

Mating pattern and mate choice in the Lapwing *Vanellus vanellus*

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We investigated the mating behaviour of Lapwings in a Hungarian grassland between 1992 and 1994. 80% of males were monogamous and 20% were polygynous (n=59 males). Polygynous males acquired two females (primary, secondary) that laid one clutch each on the males' territory. Monogamous males, that became polygynous later, spent more time on song-flight (7.5 ± 1.6 (s.e.)%) than the ones which remained monogamous (1.6 ± 0.7 %). Polygynous males tended to have more successful nests on their territories (1.0 ± 0.3) than monogamous males (0.5 ± 0.1). All females out of 104 had one social mate in a breeding season, except one female mated to two males (sequential polyandry). Secondary females laid their nests 8.4 ± 1.2 days after the primary females completed their nests and at that time several males were still unmated. We found no indication that secondary females were 'inferior' to monogamous and primary females, because body condition, clutch volume and nest survival were not different among monogamous, primary and secondary females. Our results suggest that polygyny was not forced on females by the lack of unmated territorial males; rather secondary females preferred already mated males to unmated ones.

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1. Introduction

Shorebirds (infraorder Charadriides) are ideal subjects to investigate questions about avian breeding systems, since they have an extraordinary variety of mating patterns including monogamy, polygyny and polyandry (Pitelka *et al.* 1974, Erckmann 1983). The Lapwing *Vanellus vanellus* is one of the most common shorebirds in Europe and until recently it has been considered a typically monogamous species (Cramp & Simmons 1983). Recent studies on individually marked birds

showed, however, that the Lapwings' mating behaviour is more flexible than it was previously thought. For example, it turned out that social polygyny is common in many populations and 30-50% of males are mated to several females simultaneously (Berg 1993, Byrkjedal *et al.* 1997, Parish *et al.* 1997). Some of the polygynous males are polyterritorial and they defend separate territories for each of their mates (Byrkjedal *et al.* 1997, Parish *et al.* 1997). In addition, female Lapwings appeared to mate with a single male in a breeding season, although recently both double-clutching and sequential polyandry

have been reported (Blomqvist & Johansson 1994, Parish *et al.* 1997). Studies also suggest that variation in male reproductive success may be explained by female choice (Berg 1993, Grønstedt 1996, Byrkjedal *et al.* 1997, Parish *et al.* 1997), although female preference for particular males may be counteracted by the aggressive interactions among females (Liker & Székely 1997a).

In this study we investigate three aspects of mating behaviour in Lapwings. First, we investigate their mating patterns in a Hungarian alkaline grassland ('puszta'). Although several studies have been published on the mating patterns of Lapwings (Berg 1993, Byrkjedal *et al.* 1997, Parish *et al.* 1997), these studies were carried out in Northern and Western Europe where the Lapwings often breed in arable land or cultivated grassland. Second, we investigate the reproductive success of males and females in various pair-bonds. In particular, we compare the reproductive success of polygynous and monogamous males, since a previous study by Grønstedt (1996) suggested that more eggs hatch on the territories of polygynous males than on the territory of monogamous ones. We also compare the nest survival of monogamous and polygynous females. Finally, we investigate why do some females mate with an already mated male. Previous studies suggested that neither the lack of unmated males (Byrkjedal *et al.* 1997, Parish *et al.* 1997) nor the random settlement of females provide a sufficient explanation for the polygyny in the Lapwing (Byrkjedal *et al.* 1997). Thus some females seem to prefer already mated males over unmated males. This preference may relate to the quality of males' displays (song-flights), the age

of the males, their territory size, or to the abundance of food on their territory (Berg 1993, Grønstedt 1996, Byrkjedal *et al.* 1997, Parish *et al.* 1997). However, the relative importance of the males' characteristics (or that of their territories) has remained controversial (Byrkjedal *et al.* 1997). In this paper we examine several potential mate choice cues such as the conspicuous song-flight display of males, a possible honest indicator of male quality (Andersson 1994), and the attributes of their territories such as size and abundance of food. We studied mating pattern and reproductive success between 1992 and 1994, whereas mate choice was investigated in 1994. The latter study involved a subset of closely monitored males.

