NEST DEFENCE BY LAPWINGS: OBSERVATIONS ON NATURAL BEHAVIOUR AND AN EXPERIMENT

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Lapwings *Vanellus vanellus* are ground-nesting waders and they protect their nests by aggressively attacking predators near their nests. We investigated the response of parents to natural predators and a dummy Hooded Crow *Corvus [corone] cornix* during the incubation period. First, we investigated whether the presumed value of offspring influenced defence behaviour. We found no evidence that clutch volume or the number of days the clutch had been incubated for influenced either the frequency of attacks or the time spent on attacks. The density of nests decreased over the breeding season, and both the frequency of attacks and the time spent on attacks decreased with nest density. Second, we found that male Lapwings were more active in defence than females. In particular, male Lapwings attacked natural predators more often than females and they spent more time on attacks than females. These results were corroborated by the dummy experiment.

Key words: *Vanellus vanellus* - nest defence - antipredator behaviour - parental care

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INTRODUCTION

Most parent birds face the decision of how much time and energy they should invest in caring for and defending their offspring (reviewed by Montgomerie & Weatherhead 1988; Redondo 1989; Clutton-Brock 1991; Székely *et al.* 1996). By defending their nest or young the parents may increase the survival chance of their offspring (e.g. Greig-Smith 1980; Byrkjedal 1987). However, defence behaviour may be costly, because the parent risks of being injured by predators (e.g. Myers 1978; Brunton 1986; Sordahl 1990), or because defence takes time that can be used for other activities such as feeding or brooding the chicks (Walters 1982). The cost of defence may differ between the sexes; for example one parent may incur higher risk of being injured than the other or it may lose more with the time spent on defence than the other (Montgomerie & Weatherhead 1988).

Nest defence has often been studied in altricial birds (e.g. Regelmann & Curio 1983; Winkler 1992; Rytkönen *et al.* 1995; Dale *et al.* 1996). These birds commonly breed in nest-boxes where nest predation is not severe. However, in ground-nesting birds the nest is accessible to a large number of predators, therefore parental defence behaviour, i.e. chasing or luring predators away from the nest, is often vital for the survival of their nest (Gochfeld 1984).

We investigated a ground-nesting precocial wader, the Lapwing *Vanellus vanellus* (suborder Charadrii) in which both parents incubate the
clutch and defend the nest (Cramp & Simmons 1983; Liker & Székely 1997, 1999a). Lapwings are territorial and they have a variety of nest defence behaviour such as alarm calling and predator mobbing (Elliot 1985a, b; Blomqvist 1996). The objective of our study was to investigate two aspects of nest defence behaviour. First, we were interested in whether the parents defend valuable offspring more intensively than less valuable ones. In particular, we investigated whether Lapwings invested more in defence of clutches that contained large eggs or the ones that were closer to hatching (Andersson et al. 1980; Montgomerie & Weatherhead 1988). Since the survival prospects of Lapwing chicks decrease over the breeding season (Galbraith 1988; Thompson et al. 1994), we also investigated whether the parents defended more intensively the clutches laid early in the season than late ones. Second, we compared the defence behaviour between males and females. Male Lapwings tend to be larger than females (Cramp & Simmons 1983), and if size relates to the success of driving predators away from the nest, then males are expected to defend their nest more intensively than females (Montgomerie & Weatherhead 1988).

**METHODS**

We studied the Lapwings in Miklapuszta, an alkaline grassland of about 2000 ha in Central Hungary, near the villages of Harta and Akasztó (46°40'N, 19°10'E). The vegetation of the study site was dominated by halophytic plants such as Festuca pseudovina, Puccinellia limosa, Artemisia maritima, Lepidium cartilagineum and Camphorosma annua (Székely et al. 1994; Liker & Székely 1997). About 200-300 Lapwings bred annually in the area between 1992 and 1994 (A. Liker unpubl. data).

