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Communications

Polygynous great reed warblers *Acrocephalus arundinaceus* suffer more cuckoo *Cuculus canorus* parasitism than monogamous pairs

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There is increasing evidence that hosts within a population may not be parasitized by common cuckoos *Cuculus canorus* with equal probability. Such non-randomness has been documented, for example, for host nest sites and host quality. In this study we demonstrate association between successful cuckoo parasitism and host social mating system. We found that nests of socially polygynous great reed warblers *Acrocephalus arundinaceus* were more often successfully parasitized than the nests of their monogamous counterparts. We hypothesize that lack of parental assistance provided by polygynous males to their mates during egg laying period and higher nest activity in their territories could contribute to this discrepancy. These data imply that social mating system should be taken into account in future studies of brood parasitism.

The breeding success of common cuckoos (*Cuculus canorus*, hereafter ''cuckoo'') depends on duping hosts that will successfully raise their parasitic chicks. Cuckoo breeding success is therefore limited by the discriminatory and parental abilities of their hosts, and so cuckoos may choose hosts with low egg-recognition capabilities or high parental abilities (Grim 2002, Cherry et al. 2007, Polačiková et al. 2009, but see Stokke et al. 2004). This should be reflected in non-random distribution of successfully parasitized nests within a host population.

Brood parasites, including cuckoos, may use various cues when searching for the most suitable hosts (reviewed by Poláčiková et al. 2009). First, cuckoos may choose hosts with a high song repertoire and territory quality, cues that are also used in selection of high quality mates (Garamszegi and Avilés 2005). As they are also two main factors that influence mating status in facultatively polygynous passerines (Orians 1969, Hasselquist et al. 1996, Hasselquist 1998), this implies that there should be association between cuckoo parasitism and social mating system. Second, cuckoos may choose younger (naive) host individuals, as they are generally assumed to be less able to discriminate between their own and cuckoo eggs (Lotem et al. 1992, 1995, Grim 2002).

The great reed warbler *Acrocephalus arundinaceus* serves as a good model for studying the relation between the social mating system and rates of cuckoo parasitism. It is a well-known cuckoo host in Central Europe which suffers relatively high rates of cuckoo parasitism (Moskát and Honza 2002, Kleven et al. 2004) and some great reed warbler populations may reach high levels of social polygyny (Leisler et al. 1995, Bensch 1996, Trnka et al. 2010). Importantly, socially polygynous males provide less feeding and nest defence assistance to their females (Sejberg et al. 2000, Trnka and Prokop 2010) including nest guarding during egg laying period (Požgayová et al. 2009) than do monogamous males to their females.

The aim of the present study was to investigate whether the rate of successful parasitism in the great reed warbler varies with the type of social mating system. We hypothesized that socially polygynous great reed warblers should suffer more cuckoo parasitism than monogamous pairs. To test this prediction, we examined the distribution of successfully parasitized nests in relation to their social status. Furthermore, because previous findings suggested that cuckoos may preferentially parasitize the nests of older and better body condition host females and those nearer to trees (Moskát and Honza 2000, Avilés et al. 2009, Poláčiková et al. 2009), we also measured these variables to test whether cuckoo parasitism is directly related to the mating system or to some other correlates.

Methods

The study was conducted in 2007 and 2008 at three fishponds near Štúrovo (47° 51′N, 18° 36′E, 115 m a.s.l.), southwestern Slovakia. Here great reed warblers breed in narrow (approximately 5-10 m wide) strips of the reed, *Phragmites australis,* which border the ponds.

Each year, we mist netted the majority of territorial males and breeding females in the study area. Males were