2. Study area and methods

2.1. Study site

We studied the Lapwings in Miklapusztá, Central Hungary (46° 40' N, 19° 10' E) between 1992 and 1994. Miklapusztá (2000 ha) consists of alkaline grasslands, temporary and permanent wetlands and plateaus formed of loess, where 200-300 Lapwings bred during the study. We investigated an area of approximately 700 ha each year. Halophytic plants such as *Festuca pseudovina*, *Puccinellia limosa*, *Artemisia maritima*, *Lepidium cartilagineum* and *Camphorosma annua* grew in patches of the alkaline grassland (Székely *et al.* 1994). The loess plateaus were 0.5-4 m high and they rose steeply from the surrounding flat alkaline grassland. These plateaus were covered by *Muscari racemosum*, *Verbascum phoeniceum*, *Filipendula vulgaris* and

Orchis morio. Lapwings bred mainly on the flat alkaline grassland, although they often fed on the plateaus. In March 1994 we estimated the densities of earthworms in some loess plateaus and flat alkaline grasslands by using the formalin method (Raw 1959). The abundance of earthworms was about 90 times higher on the loess plateaus (8.9 ± 2.5 (s.e.) earthworms $\times 0.5 \text{ m}^{-2}$, $n=14$ samples) than on the flat alkaline grassland (0.1 ± 0.1 earthworms $\times 0.5 \text{ m}^{-2}$, $n=23$ samples; Mann-Whitney U test, $z=5.217$, $P<0.0001$).

2.2. Field work

Field work was carried out between the first week of April and the last week of June except in 1994, when it was started in the second week of March. Laying dates were known for clutches found during egg-laying. For clutches found during incubation, the egg-laying dates were estimated by floating the eggs in water (A. Liker unpublished data, see also van Paassen *et al.* 1984) or by calculating them from the date of hatching by assuming 26 days of incubation (A. Liker & G. Noszály, unpublished data). Laying dates refer to the laying of the last egg in a clutch which coincides with the start of incubation (Cramp & Simmons 1983). In each clutch we measured breadth and length of eggs to the nearest 0.1 mm and estimated egg volumes by using 0.457 as the volume constant (see Galbraith 1988). Clutch volumes were estimated for each clutch by multiplying mean egg volumes by clutch size. Nests were visited every second or fourth days. Successful nests (i. e. those that hatched at least one chick) were identified by the presence of chicks or by the occurrence of eggshell frag-

ments in the nest lining. Location of each nest was recorded on a map of 1:10 000 scale.

2.3. Identification of adults and determination of mating patterns

We used two methods to identify Lapwings. First, adults were captured on their nest by a funnel trap and they were ringed with a metal ring and an unique combination of colour rings ($n=9$ males and 92 females). Captured adults were also weighed to the nearest 1.0 g and their tarsus length were measured to the nearest 0.1 mm. Second, we used individual plumage characteristics to recognise adults within a breeding season ($n=50$ males and 12 females). We made a drawing chart for each individual by sketching facial markings, white markings on their black breast stripe and length of their crest. Plumage variation among individuals has often been used to identify Lapwings (e.g. Berg 1993, Blomqvist & Johansson 1994, Byrkjedal *et al.* 1997, Parish *et al.* 1997). Our charts were reliable to identify individuals within a breeding season as evidenced by three colour ringed males which we repeatedly identified solely by using their chart. Pair-bonds were determined during nest checks and behavioural observations (see Liker & Székely 1999). One female bred on the territory of each monogamous male. Polygynous males had simultaneous pair-bonds with two females on their territories. Female that laid the first clutch on the territory of a polygynous male was termed primary female, whereas female that laid her clutch second was termed secondary female. This notation does not imply any dominance relation between females.

2.4. Observations of male behaviour and territory size

We observed the behaviour of 17 males between 15 March and 30 March in 1994. The observations were carried out between 06:00-10:00 and 15:00-18:00 from a hide or a car about 100 m away. Three observations of 60 minutes each were collected from each male with 5.3 ± 0.3 (s.e.) days between successive observations. For each male the day of observation was randomly chosen and we also randomised the observations among males in a day. Behaviour of males, such as song-flight and ground-display, was recorded at every minute by instantaneous sampling. The ground-display included rocking-display, scraping-ceremony and mating-ceremony (see Cramp & Simmons 1983 for definitions). We recorded the position of the male on a map of 1: 6 500 scale at every five minutes when the male was on the ground. All observations were carried out by A. L.