Fieldwork was carried out between 1992 and 1994. Laying dates were known for clutches found during laying. When a clutch was found during incubation, egg-laying date was estimated either by floating the eggs in water (A. Liker & G. Noszály unpubl. data, see also van Paassen et al. 1984), or by back-dating the laying date from the date of hatching and assuming 26 d as the length of incubation from clutch completion (length of incubation (mean ± SE): 26 ± 0.4 d, n = 37 clutches; A. Liker & G. Noszály unpubl. data). Length and breadth of eggs were measured to the nearest 0.1 mm. Egg volume was calculated as length × breadth² × 0.457 × 10⁻³ ml, where the volume coefficient (0.457) is given by Galbraith (1988). Clutch volume was the sum of the volume of all eggs in a clutch. The location of nests was recorded on a map. Density of nests (nests ha⁻¹) was calculated as the number of nests within a 200 m radius circle around the focal nest on the date of observation (see Elliot 1985a). Using radii of 150 m, 250 m and 300 m do not change our conclusions (results not shown). Date of observation was the number of days elapsed since 1 March.

We used two methods to identify individuals. First, 6 males and 24 females were trapped at their nests and banded with an individual combination of colour rings. Second, unringed birds were recognised by individual plumage characteristics, such as the pattern of their facial markings, the light markings and spots on their black breast stripe and the length of their crest (n = 27 males, n = 5 females). Plumage variability is often used for individual identification in the Lapwing (Blomqvist & Johansson 1994; Byrkjedal et al. 1997; Liker & Székely 1999). Behavioural data were also collected at nests where one or both parents were not individually recognised by either of these methods (n = 20 nests). Parents at these nests were unambiguously identified during the observations, e.g. they incubated or guarded their nests. Lapwings are highly territorial (Cramp & Simmons 1983; Liker & Székely 1997; Parish & Coulson 1998), so it is unlikely that we recorded any other bird at the nest but the parents. Behaviour was recorded only if the focal individuals remained in full view. Plumage of males and females are sufficiently dimorph to allow unambiguous identification of the sexes.

The nesting period, i.e. completion dates of
the first and the last clutches in each year, were 29 March and 10 June, 30 March and 6 June, and 14 March and 9 June in 1992, 1993 and 1994, respectively. Nest predators were common over the study period. In particular, Foxes Vulpes vulpes, stray dogs Canis domesticus and Hooded Crows Corvus [corone] cornix were all-year-round residents, whereas Marsh Harriers Circus aeruginosus and Montagu’s Harriers C. pygargus returned to the study site in March and stayed there until late summer.

**Defence behaviour against natural predators**

Defence behaviour against natural predators was observed during day-time between 05:00-21:00 h (Central European Time), from April to June between 1992 and 1994. We observed the Lapwings from a hide at least 100 m from the nest. We recorded the behaviour of both parents simultaneously at the focal nest every minute for one hour by instantaneous sampling. When a Lapwing spotted a potential nest predator it took off, flew towards the predator, circled over the predator and dived at it. We defined the attacks as the time from when the parent took off until it returned to its nest. The total number of attacks, as well as the species of predators attacked were also recorded during the behavioural observations. 46 Lapwing pairs were observed during 77 observations. All observations were collected by AL.

**Defence behaviour against a dummy crow**

We conducted an experiment on defence behaviour by presenting a taxidermy mounted Hooded Crow to nesting Lapwings. The experiment was carried out between 19 April and 10 June in 1994. We placed the dummy hidden in a box about 100 m from the nest. The dummy, fixed on a wooden sleigh, was pulled by a thin wire toward the nest through a pulley and it was stopped at about 20 m from the nest. The observer pulled the sleigh at an approximately constant speed from a hide that was about 140 m from the nest and 160 m from the initial position of the dummy.

Each trial was initiated three minutes after one of the parents started to incubate the clutch or returned to within 5 m of its nest. Behaviour of the parent was recorded from the beginning of a trial every 20 second for ten minutes. Behaviour was recorded as standing, walking, pecking at the ground (i.e. foraging), flying, circling above the dummy, diving at the dummy and incubating. The total number of dives by the focal parent was also recorded during each trial. At 31 nests, 10 males and 27 females were investigated. All observations were carried out by JK.

