Aggression among female lapwings, Vanellus vanellus

ANDRÁS LIKER & TAMÁS SZÉKELY
Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, Kossuth University, Debrecen, Hungary

(Received 17 April 1996; initial acceptance 13 July 1996; final acceptance 1 November 1996; MS. number: 5229)

Abstract. Social monogamy is the most common pair bond in birds and one hypothesis for its prevalence is that already mated females (‘residents’) prevent other females from establishing a pair bond with their mates (‘competition for male parental care’ hypothesis). To investigate this hypothesis we experimentally induced aggressive behaviour in resident female lapwings by presenting a female dummy conspecific, and a male dummy as control, near their nests. Females attacked both dummies. However, the female dummy was attacked more often than the male during the 5-min trials. Attacks on the female dummy were mostly on the ground (88%, N = 27 resident females) whereas the male dummy was attacked either by aerial dives (53%) or on the ground (47%, N = 24 resident females). Frequency of attacks on the female dummy decreased over the incubation period, whereas there was no such trend with the male dummy. These results suggest that female lapwings attempt to prevent their mates from attracting a new mate and thus try to monopolize their parental care. Other competing hypotheses for the explanation of aggressive behaviour in female lapwings are also discussed but were not supported by our data.

© 1997 The Association for the Study of Animal Behaviour

Sexual competition among males has been recognized as an important driving force behind mating patterns and parental care (reviews: Davies 1991; Harvey & Bradbury 1991; Andersson 1994; Möller 1994; Reynolds & Harvey 1994; Andersson & Iwasa 1996). Sexual competition among females has received much less attention, although recent studies suggest that it may be widespread in birds. Female–female competition may affect several aspects of mating systems and parental care (reviews: Berglund et al. 1993; Slagsvold & Lifjeld 1994). For example, aggression among females may maintain monogamy (Hannon 1984; Veiga 1992; Slagsvold 1993), reduce harem size (Hurly & Robertson 1985) and force males into defending multiple territories (Slagsvold et al. 1992; but see K lớnimaa et al. 1995).

Females may gain different sorts of benefits by being aggressive. First, already mated females (‘residents’) may prevent their mates from courting and attracting a new female to their territory. If this behaviour is successful, then resident females may monopolize the parental care of their mates (‘competition for male parental care’ hypothesis). This hypothesis appears to explain female aggression in several monogamous and polygamous birds (Yasukawa & Searcy 1982; Davies 1992; Slagsvold et al. 1992; Slagsvold 1993). Second, a breeding female may behave aggressively to prevent other females from using resources such as food on the territory (Berglund et al. 1993). Third, a resident female may use aggression to defend her nest against other females that attempt to destroy her nest or dump their eggs into it (Dunn & Hannon 1991; Davies 1992; Bensch & Hasselquist 1994).

We investigated one of these hypotheses, the ‘competition for male parental care’, in a precocial bird, the lapwing. Although most previous studies have focused on altricial birds (e.g. Sandell & Smith 1996; review: Slagsvold & Lifjeld 1994), we believe that investigating precocial birds is particularly important. It is often assumed that parental care in precocial birds is less demanding than in altricial ones and either parent may be freed from parental duties (Siller-Tullberg & Temrin

Correspondence and present address: A. Liker, Zoology Centre, University of Veterinary Science, P.O. Box 2, H-1400 Budapest, Hungary (email: aliker@ns.univet.hu). T. Székely is now at the School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, U.K.

0003–3472/97/100797+06 $25.00/0/ar960491

© 1997 The Association for the Study of Animal Behaviour
1994; Székely & Reynolds 1995). Thus the significance of competition for male parental care is less obvious in precocial birds than in altricial ones.

The competition for male parental care hypothesis predicts that (1) resident females should be more aggressive towards a female conspecific than towards a male. (2) A resident female may be at most risk of losing her mate's help if a new female begins incubation shortly after the resident (Slagsvold & Lifjeld 1994). Thus resident females should be most aggressive at the beginning of incubation and the frequency of aggressive interactions with female intruders should decrease over the incubation period. Such a trend is not predicted in aggressive behaviour with male intruders (Slagsvold & Lifjeld 1994). We investigated these predictions by presenting a female dummy, and a male dummy as a control, to resident females. We also investigated whether female body size, clutch size and timing of trials over the breeding season were related to the aggressive behaviour of resident female lapwings.