2.5. Data processing and statistical testing

Each clutch or individual was used once in each analysis. Some males were polygynous in one breeding attempt although they bred monogamously in other breeding attempt(s) e.g. initiated a new nest after the failure of their first nest or bred in a different year. We include these males as polygynous in the analyses. Daily probabilities of nest survival were estimated by the Mayfield method (1975), and their standard errors and tests were calculated by following Hensler & Nichols (1981). Display behaviour of males was analysed as percentages of total observation time

during which the focal male was in view. Territory size was estimated by drawing a maximum convex polygon around the position of males during each 60 minute observation period. We took the mean area of these three polygons. We also mapped the loess plateaus onto the territory maps, and the size of loess plateaus within each territory was estimated from these maps. Date of egg-laying was the number of days since 1st March. Body condition of incubating females was estimated as residuals of body mass regressed on tarsus length i.e. $BODY\ MASS\ (\ln(g)) = 2.855 + 0.650 \times TARSUS\ LENGTH\ (\ln(mm))$ ($r^2 = 0.149$, $P < 0.001$, $n = 91$ females). The number of days incubated at the time of weighing were not different between monogamous (14.5 ± 0.8 (s.e.) days, $n = 23$), primary (20.3 ± 2.4 days, $n = 6$) and secondary females (15.1 ± 2.3 days, $n = 6$; Kruskal-Wallis test, $\chi^2 = 4.695$, d.f. = 2, $P > 0.05$). As we had few cases of polygyny we pooled the data from all three years. Non-parametric tests were used such as Spearman rank correlations (r_s) since the normality or the homoscedasticity assumptions of parametric tests were often violated. Partial correlations were performed on ranked data as suggested by Daniel (1990). In multiple independent comparisons the critical level of significance was corrected as suggested by Motulsky (1995). Statistical analyses were carried out by SPSS 4.0 for the Macintosh. Mean \pm s.e. and two-tailed probabilities are given.

Tab. 1. Mating pattern of male Lapwings in 1992-1994. Each male was included once in each year and once in the 'all years' category. One male had a monogamous pair-bond and a polygynous pair-bond in two breeding attempts in 1994; his polygynous pair-bond is included.

Year	Mating pattern of males	
	Monogamous (%)	Polygynous (%)
1992	4 (100.0)	0 (0)
1993	23 (92.0)	2 (8.0)
1994	23 (69.7)	10 (30.3)
All years	47 (79.7)	12 (20.3)

3. Results

3.1. Mating patterns

3.1.1. Males

80 nests were laid on the territories of 59 males. 56 nests were laid on the territories of monogamous males ($n=49$ males), and 24 nests were laid on the territories of polygynous males ($n=12$ males; two males had both a monogamous and a polygynous pair-bond, see below). Thus 20.3% of the 59 males were polygynous at least in one breeding attempt (Tab. 1). Six males out of 59 were involved in more than one breeding attempt. The mating pattern of two individually marked males changed within or between years. One male (H97) was monogamous in 1992, but he had both a polygynous and a monogamous pair-bond

in 1994. The other male (H214) was polygynous in 1993 and monogamous in 1994. Both of these males changed their mates between years, but we do not know whether H97 changed his mate between successive nesting attempts in 1994. On the other hand, four males mated only monogamously. Two males (HP58, HP53) bred twice monogamously in 1994 and one male (HP42) bred three times monogamously in 1994. One male (H44) mated monogamously twice in 1992 and once in 1994. HP58 kept the same mate for both of his breeding attempts although we do not know whether the other three males (HP53, HP42, H44) changed their mates between successive pair-bonds.