Hooded Crows are common nest predators of ground-nesting birds and Lapwings intensively attack them around their nests (Götmark et al. 1990; Blomqvist 1996). Hooded Crows were common on our study site (Table 1). We believe that Lapwings responded to the dummy as to a potential nest predator. Elliot (1985a) showed that a dummy Carrion Crow Corvus [c.] corone elicited more intensive response from Lapwings than a dummy Woodpigeon Columba palumbus. Also, other objects such as cardboard boxes are not attacked even at the vicinity of the nests (A. Liker pers. observ.). Finally, during one of our pilot trials two Hooded Crows joined the dummy. The

<table>
<thead>
<tr>
<th>Predators</th>
<th>Males</th>
<th>Females</th>
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<tbody>
<tr>
<td>Harriers¹</td>
<td>32 (47.1%)</td>
<td>11 (52.3%)</td>
</tr>
<tr>
<td>Falcons²</td>
<td>7 (10.3%)</td>
<td>0 (0.0%)</td>
</tr>
<tr>
<td>Corvids³</td>
<td>23 (33.8%)</td>
<td>9 (42.9%)</td>
</tr>
<tr>
<td>Others⁴</td>
<td>6 (8.8%)</td>
<td>1 (4.8%)</td>
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<tr>
<td>Total</td>
<td>68 (100%)</td>
<td>21 (100%)</td>
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¹Include attacks against Marsh Harrier (no. of attacks by male and female Lapwings, respectively: 20, 6) and Montagu's Harrier C. pygargus (12, 5); ²Kestrel Falco tinnunculus (2, 0) and Red-footed Falcon F. vespertinus (5, 0); ³Hooded Crow (16, 8), Rook C. frugilegus (3, 0) and Magpie Pica pica (4, 1); ⁴White Stork Ciconia ciconia (1, 1) and Black-headed Gull Larus ridibundus (5, 0).
defence behaviour of Lapwings appeared to be as intensive against solely the dummy as against the two alive crows plus the dummy.

Data processing

We used two variables each to describe defence behaviour. In the observational data set, we investigated the frequency of attacks (the total number of attacks h\(^{-1}\) against any predator) and the time spent on attacks (\%). The latter variable was the percentage of time a parent spent on attack out of total observation time. Similarly, in the dummy experiment we investigated the frequency of dives defined here as dives h\(^{-1}\) at the dummy and the \% of time spent on attacks. The latter variable was calculated as percentage of circling and diving records out of the total number of behavioural records during each trial.

The dummy was presented one to six times on different days at each nest (1.81 ± 0.2, mean ± SE). Knight and Temple (1986) argued that the number of presentations may influence the intensity of nest defence. We investigated this idea in two ways, but none of them supported the argument of Knight and Temple (1986). First, we found no evidence that the number of presentations at a nest was related either to the frequency of dives (Spearman rank correlations, males: \(r_s = 0.485, n = 10, n.s.\), females: \(r_s = 0.112, n = 27, n.s.\)) or to the time spent on attacks (males: \(r_s = 0.276, n = 10, n.s.\), females: \(r_s = 0.017, n = 27, n.s.\)). Second, the effect of the number of presentations may be confounded by incubation stage i.e. the number of days the clutch had been incubated, thus we also investigated the relationship between defence behaviour and the number of presentations by statistically controlling for incubation stage using partial rank correlation (Daniel 1990). Nevertheless, defence behaviour remained unrelated to the number of presentations (frequency of dives: males: \(r_s = 0.424, n = 7, n.s.\), females: \(r_s = -0.008, n = 24, n.s.\); time spent on attacks: males: \(r_s = 0.248, n = 7, n.s.\), females: \(r_s = -0.158, n = 24, n.s.\)).

Statistical analysis

Each parent was represented by one data point; if several observations were available for an individual we took their mean. We used non-parametric tests such as Spearman rank correlation (\(r_s\)) because the distribution of response variables violated the normality assumption of parametric tests. We investigated two inter-related variables to describe defence behaviour and three variables to describe the value of offspring. We followed Motulsky (1995) and did not correct the critical levels of significance, since we were not interested in the effects of single variables in isolation from the others. Statistical analyses were carried out using SPSS for the Macintosh 4.0. To facilitate the comparison of our results with other studies, we provide mean ± SE. Two-tailed probabilities are given.