Lapwings are ground-nesting shorebirds. They are particularly suitable for such a study, because their breeding system includes both monogamy and simultaneous polygyny (Cramp & Simmons 1983; Berg 1993; Matyjasaki 1994). Both parents incubate the clutch and the male parent often cares for the chicks (Cramp & Simmons 1983; Blomqvist & Johansson 1994).

**METHODS**

We studied lapwings in Miklapuszta, Central Hungary (46°40'N, 19°10'E), between 29 April and 16 June 1994 and between 11 and 14 May 1995. The study area was an alkaline grassland of about 2000 ha (see Székely et al. 1994 for a description of the study site) where 200-300 lapwings bred in both years.

We used taxidermic mounts of a female and a male lapwing to mimic the presence of an intruder in the resident female's territory during her incubation. The dummies were mounted in a neutral standing posture. Either of the two dummies was placed on the open ground 10 m from the nest of the resident female. The dummy faced the nest and was clearly visible to the female when she returned to it. We recorded the behaviour of the resident female from a hide or a car approximately 100-300 m away. We started to record the behaviour of the female when she approached the dummy to within 30 m, and then noted her behaviour for 5 min. We recorded the number of attacks she performed against the dummy. Three types of aggressive behaviour were distinguished and their frequencies were recorded separately. First, a quick aggressive dash towards the dummy was characterized by a retracted neck, fluffed breast feathers and erected crest. Females often approached the dummy to within 1 m during these dashes. At the dummy they performed crouching and various other displays such as high-upright posture, rocking display, scraping and side-throwing (see terminology in Cramp & Simmons 1983). Second, during ground attacks the female contacted the dummy by either pecking, hitting it with her wing or kicking it. Third, females dived at the dummy from the air during which they sometimes hit it with their wings. We followed the same experimental procedure for the male dummy as for the female one. There was a 1-day interval between the presentation of these two dummies, and we randomized whether the male or the female dummy was presented first. We presented the female dummy to 27 resident females and the male to 24 resident females but four nests and one nest, respectively, were predated before the other dummy could be presented; thus we presented both models to 23 females.

Resident females were either colour ringed (N = 8) or were identified by their nests. All nests were incubated by only one female (A. Liker & T. Székely, unpublished data). The plumage of males and females was sufficiently dimorphic to allow unambiguous identification of the sexes. We captured females on their nests by a funnel trap, banded them with a metal ring and a unique combination of colour rings, weighed them to the nearest 1.0 g, and measured their tarsus length and crest length to the nearest 0.1 mm and 1.0 mm, respectively. Crest length was measured as the length of the longest crest feather from its base to the tip. We estimated body condition by regressing the body mass of females on to the number of days since the beginning of incubation and taking the residuals from this regression equation. The start of incubation was known for clutches found during egg laying; for incubated clutches we estimated it either by floating the eggs in water or back-dating it from the date of hatching (A. Liker & G. Noszály, unpublished data). Length and breadth of the eggs were measured to
the nearest 0.1 mm, and egg volumes were calculated as \( V = K_V \times L \times B^2 \), where \( V \) is the volume, \( L \) and \( B \) are the length and breadth of the egg, and \( K_V = 0.457 \) is the volume constant (Galbraith 1988). We recorded clutch size in each trial and calculated clutch volume by multiplying clutch size by the average egg volume. Timing of trials is given as number of days from 1 March.

Each female was represented by one data point in the analyses; thus \( N \) refers to the number of resident females. We used non-parametric tests because the distribution of attack behaviour strongly deviated from normal, and our sample size was too small to disregard this deviation (Motulsky 1995). Post hoc hypotheses of multiple comparisons may inflate the true level of significance (‘family-wise error’, Zolman 1993). To control for this source of error we identify \( \alpha(c = 3) = 0.017 \) as a critical level of significance for three pair-wise relations between attack behaviour, female body condition, tarsus length and crest length. Mean \( \rho \) coefficients of Spearman’s rank correlation \( (r_S) \) and two-tailed probabilities are given. Statistical analyses were carried out by SPSS 4.0 for the Macintosh.

## RESULTS

Resident females responded to both dummies as they do to real conspecifics. They displayed all three types of aggressive behaviour towards them such as aggressive dash, ground attack and aerial dive (Table I). The most common aggressive behaviour towards the female dummy was attack on the ground (78%; 163 attacks, \( N = 27 \)), whereas the male dummy was either attacked by aerial dives (53%) or by ground attacks (37%; 43 attacks, \( N = 24 \)). The frequency of attacks on the female and the male dummies was highly correlated \( (r_S = 0.712, N = 23, P < 0.0001) \).