3.1.2. Females

122 clutches were laid by 104 females. All females had a social pair-bond with one male at a time. 17 females out of 104 laid more than one clutch (16 females laid two clutches each and one female laid three clutches) and we identified the mate of two such females. One of these females (T366) laid both of her clutches for the same male (HP58, see above). The other female (T379) laid one clutch each for a polygynous and monogamous male in 1994 and she changed mates between the two nests (sequential polyandry). Four

Tab. 2. Hatching success of Lapwing nests. Daily probabilities of nest survival and their standard errors were estimated by the Mayfield method (see 'Methods'). Daily probabilities of nest survival were not different between nests of polygynous females (primary and secondary females combined: 0.9728 ± 0.0077) and monogamous females ($z=0.778$, $P>0.4$).

	Mating pattern of females		
	Monogamous	Primary	Secondary
Daily probability of nest survival (mean \pm s.e.)	0.9650 ± 0.0063	0.9779 ± 0.0098	0.9674 ± 0.0121
No. of nests found	55	11	12
No. of nests lost	30	5	7
Exposure (no. of days)	858	226	215

Tab. 3. Body condition, clutch volume and date of egg-laying in female Lapwings, mean \pm s.e. (no. of females). Condition of incubating females is given as residuals of a linear regression of $\ln(\text{body mass})$ on $\ln(\text{tarsus length})$ (see 'Methods'). Laying dates are the no. of days after 1st March. To correct for the four independent comparisons at 5% significance level we identify $P=0.0127$ as corrected critical significance level. χ^2 values and uncorrected probabilities of Kruskal-Wallis tests are given.

	Mating pattern of females			χ^2	P
	Monogamous	Primary	Secondary		
Female					
condition ($\ln(g) \times 10^{-2}$)	1.9 \pm 1.2 (23)	-0.8 \pm 0.9 (6)	0.2 \pm 2.6 (6)	2.257	>0.3
tarsus length (mm)	48.1 \pm 0.4 (23)	48.0 \pm 0.5 (6)	48.1 \pm 0.7 (6)	0.016	>0.9
Clutch volume (cm ³)	87.3 \pm 2.1 (56)	86.9 \pm 2.6 (12)	93.8 \pm 2.9 (12)	1.794	>0.4
Laying date (day)	50.0 \pm 2.9 (55)	38.1 \pm 6.9 (11)	46.1 \pm 6.3 (12)	3.353	>0.1

females deserted their clutch or brood, although none of these females remated or re-nested after desertion (Liker & Székely 1999).

3.2. Reproductive success

3.2.1. Males

3.81 \pm 0.09 and 7.58 \pm 0.36 eggs were laid on the territories of monogamous ($n=47$ males) and polygynous males ($n=12$ males), respectively (Mann-Whitney U test, $z=5.862$, $P<0.001$). Since daily survival was not different between monogamous and polygynous nests (Tab. 2), polygynous males tended to have more successful nests on their territories (1.0 \pm 0.3, $n=11$ males) than monogamous males (0.5 \pm 0.1, $n=46$ males; Mann-Whitney U test, $z=1.707$, $P=0.088$).

3.2.2. Females

Females settled on the territories of already mated males throughout the breeding season (Fig. 1). Several females chose mated males when unmated males were still available since laying dates were not different between monogamous, primary and secondary females (Tab. 3).

Secondary females laid their nest 8.4 \pm 1.2 days after the primary ones on the same territory. It took 5 days to lay the modal clutch size of four eggs (A. Liker & G. Noszály, unpublished data), thus secondary females started to lay their eggs on average three days after the primary females completed theirs. The difference

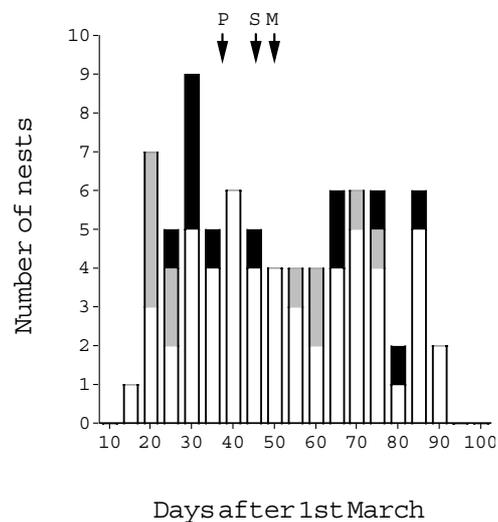


Fig. 1. Distribution of egg-laying dates of monogamous (M), primary (P) and secondary (S) female Lapwings (white, hatched and black bars, respectively). Nests laid over each five-day periods are pooled from 1992, 1993 and 1994 ($n=78$ nests). Arrows indicate mean dates of egg-laying.