RESULTS

Nest defence against natural predators

We observed 89 attacks against predators (Table 1). All attacks were aimed at avian predators. Frequency of attacks was not influenced either by clutch volume (males: \(r_s = -0.074, n = 44, n.s.\), females: \(r_s = 0.011, n = 46, n.s.\)) or incubation stage (males: \(r_s = 0.186, n = 43, n.s.\), females: \(r_s = -0.048, n = 45, n.s.\)). Furthermore, time spent on attacks was not related either to clutch volume (males: \(r_s = -0.108, n = 44, n.s.\), females: \(r_s = 0.096, n = 46, n.s.\)) or incubation stage (males: \(r_s = -0.001, n = 43, n.s.\), females: \(r_s = -0.072, n = 45, n.s.\)).

Both the frequency of attacks and the time spent on attacks increased over the season in males (frequency of attacks: \(r_s = 0.401, n = 44, P < 0.01\), time spent on attacks: \(r_s = 0.278, n = 44, P = 0.06, \) Fig. 1a). We also observed positive, albeit non-significant, relationships in females (frequency of attacks: \(r_s = 0.247, n = 46, n.s.\), time spent on attacks: \(r_s = 0.161, n = 46, n.s.\), Fig. 1b).

One reason for the seasonal variation in defence behaviour may be that the density of nests decreased over the season (\(r_s = -0.654, n = 34, \)
Fig. 1. Frequency of attacks (attacks h^{-1}) against natural predators in relation to the season (A) in male \( r_s = 0.401, n = 44, P < 0.01 \) and (B) in female Lapwings \( r_s = 0.247, n = 46, \text{n.s.} \). Season is given as the number of days since 1 March.

\( P < 0.001 \) and both the frequency of attacks (males: \( r_s = -0.683, n = 32, P < 0.001 \), females: \( r_s = -0.537, n = 34, P < 0.002 \)) and the time spent on attacks decreased with the density of nests (males: \( r_s = -0.511, n = 32, P < 0.004 \), females: \( r_s = -0.436, n = 34, P < 0.02 \)). To separate whether the significant increase in male defence behaviour was related to the date of the observation, or to density of nests \textit{per se}, we carried out partial correlation analyses. It turned out that the frequency of attacks by males remained highly correlated with the density of nests when the date of the observation was controlled for (partial correlation, \( r_s = -0.597, n = 29, P < 0.001 \)), whereas the frequency of attacks was no longer related to the date of the observation when the density of nests was controlled for (partial correlation, \( r_s = -0.058, n = 29, \text{n.s.} \)).

Fig. 2 (A) Frequency of attacks (attacks h^{-1}) and (B) percentage of time spent on defence by male and female Lapwings against natural predators. Wilcoxon matched-pairs sign-ranks tests between males and females, frequency of attacks: \( z = 3.920, n = 44, P < 0.001 \); \% of time spent on attacks: \( z = 2.845, n = 44, P < 0.005 \). The lines are the medians, boxes represent 10 and 90 percentiles, the whiskers show the range without outliers and extremes, and the dots are the outliers. One outlier (a male, see Results) is not shown. Note that medians and 10 percentiles are equal to zero.

Fig. 3. (A) Frequency of dives (dives h^{-1}) and (B) percentage of time spent on defence by male and female Lapwings against a dummy Hooded Crow. Mann-Whitney U-tests, frequency of dives: \( z = 2.15, P < 0.04 \), \% of time spent on attacks: \( z = 2.54, P < 0.02, n = 10 \) males and 27 females. The lines are the medians, boxes show 10 and 90 percentiles, the whiskers show the range without outliers and extremes.

Males attacked predators more frequently than females (males: 0.99 ± 0.3 attacks h^{-1}, females: 0.28 ± 0.1 attacks h^{-1}) and they spent more time
attacks as well (males: 1.12 ± 0.6 % of time, females: 0.37 ± 0.2 % of time, Table 1, Fig. 2). One male, whose nest was taken by a Marsh Harrier during a behavioural sample, spent 26.42 % of his time on attacking the intruder. After excluding this nest from the analysis, the difference between the sexes remained significant (Wilcoxon matched-pairs sign-rank test, z = 2.701, \( P < 0.01 \), \( n = 43 \)).