Resident females attacked the female dummy more often than the male one (Fig. 1). The frequency of attacks on the female dummy decreased over the incubation period (Fig. 2), whereas the frequency of attacks on the male dummy was unrelated to incubation period \( (r_S = -0.038, N = 24, NS) \).

The frequency of attacks was not different for females with different clutch sizes (Kruskal–Wallis tests: female dummy: \( H = 0.141, NS \); male dummy: \( H = 3.698, NS \)), and it was unrelated to the volume of their clutches (female dummy: \( r_S = 0.073, N = 18, NS \); male dummy: \( r_S = 0.319, N = 15, NS \)). The frequency of attacks was unrelated to the timing of the trials over the breeding season (female dummy: \( r_S = -0.026, N = 27, NS \); male dummy: \( r_S = -0.037, N = 24, NS \)). Finally, we found no significant relation between frequency of attacks and the condition of the female, her tarsus length and crest length (Table II).

## DISCUSSION

### Female–Female Competition

Our results support both predictions of the competition for male parental care hypothesis.
First, resident females were more aggressive towards the female dummy than the male one. Second, the frequency of aggression towards the female dummy decreased over the incubation period, whereas we found no such trend with the male dummy. Thus female lapwings attempt to prevent or delay other females from laying their eggs on the territory of their mates. This behaviour is significant, because if the resident female is successful then her brood will receive the full care of her mate. Thus she may be able to desert her offspring before or after her eggs hatch, and may leave her brood to the care of her mate (Blomqvist & Johansson 1994; A. Liker & T. Székely, unpublished data).

Aggression by a resident female may be particularly successful, if she can interrupt the courtship between her mate and a new female. We observed three resident females that attacked the potential new mate of their males. The attacks took place 20–40 m from the nests of resident females and they were timed when their mate courted new females. This behaviour may sometimes be successful, because one out of these three males failed to get the new mate (A. Liker & T. Székely, unpublished data). Clearly, many females do not succeed in preventing their males from re-mating, since in one year 30% of males became bigamous in our population (A. Liker & T. Székely, unpublished data). The frequency of polygyny appears to be higher in other populations of lapwings: 50% in Sweden (Berg 1993) and 40% in Poland (Matyjasiak 1994). We predict that in these latter populations the females may be less aggressive towards each other or their attacks may be less successful than in Hungary.

Although our study was not specifically designed to exclude alternative explanations for the aggressive behaviour of resident females, we argue that they are unlikely. First, females may be aggressive to defend resources, such as food, on their territory. This hypothesis predicts that females should attack males and females indiscriminately and the frequency of their aggressive behaviour should remain constant over the incubation period. However, neither of these predictions was supported by our study. Furthermore, female lapwings spend much of their time foraging on communal feeding areas outside their territories in our study site; thus the food on their territories may constitute an insignificant part of their diet.

Third, a female may be aggressive towards other females to prevent them from dumping an
egg in her nest. However, egg dumping has not been reported in lapwings. Lapwings lay clutches of four eggs, and clutches of five (or more) eggs are very rare; in our population two out of 335 clutches contained five eggs (A. Liker & T. Székely, unpublished data).

### Signalling Fighting Ability

We found high correlations between frequency of attacks on the dummies and crest length of resident females (Table II). Although neither of these relations was statistically significant, perhaps because of small sample sizes, we argue that they may be biologically important. Previous studies of signalling fighting ability have investigated the role of plumage characters in establishing a dominance hierarchy (Butcher & Rohwer 1989; Savalli 1995). We propose that crest length may be important to indicate the ability of a female lapwing to attack. Lapwings are territorial and both sexes spend a considerable proportion of their time on territorial displays and fighting. Thus it may be beneficial for females to have an ‘honest’ indicator of their ability to fight.

In conclusion, our experiment shows that resident females behave differently towards male and female intruders. The results are most consistent with the competition for male parental care hypothesis, that is, resident females try to gain full parental contribution from their mates. Although these results are suggestive we need further evidence on the reproductive advantage of this behaviour. Comparisons with other lapwing populations on the frequency and success of female aggressive behaviour would be valuable.

### ACKNOWLEDGMENTS

We thank G. Noszály, J. K is, S. Kovács and M. Castro for their help in the field, and A. I. Houston and two anonymous referees for their comments on the manuscript. Állampuszta State Farm gave logistic help to the field study. Permission for the field work was provided by the Kiskunság National Park. The study is part of the Ph.D. fellowship of A.L. and it was funded by an OTKA grant to T.S. (No. T 5492).

### REFERENCES