between laying dates of primary and secondary females was unrelated to the date of egg-laying of the primary female ($r_s = -0.339$, $P > 0.3$, $n = 11$ territories). The distance between the nests of primary and secondary females was 95.9 ± 8.8 m ($n = 12$ territories).

We found no indication that secondary females were of lower 'quality' than primary and monogamous ones, since monogamous, primary and secondary females were not different in body condition, tarsus length and clutch volume (Tab. 3). Finally, the daily survival of nests was not different between monogamous and polygamous females (Tab. 2).

3.3. Mate choice

Six males attracted two females each, nine males attracted one female each and two males remained unmated in March 1994. Polygynous, monogamous and unmated males often defended neighbouring territories, thus females were able to sample these males before they settled (Fig. 2). We investigated whether the display behaviour of males, the size of their territories, or the area of abundant food in their territories influenced mate choice of females.

3.3.1. Display behaviour

Initially, we found a negative relation between display behaviour of males and

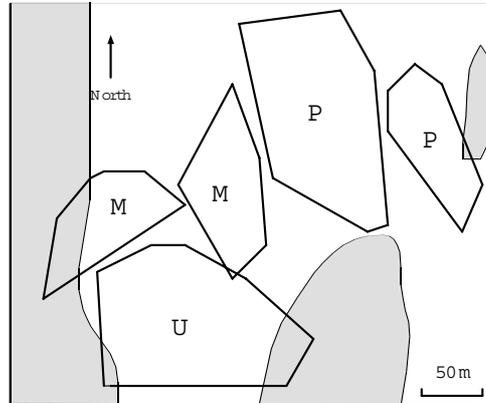


Fig. 2. An example of five male territories in Lapwing. The males were unmated (U), monogamous (M) or polygynous (P) at 30 March 1994. Loess plateaus are dotted.

number of females they attracted (ground-display: $r_s = -0.491$, $P < 0.05$, song-flight: $r_s = -0.468$, $P = 0.058$, $n = 17$ males). This may be because already mated males reduced their display behaviour; perhaps they were occupied with nest-building or incubation. We therefore re-analysed the relation between display behaviour and mating success by dividing males into two groups: (1) unmated and monogamous males which obtained a new mate after the observations of display behaviour and became monogamous or polygamous, respectively (successful males) and (2) males which did not obtain a new mate after the observations and remained unmated or monogamous, respectively (unsuccessful males). We found that before obtaining a mate all males spent a

Tab. 4. Territory size and area of loess plateau in territories of male Lapwings (mean \pm s.e.). χ^2 values and probabilities of Kruskal-Wallis tests are given.

	Mating pattern of males			χ^2	P
	Unmated (n=2)	Monogamous (n=9)	Polygynous (n=6)		
Territory size (ha)	0.48 \pm 0.15	0.43 \pm 0.14	0.47 \pm 0.06	0.985	>0.6
Area of loess plateau (ha)	0.01 \pm 0.01	0.07 \pm 0.03	0.11 \pm 0.05	1.307	>0.5

high proportion of their time on song-flight displays, regardless their subsequent success (no difference between unmated successful and unmated unsuccessful males, Fig. 3). This pattern changed, however, after the settlement of the first female on the male's territory: six males out of fifteen monogamous ones that eventually attracted a secondary female spent significantly more time on song-flight ($7.5 \pm 1.6\%$) than the nine monogamous males which did not attract an additional mate ($1.6 \pm 0.7\%$, Mann-Whitney U test, $z=2.520$, $P<0.02$, Fig. 3; this result remains significant at $P=0.05$ when we control for the two comparisons by sequential Bonferroni correction). After obtaining a second mate polygynous males decreased their display to that of the level of unsuccessful monogamous males (Fig. 3). The time spent on ground-displays was not related to male mating success: we found no difference between monogamous males that attracted a new female ($8.2 \pm 3.7\%$, $n=6$ males) and the ones that did not ($10.2 \pm 5.4\%$, $n=9$ males, Mann-Whitney U test, $z=0.354$, $P>0.7$).