Attack behaviour of parents was related to the behaviour of their mates: both the frequency of attacks (\( r_s = 0.602, n = 44, P < 0.001 \)) and the time spent on attacks were highly correlated within pairs (\( r_s = 0.737, n = 44, P < 0.001 \)).

**Experiment with the dummy crow**

The frequency of dives against the dummy Hooded Crow was not influenced either by clutch volume (males: \( r_s = -0.334, n = 10, \text{n.s.} \), females: \( r_s = -0.201, n = 27, \text{n.s.} \)), or incubation stage (males: \( r_s = 0.298, n = 10, \text{n.s.} \), females: \( r_s = 0.067, n = 27, \text{n.s.} \)). Also, the time spent on attacks was unrelated to clutch volume (males: \( r_s = -0.370, n = 10, \text{n.s.} \), females: \( r_s = -0.246, n = 27, \text{n.s.} \)) or incubation stage (males: \( r_s = 0.418, n = 10, \text{n.s.} \), females: \( r_s = 0.226, n = 27, \text{n.s.} \)). The frequency of dives tended to increase, albeit non-significantly, over the season in males (\( r_s = 0.488, n = 10, \text{n.s.} \)) and in females (\( r_s = 0.250, n = 27, \text{n.s.} \)), whereas the time spent on attacks increased over the season (males: \( r_s = 0.442, n = 27, P < 0.025 \); females: \( r_s = 0.590, n = 10, P = 0.07 \)). Males responded more vigorously to the dummy crow than females (Fig. 3). Males dived more frequently at the dummy than females (males: 54.2 ± 19.3 dives h⁻¹, females: 23.77 ± 9.3 dives h⁻¹) and they also spent more time on attacking (males: 43.98 ± 9.0 % of time, females: 17.56 ± 4.7 % of time). Neither the frequency of dives (\( r_s = 0.580, n = 6, \text{n.s.} \)), nor time spent on attacks (\( r_s = 0.029, n = 6, \text{n.s.} \)) were related between males and females of a pair.

**DISCUSSION**

The observations on the natural behaviour and the experiment provided consistent results on the nest defence behaviour of Lapwings. First, they showed that the value of offspring (measured either by clutch volume or incubation stage) was unrelated to the intensity of defence behaviour. Second, the intensity of defence behaviour increased over the season, although this increase was significant only in males (observations) or in females (experiment). Third, males defended the nest more intensively than females. Although some of these results might be confounded by the temporal variation in predator density and their persistence to attacks by Lapwings, we think that this is unlikely, since nest predators (harriers, crows and foxes) were common throughout the study period.

Lapwings showed an intensive defence behaviour against both natural predators and the dummy Hooded Crow. In line with several other studies (Breitwisch 1988, Rytkönen et al. 1995), defence behaviour of Lapwings was unrelated to clutch size. This supports the argument of Lazarus and Inglis (1986) that parents are unlikely to take brood size into account when the number of offspring taken by the predator is independent of brood size. We found no evidence that defence behaviour was related to the age of the offspring, although other studies in birds have found that the intensity of nest defence increased with the age of the young (e.g. Regelmann & Curio 1983; Sjöberg 1994). We offer two explanations why the defence behaviour of Lapwings was unrelated to the incubation stage. First, the intensity of defence may relate to the vulnerability of offspring e.g. conspicuousness, rather than age *per se* (Gochfeld 1984; Brunton 1990; Dale et al. 1996). Since conspicuousness of eggs does not change during incubation, this hypothesis predicts constant intensity of nest defence during incubation. It is also unlikely that the conspicuousness of nests has changed during incubation, since the height of vegetation was kept approximately at the same level by grazing sheep. Furthermore, if conspicuousness of clutches had been changed because of vegetation growth, nest defence intensity would have been decreased instead of being increased. Second, we suggest that in order to increase the level of defence, parents need an obvious cue of
the age of their offspring. If such cues are not present, then parents may not be able to identify the age (and hence, the presumed reproductive value) of their offspring. Thus, when chicks start to peep in the eggs near hatching then parent Lapwings may increase the intensity of their defence behaviour as it was documented in Killdeer Charadrius vociferous (Brunton 1990).