mainly caught during territory establishment and females during egg incubation to avoid disturbing them at the initiation of breeding. All captured birds were marked with both aluminium and colour rings, measured and weighed. The physical condition of each bird was calculated using the residuals of the regression of body mass against wing length as a body size indicator (see also Young and Moor 1997). Great reed warbler nests were searched for systematically at 4–5 day intervals between May and late July. Each nest was checked immediately after hatching for the presence of cuckoo chick. A nest was considered successfully parasitized if a cuckoo chick successfully evicted host eggs or chicks. The social mating status of each male and female was determined on the basis of captures of birds at or near their nests and direct observations of colour-ringed males and females defending their nests. As nesting status of females can change during the season (see also Sejberg et al. 2000), in this study we estimated female nesting status twice, when incubating the eggs and when feeding young. We then categorized nesting females as being monogamous (the only female incubating eggs or feeding young with the same male), or primary, secondary or tertiary females (the first, second or third female incubating eggs or feeding young with the same male). Male status was divided into two categories: monogamous (males who defend nest or feed young of one female only during breeding season) and polygynous (males defending the nests or feeding young of two or three females during breeding season). Overall 31.2% of nesting males were polygynous and this did not differ between years (33.3% of 45 nesting males in 2007 and 29.2% of 48 nesting males in 2008; Fisher's exact test, $p = 0.82$). Socially polygynous males formed pair bonds almost exclusively with two females, and only one male was paired with three females.

We estimated distance to cuckoo vantage points for each nest, defined as a distance (m) from the nest to the closest tree on which cuckoos could land. We used Garmin geographic positioning system and Google Earth (ruler) to specify the position of closest vantage points from bird's eye view. Similarly, the age of great reed warblers was also estimated on the basis of our ringing data because of difficulty to determine the exact age of these birds in spring due to their complete moult in Africa (but see Bensch et al. 1998).

We used multiple logistic regression to test whether successful nest parasitism (binomial dependent variable) is influenced by great reed warbler social mating system, differences between years (categorical predictors) or time of season (continuous predictor). The single nest of a tertiary female found in 2008 was removed from analyses. Results are presented as means $\pm$ SE. Data were analysed using SPSS software. Normality of data was checked using the Shapiro-Wilks test for normality. When the data were not normally distributed, nonparametric statistical tests were used. All statistical tests were two-tailed.

Results

Rate of successful cuckoo parasitism

Polygynous great reed warblers suffered much higher rates of successful cuckoo parasitism than monogamous warblers (Fig. 1). The overall rate of successful parasitism was 18.9% of 58 nests in 2007 and 16.4% of 61 nests in 2008. Multiple logistic regression revealed that only the mating system had significant effect on the likelihood of successful cuckoo parasitism (Wald's $\chi^2 = 7.79$, $DF = 2$, $p = 0.02$). Other variables including season, year and mating system $\times$ year interaction were not significant (all p-values > 0.41). In no case was both primary and secondary nests of the same male successfully parasitised, so it is valid to analyse them separately. Furthermore, when we pooled all primary and secondary great reed warbler nests into one category and compared them against monogamous nests, the results of multiple logistic regression became even more significant (Wald's $\chi^2 = 7.78$, $DF = 1$, $p = 0.005$).

Body condition, age and nest location

Female body condition did not differ between monogamous, primary and secondary females (mean $\pm$ SE residual values: -0.246 ± 0.281, 0.684 ± 0.517 and 0.108 ± 0.437, $n_1 = 34$, $n_2 = 10$ and $n_3 = 14$, respectively, Kruskal-Wallis ANOVA, $H = 3.631$, $DF = 2$, $p = 0.16$). Body condition of monogamous and polygynous males was also similar (mean $\pm$ SE residual values: -0.137 ± 0.211 and 0.289 ± 0.306, $n_1 = 61$, $n_2 = 29$, respectively, $t = 1.147$, $DF = 88$, $p = 0.25$).

Based on ringing (capture-recapture) data, there was no difference in two age groups (2 yr and >2 yr birds) between great reed warbler males ($\chi^2 = 0.18$, $df = 1$, $n_1 = 30$, $n_2 = 15$, $p = 0.67$) and females ($\chi^2 = 0.05$, $DF = 1$, $n_1 = 32$, $n_2 = 39$, $p = 0.82$) of the two social mating systems in our population.

There were also no differences in distances to nearest vantage point (tree) between socially monogamous, primary and secondary nests (mean $\pm$ SE $= 30.744 \pm 4.568$ m, 32.977 ± 7.167 m and 30.236 ± 6.607 m, $n_1 = 64$, $n_2 = 29$ and $n_3 = 25$, respectively, Kruskal-Wallis ANOVA, $H = 1.829$, $DF = 2$, $p = 0.401$).