3.3.2. Territory size

We found no evidence that territory size or the area of abundant food in the males' territory ('loess plateaus') were important in female choice, because neither territory size nor area of loess plateaus were different among unmated, monogamous and polygynous males (Tab. 4). The area of loess plateaus remained unrelated to the number of mates when we controlled for territory size by partial correlation ($r_s=0.271$, $d.f.=14$, $P>0.3$). Also, laying date of the first clutch on a male's territory was unrelated to territory size

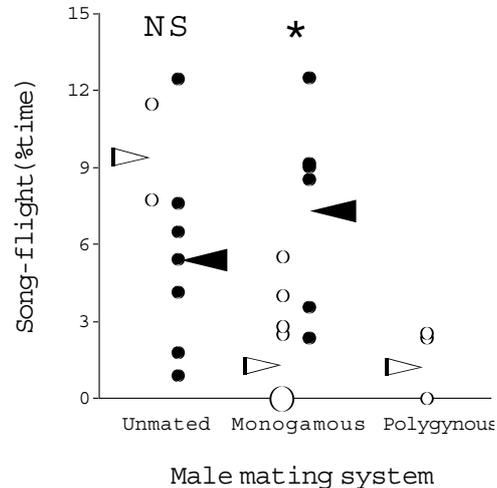


Fig. 3. Time spent on song-flights in relation to the number of mates at the time of the observations ($n=17$ males). Successful males attracted a new mate after the behavioural observations (filled dots, mean: black arrow), whereas unsuccessful males did not (circles, mean: white arrow). The large circle includes five males. Mann-Whitney U tests between successful and unsuccessful unmated males ($P>0.1$), and between successful and unsuccessful monogamous males ($P<0.02$).

($r_s=0.305$, $P>0.2$, $n=14$ males) and to the area of loess plateaus ($r_s=0.178$, $P>0.5$, $n=14$ males).

Since display behaviour tended to decrease with the number of mates (see above), we analysed the relations between display behaviour and territory size by controlling for the number of mates at the time of observation. Nevertheless, territory size was unrelated both to the time spent on song-flights (partial correlation by controlling for the number of mates, $r_s=0.395$, $d.f.=13$, $P>0.1$) and to the time spent on ground-display ($r_s=0.205$, $d.f.=13$, $P>0.4$).

4. Discussion

4.1. Mating pattern

We found that polygyny was a common mating behaviour of Lapwings in a Hungarian grassland, although the frequency of polygyny appeared to be lower (20% of males) than in Western Europe, where 30%-50% of male Lapwings were polygynous (Berg 1993, Byrkjedal *et al.* 1997, Parish *et al.* 1997). Furthermore, males paired with at most two females in Hungary, whereas in other populations males pair with up to three or four females (Kelly 1989, Berg 1993, Byrkjedal *et al.* 1997, Parish *et al.* 1997). We offer three explanations for the differences among these populations. First, abundance of food may be higher in cultivated habitats in Western Europe than in alkaline grasslands, which may facilitate the aggregation of the females in the former habitat type. Concentration of females probably increases the ability of males to monopolise a number of females. In line with this argument, density of earthworms was about 20 times and 15 times higher in England and in Norway, respectively, than in our study site (Baines 1990, Grønstedt 1996). Second, Lapwings often breed at high densities presumably to defend their nest from predators (Berg *et al.* 1992). This predicts that clumped breeding and thus higher potential for polygyny should be more prevalent at sites where nest predation is high. This argument, however, is unlikely since nest predation was about 60% and 15% in England and Sweden, respectively, whereas nest predation was about 60% in our site (Baines 1990, Berg *et al.* 1992, Liker & Székely 1997b).