Male Lapwings increased the amount of time they spent on attacking predators over the breeding season. However, this result is the opposite what would be expected if the early broods are more valuable than late ones (Galbraith 1988; Thompson et al. 1994; but see Klomp & Speek 1971). It is unlikely that the seasonal increase in defence behaviour is due to increased abundance of nest predators over the season. First, the most common predators were present throughout the breeding season in our study site. Second, seasonal increase in nest defence became statistically non-significant when nest density was statistically controlled for. Thus we showed that the seasonal variation in male defence behaviour was related to nest density and not to the date of the season per se. Elliot (1985a) also found that the number of participants in nest defence increased with the number of active nests in a breeding group. We suggest that breeding density may influence defence behaviour at least in two ways. First, parents breeding at high densities may benefit from the defence behaviour performed by their neighbours. Thus the parents at high densities may be able to spend less time on defending than solitary breeders. Second, predators may learn to avoid sites where the breeding density is high, since they are regularly confronted with attacking Lapwings (Elliot 1985b).

We found that male Lapwings defended their nest more intensively than females. This result is consistent with an other study of Lapwings in Hungary (Hegyi & Sasvári 1998; but see Elliot 1985a). We suggest that either the costs of defence behaviour or the benefits may differ between the sexes. Male Lapwings have broader and more rounded wings than females, showing remarkable manoeuvring abilities in flight (Glutz von Blotzheim 1975; Cramp & Simmons 1983; Grønstøl 1996). In passerine birds, species with rounded wingtips seem to be exposed to lower predation risk than species with more pointed wingtips, suggesting that broader wings enhance manoeuvrability (Swaddle & Lockwood 1998). If so, increased manoeuvrability and therefore the lower risk of injury may select for nest defence predominantly by the male. Also, manoeuvrability should influence the success of defence behaviour. Thus, male Lapwings may be more efficient in protecting their young from predators than females. Furthermore, defence behaviour may signal the parental capabilities of males, and therefore influences mate choice by females (Andersson 1994). Acrobatic dives on predators are remarkably similar to the aerial display behaviour of male Lapwings (song-flight). It has been shown that the angle of alternating flight (a component of the song-flight) and the rate of song-flight are significant predictors of male mating success in the Lapwing (Grønstøl 1996; Liker & Székely 1999). Therefore, females may pay attention to the attack rate of males and decide whether to keep their current mate for future breeding attempts or divorce. Future studies should separate these explanations, for instance by manipulating the wing morphology of males and females and comparing the defence behaviour of sexes.

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**SAMENVATTING**

Kieviten *Vanellus vanellus* broeden op de grond en hebben een open en kwetsbaar nest. Ze verdedigen dit nest door naderende predatoren tegemoet te treden met agressief ogende duikvluchten. In deze studie van op de Hongaarse poesta broedende Kieviten wordt in detail de nestverdediging door beide ouders tegen natuurlijke predatoren zoals kiekendieven, valken en kraaiachtigen beschreven. Tevens worden de resultaten gegeven van een experiment waarbij een opgezette Bonte Kraai *Corvus [corone] cornix* naar nesten werd getrokken en tegelijk het aanvalsgedrag werd geregistreerd. De auteurs toetsen de veronderstelling dat naarmate de verwachte waarde van het legsel toeneemt (omdat het bestaat uit grote eieren of omdat het al langere tijd bebroed is geweest), het nest waarin dit legsel zich bevindt, ook sterker verdedigd wordt. De resultaten zijn negatief, want het totale volume van het legsel, noch het aantal dagen dat het legsel bebroed werd, hingen samen met de aanvalsfrequentie of de tijd die Kieviten aan die aanvallen besteedden. De dichtheid aan nesten werd in de loop van het seizoen steeds kleiner, en parallel daarmee nam de aanvalsfrequentie af. Mannetjes Kieviten waren actiever bij de nestverdediging dan vrouwtjes, zowel tegen natuurlijke predatoren als tijdens het aanvallen van een opgezette Bonte Kraai. De relatief grote bijdrage van mannetjes bij de nestverdediging hangt misschien samen met het gegeven dat hun vleugels breder zijn dan die van vrouwtjes en hun wendbaarheid groter is dan bij vrouwtjes. (TP)

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