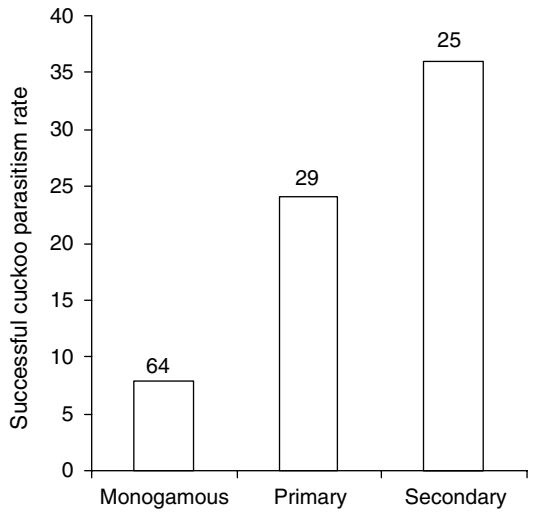

Figure 1. Percentage of successful cuckoo parasitism in relation to nest status. Numbers at the top of the bars indicate sample size.

Discussion

This study shows that polygynously mated great reed warblers may suffer more cuckoo parasitism than monogamous pairs. The fact that socially polygynous nests in our study population were more often successfully parasitized than monogamous nests may also suggest that cuckoo parasitism can represent another, previously unrecognized cost of polygyny. As far as we know, this is the first study to document a relationship between social mating system and cuckoo parasitism in a host-parasite system.

Our data relate specifically to successful parasitism, and thus they need not properly reflect natural rate of cuckoo parasitism in our study population. Observed differences in successful parasitism rate between monogamous and polygynous great reed warbler nests might arise either from different rate of natural cuckoo parasitism or from different discrimination abilities of monogamously and polygynously mated females. As previous studies have shown that discrimination behaviour in great reed warblers is age-dependent (Lotem 1992, 1995), the latter explanation seems less probable because no relevant age differences have been found between great reed warbler females of the two social mating systems in our population. We also checked the nests for cuckoo eggs but due to high egg predation and abandonment of nests (about 20%) during egg laying stage we failed to determine social status of all parasitized nests (see Methods). Although these data are incomplete, they also revealed higher natural parasitism rate for polygynous than for monogamous nests (Trnka unpubl.). However, testing whether successful parasitism does reflect natural parasitism should be a major challenge for future studies.

We suggest that the higher rate of successful cuckoo parasitism of polygynous great reed warblers follows from reduced nest defence rather than nest location or host body condition. Previous studies have shown that cuckoo females may preferentially parasitize more visible great reed warbler nests located nearer to trees or electric wire (Moskát and Honza 2000, Avilés et al. 2009) and/or they choose to parasitize host females of high quality, as reflected in host body condition (Polačiková et al. 2009). In our study population, however, we found no difference in nest location between socially monogamous and polygynous pairs. Moreover, both monogamous and polygynous nests were situated in habitats with similar vegetation structure (expressed as the number, height and diameter of reed stems in their vicinity, Trnka and Prokop 2010) with presumably similar visibility of the nests from cuckoo perches. Similarly, monogamously and polygynously mated females did not differ in physical condition in our study population (see also Bensch 1996).

However, we suggest that lack of parental assistance provided by socially polygynous males to their females (Dyrcz 1986, Bensch and Hasselquist 1994, Sejberg et al. 2000) including nest defence (Trnka and Prokop 2010) and nest guarding during egg laying period (Požgayová et al. 2009) could contribute to the higher rate of successful cuckoo parasitism of polygynous great reed warblers. Alternatively, higher nest activity in the territories of polygynous males with more than one active nest might increase the risk of nest detection by cuckoos. We therefore hypothesize that these could be reasons for why cuckoo females were more successful when parasitizing socially polygynous than monogamous great reed warbler nests. Whether other factors are responsible for these findings, however, still remains to be demonstrated.

Regardless of the cause of variation in rates of successful parasitism, our results suggest that social polygyny can influence the pattern of cuckoo parasitism in facultatively socially polygynous species, and that social mating system should be taken into account in future studies of brood parasitism.

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