partimadárnak pl. gulipánnak, széki lilének és kis lilének. A lecsapolt tófenéken költő madarak szaporodási sikere nem ismert. Ezért a jövőben fokozott figyelemmel kell kísérnünk a lecsapolt halastavak fészkelő madarainak sorsát és lehetőséget kell keresnünk a halastavi fészkek hatékony védelmére. A célok elérésének egyedüli útja, ha a természetvédelmi hatóságoknál és a független természetvédő szervezeteknél dolgozó ornitológus szakemberek a kutatókkal és az amatőr ornitológusokkal együttműködnek.

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