Third, aggressive behaviour of females against other females may also influence the frequency of polygyny. In particular, we found that female Lapwings were very aggressive towards a female intruder, especially at the beginning of incubation (Liker & Székely 1997a). The pattern of such aggressiveness suggests that resident females attempt to constrain their males' attempt to attract a new female in order to monopolise the full paternal care of their mate (Slagsvold & Lifjeld 1994). The significance of male help for the survival of the young may vary among populations (Lyon *et al.* 1987, Dunn & Robertson 1992, Gowaty 1996), therefore the intensity of female-female aggression for male care is also expected to vary. The latter argument predicts that female-female aggression will be less intensive in such populations where polygyny is common. Behavioural data are required from other populations of Lapwings to evaluate fully the significance of female-female aggression in their mating system. Nevertheless, these arguments demonstrate the validity of Davies (1989) warnings that to understand mating patterns of a given sex (e.g. males) we need to investigate the behaviour of both sexes, because the observed mating pattern (e.g. polygyny) may be the result of different interests of males and females ('sexual conflict').

Genetic relatedness between offspring and their putative parents may indicate deviation from the observed pattern of social polygamy. In particular, extra-pair copulations (EPCs) have been reported in Lapwing (Cramp & Simmons 1983, Parish *et al.* 1997). EPCs also occur in Hungary, since we observed twelve copulations among individually identified Lapwings, of which one copulation was an extra-pair

copulation and eleven were within-pair copulations (A. Liker unpublished data). These observations suggest that a proper quantification of reproductive success of each mating pattern requires genetic studies of the relatedness between offspring and parents.

4.2. Reproductive success

Our study suggests that polygyny is advantageous for males. We suggest that secondary females do not pay a cost (in terms of reduced reproductive success) at least during incubation. However, we consider both results preliminary. First, our data refer only to one component of reproductive success: the hatching success. Clearly, one needs to take into account subsequent stages of offspring development such as survival of chicks until fledging and the probability that the young are recruited into the breeding population. Given the mobile nature of the precocial chicks and the high dispersal of juvenile Lapwings (Thompson *et al.* 1994), estimating such values seems to be a formidable task. Second, we do not have data on the full costs of polygyny for male and female Lapwings. Polygynous males may achieve higher reproductive success in a given year, but this benefit may be negated if territorial fights or displays incur costs in survival or future reproduction. Similarly, secondary females may have lower survival prospects or may be handicapped in future breeding attempts.

4.3. Mate choice

Why do some females mate with an already mated male? We showed that polygyny was not forced on females by the

lack of unmated males. Another possibility is that random settlement of females produced the observed variation in male mating success (Hartley & Shepherd 1995). The latter explanation, however, is unlikely for Lapwing, since we found that female settlement was not random in relation to male behaviour and females preferred those males which spent a lot of their time on song-flights. Deception of females about the mating status of males (as proposed by Lundberg & Alatalo 1992) is also unlikely, since secondary females laid their eggs on the same territory as primary females so they must have been aware of the presence of the primary females. Thus it seems to us that some males (or their territories) were genuinely more attractive to females than others.

Recent studies suggest that female Lapwings use either the characteristics of the males or that of their territory in mate choice (Berg 1993, Grønstedt 1996, Byrkjedal *et al.* 1997, Parish *et al.* 1997). For instance, Grønstedt (1996) observed that male Lapwings with a large roll angle in song-flights were preferred by females. We suggest that the time spent on song-flights may also be important. Aerial displays such as song-flights are energetically costly, therefore they may signal the condition, health or overall quality of the males (Andersson 1994, Buchanan & Catchpole 1997). In a line with this argument Blomqvist *et al.* (1997) suggested that song-flight in male Dunlins *Calidris alpina* serves primarily mating advertisement. It is also possible that display behaviour varies over the age of males. For example, old males may be better at displaying than young ones simply because they are able to spend more time on displaying or they may be able to per-

form more sophisticated aerial manoeuvres. Indeed, male age and experience seem to be important, since old male Lapwings are more likely to become polygynous than young ones (Parish *et al.* 1997).

