



Is shared male assistance with antiparasitic nest defence costly in the polygynous great reed warbler?

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Polygyny typically has negative fitness consequences for secondary females, but may equally impose costs on primary females or even on polygynous males. We investigated how polygynous and monogamous great reed warbler, *Acrocephalus arundinaceus*, males assist their mates with aggressive nest defence against the common cuckoo, *Cuculus canorus*, and whether the females adjust their nest defence intensity according to male investment in aggression. Additionally, we investigated whether host social mating status affects host vulnerability to parasitism. We presented taxidermic cuckoo mounts at nests of primary, secondary and monogamous females, and recorded aggressive responses of nest owners. We found that monogamous males defended their nests most aggressively while polygynous males allocated their nest protection effort unevenly between their two mates, responding more vigorously on the primary than secondary nests. In contrast, nest defence intensity of females did not differ with respect to their social status, indicating that females of polygynous males did not compensate for low levels of male aggression. Similarly, we found no differences in natural cuckoo parasitism rates between monogamous, primary and secondary nests. Our results thus suggest that while monogamous females receive more assistance with nest defence than females of polygynous males, this has no effect on the probability of parasitism.

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Social polygyny, the bond of one male with two or more females at a time, is the most prevalent and perhaps also the most intensively studied polygamous mating system in birds (Møller 1986; Davies 1991; Ligon 1999). Adoption of this strategy is regarded as beneficial to males, since by having multiple broods, they may significantly enhance their reproductive success (Hannon & Dobush 1997; Pearson et al. 2006; Ferretti & Winkler 2009). In contrast, females sharing one male's territory are expected to compete with each other for resources or for male assistance with parental care and such competition may negatively affect their reproductive output (Verner 1964). It is then natural to expect that females confronted with the cost of polygyny may prefer to breed monogamously.

The polygyny threshold model (Verner 1964; Verner & Willson 1966; Orians 1969) is the most widely accepted theoretical explanation of territorial polygyny in birds, although no less important additions and alternatives to this model have been suggested (reviewed by Searcy & Yasukawa 1989; Slagsvold & Lifjeld 1994; Ligon 1999). According to this model, there is a selective advantage for females to mate with a polygynous male rather than with

a bachelor, if the cost of polygyny is compensated for, for example through access to a territory or a male of superior quality. However, polygyny cannot be viewed only as an outcome of female decisions in relation to the variation in male genetic, phenotypic or territorial quality, but also in the context of sexual conflict (Davies 1989; Kempenaers 1995; Smith & Sandell 2005) or as a result of variation in female qualities or condition (Forstmeier et al. 2001; Griggio et al. 2003).

It is generally known that polygynous males provide less parental care per nest than monogamous males and often invest more in offspring of their primary (i.e. first mated) than secondary (i.e. second mated) females (e.g. Johnson et al. 1993; Sandell et al. 1996; Forstmeier et al. 2001). However, owing to a trade-off between male sexual advertisement to the secondary females and paternal behaviour at the primary nests, sometimes it is the primary females that are left with a smaller contribution from their mates (Muldal et al. 1986; Pinxten & Eens 1994; Slagsvold & Lifjeld 1994). Females of polygynous males are thus expected to compensate for the reduced paternal help by increasing their own workload (Pinxten et al. 1993; Pinxten & Eens 1994; Sejberg et al. 2000; Redpath et al. 2006), but may not be able to compensate for it completely and therefore fledge fewer or lower quality offspring than monogamously paired females. Such fitness costs are typically reported for the less assisted secondary females (Pinxten

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& Eens 1990; Johnson & Kermott 1993; Pribil 2000). Less attention has been paid to the issue of how mate sharing affects primary females (Hansson et al. 1997; Czapka & Johnson 2000; Trnka et al. 2010) or whether polygyny imposes some costs also on males (e.g. Dunn & Robertson 1993; Lubjuhn et al. 2000; Pilastro et al. 2002).

The predominantly investigated form of male parental care in polygynous systems is nestling provisioning (e.g. Alatalo et al. 1981; Urano 1990; Yasukawa et al. 1990). Other forms, such as male incubation behaviour (Pinxten et al. 1993; Smith et al. 1995; Grønstøl 2003) or male feeding of the incubating female (Altenburg et al. 1982; Lifjeld et al. 1987), are less intensely studied in this context. In addition, only a few studies have examined how polygynous males allocate their nest defence effort among the mates of different social status (Knight & Temple 1988; Weatherhead 1990; Yasukawa et al. 1992; Johnson & Albrecht 1993; Trnka & Prokop 2010). Of these studies, none have investigated male assistance with nest defence against brood parasites, although in some host populations, brood parasitism may be as detrimental to host fitness as nest predation if not more so (Rothstein 1990). Moreover, the male role in antiparasitic aggression is thought to be of importance because two defending parents may be more likely to prevent the nest from being parasitized than one parent alone. Indeed, there is some evidence that a higher number of nest defenders decreases the probability of brood parasitism. In colonial nesters, larger groups of hosts may be parasitized at lower rates than smaller groups, which is most probably caused by collective nest defence by the host (Brown & Lawes 2007). In cooperatively breeding birds, an incubating female fed by helpers may spend more time on the nest. Increased host nest attendance may then significantly reduce the likelihood of parasitism (Canestrari et al. 2009). Therefore, lower assistance with nest defence by polygynous males or their lower nest attentiveness might sometimes explain significantly higher parasitism rates in polygynous than monogamous territories (Trnka & Prokop 2011).