Song-flights may also signal the ability of males to fight against other males (Dabelsteen 1978). For instance, males that spend large amount of time on song-flights may obtain the best territories, and females may in fact choose their territory - and not the males *per se*. However, the importance of territory in mate choice is controversial in the Lapwing. On the one hand the observations of both Grønstedt (1996) and Parish *et al.* (1997) suggest that territory quality did not influence the mating success of males. On the other hand Berg (1993) showed that polygynous male Lapwings defended larger territories than monogamous ones, and that the large territories possessed larger foraging areas (flooded fields) than the small ones. Finally, Byrkjedal *et al.* (1997) found that male mating success was related to territory size in some years, but not in others. This controversy may be settled in two ways. First, by assessing the abundance of food on both breeding and feeding territories and estimating how significant is the territory in provisioning of the adults and their young. Thus choosing a territory with abundant food may be more important in such a population, where the Lapwings spend most of their time feeding on their territory. For example, Lapwings spend over 90% of their time on their territory in Sweden and they usually fed there (Berg 1993), whereas in Hungary they spend 70-80% of their time on the territory and they feed mostly off-territory (A. Liker, unpublished data). However, if food is

uniformly superabundant in all territories then females should find another a cue which may be used to discriminate among males (Grønstedt 1996, Byrkjedal *et al.* 1997, D. M. B. Parish pers. com.). Second, experimental studies would be invaluable to separate the significance of males' characteristics from that of their territories in mate choice. For example, experimental manipulations of the ability of males to display acrobatic displays or the amount of earthworms on some territories would test unequivocally the significance of display behaviour and food abundance, respectively.

In conclusion, we showed that 20% of male Lapwings were polygynous whereas the rest bred monogamously in Hungary. Females that settle second on the territory of mated males do not seem to pay a cost, at least not until their eggs hatch. Polygynous males spent more time on song-flight than monogamous ones, supporting the idea that sexual selection (either by female choice or by male-male competition) has influenced the evolution of this display. We point out that further investigations are required on the long-term costs and benefits of each mating patterns by estimating the genetic relatedness between the offspring and their putative parents. Finally, we call for experimental manipulations to tease apart the various hypothesised cues in the mating behaviour of Lapwings.

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Összefoglalás

A búbicek *Vanellus vanellus* párzási rendszere és párválasztása

Búbicek párzási viselkedését vizsgáltuk 1992-1994 között Miklapusztán. A párt kapott hímek 80%-a monogám, 20%-a poligín párzási rendszerben költött ($n=59$ hím). A poligín hímek territóriumán egy időben két tojó fészkel. Nem találtunk különbséget a monogám és poligín hímek között a territóriumok méretében és táplálék-ellátottságában, viszont különbözött a hímek udvarlási viselkedése: párválasztás idején a poligín hímek több időt töltöttek a territórium fölötti csapongó repüléssel (7.5 ± 1.6 (s.e.) %), mint a monogám hímek ($1.6 \pm 0.7\%$). A poligín hímek szaporodási sikere feltehetőleg nagyobb a monogám hímek szaporodási sikerénél, mivel több sikeres fészkelési kísérlet volt a poligín hímek territóriumán (1.0 ± 0.3), mint a monogám hímekén (0.5 ± 0.1). A tojók egyetlen szociális partnerrel álltak párba a fészkelési időszak során ($n=104$ tojó), kivéve egy tojót, amely két hímmel rakott fészket egy szaporodási időszakon belül (szekvenciális poliandria). Poligíniában az egy territóriumon fészkelő tojók tojásrakása között 8.4 ± 1.2 nap különbség volt, a másodiknak megtelepedő tojók fészkerakása idején a populációban még jelen voltak párnélküli hímek is. Nem találtunk különbséget a monogám, az elsőnek megtelepedő valamint a másodikként megtelepedő poligín tojók kondíciója, fészkealmérete és fészkeik kelési sikerre között, ami arra utal, hogy nincs különbség a különböző párkapcsolatban fészkelő tojók "minőségében". Az eredmények azt mutatják, hogy a búbiceknél a poligín párzási rendszer nem a párnélküli hímek hiányának, hanem a tojók párválasztásának a következménye. A poligín tojók számára a jó minőségű partner választása indirekt nyereséggel (pl. előnyös genetikai tulajdonságú utódok) vagy közvetlen nyereséggel (pl. utódgondozás) egyaránt járhat, a párválasztásból származó előny tisztázása azonban további kutatást igényel.

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