We investigated whether the social mating system of the great reed warbler, *Acrocephalus arundinaceus*, affects its aggressive behaviour towards the cuckoo, *Cuculus canorus*, and whether it is costly in terms of increased parasitism rate. More specifically, we explored how polygynous and monogamous males assist their mates with nest defence against the cuckoo and whether females of particular mating status adjust their nest defence intensity according to that of their mates. Additionally, we compared natural cuckoo parasitism rates among monogamous, primary and secondary nests. We predicted primary females would get less assistance from males than secondary or monogamous females, because during egg laying of primary females, polygynous males may be distracted by activities connected with the acquisition of secondary females. As a consequence, the competing activities of the polygynous males may result in lower male attentiveness at the primary nests and thus these nests may be more vulnerable to parasitism. According to this scenario, we expected a higher parasitism rate on primary than secondary or monogamous nests (see also Trnka & Prokop 2011). We assumed that shared male assistance with antiparasitic nest defence will be costly for primary females and, eventually, also for polygynous males. However, this cost may be prevented if females increase their aggressive behaviour to compensate for the lower male contribution.

METHODS

Study Species

The facultatively polygynous great reed warbler is an important cuckoo host (Moskát & Honza 2002; Kleven et al. 2004; Campobello

& Sealy 2009) known to behave aggressively towards nest intruders, including parasitic cuckoo females (Bártol et al. 2002; Røskft et al. 2002; Požgayová et al. 2009; Trnka & Prokop 2012). In this passerine, only females are responsible for incubation while males guard the nests by watching for enemies, participate in nest defence and help females with caring for the chicks (Cramp 1992). The rate of male polygyny in the great reed warbler varies between 8% and 43% (Dyrz 1986; Hasselquist 1998; Leisler & Wink 2000; Trnka et al. 2010), depending on the particular year and population studied.

Fieldwork

We carried out the study on a colour-ringed great reed warbler population, from late April to mid-July 2009 and 2010. During that period, the population consisted of about 100 breeding pairs and, in the 2 years, exhibited a 29% and 21% male polygyny rate, respectively. Polygynous males were almost exclusively bigamous; only two males (one in each year) mated with three females.

We systematically searched for nests in littoral vegetation. The nests were found during the nest-building stage or at the beginning of egg laying and were checked daily until clutch completion. At each visit, we numbered a newly laid egg with a waterproof pen according to its laying order (to detect discrepancies in the laying sequence and to ascertain the clutch size) and checked the nest contents for the presence of a parasitic egg. Only clutches containing a cuckoo egg during our nest checks were considered parasitized; otherwise they were considered nonparasitized.

Birds were mist-netted and colour-ringed soon after their territory establishment (males) or during the nest-building, egg-laying or incubation stages (females). To make the mist-netting more effective, we used mp3 recordings of conspecific song to attract the birds. However, as many birds were colour-marked from previous years, we avoided unnecessary disturbance and confirmed their identity and social mating status based on the resightings of the colour rings. As the mating status of both males and females may change because of the settlement of new females or because of nest failure, we checked the status of each individual several times over the breeding season. Accordingly, a monogamous female was the only female of a monogamous male. A primary female was the first mated female of a polygynous male, sharing the territory simultaneously with a secondary female. Analogously, the secondary female was the second mated female of a polygynous male, sharing the same territory simultaneously with the primary female.

At the end of egg laying (mean \pm SD = 4.7 \pm 1.0 days after clutch initiation; mean clutch size \pm SD = 4.1 \pm 0.8 eggs, $N = 67$), nesting pairs were presented with a taxidermic cuckoo mount, randomly chosen from three specimens. The experimenter attached the mount to a pole < 1 m from the focal nest, levelled it with the nest rim, and retreated to a distance of 15–20 m. From there she observed the behaviour of the nest owners with binoculars, allowing each pair member to respond for 2 min from its first arrival within a 5 m diameter around the dummy. If there was no reaction and no bird(s) visible in the vicinity of the nest for 15 min from when the dummy was attached to the pole, the experiment was stopped and the dummy was removed. All experiments were carried out between 0800 and 1900 hours CET.

We chose the cuckoo for the experiments because it is a natural enemy of great reed warblers at our study site, where it parasitizes them at a rate of 30–40% (our own data). The cuckoo is only dangerous for host clutches, but not for the adults, which should not bias host aggressive behaviour. Indeed, many previous studies demonstrated that hosts (including the species used in this study) are aggressive towards brood parasites (e.g. Røskft et al. 2002,

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