Does Social Mating System Influence Nest Defence Behaviour in Great Reed Warbler (*Acrocephalus arundinaceus*) Males?

Alfréd Trnka* & Pavol Prokop*,†

* Department of Biology, University of Trnava, Priemyselná, Trnava, Slovakia

† Institute of Zoology, Slovak Academy of Sciences, Dúbravská cesta, Bratislava, Slovakia

Correspondence

Alfréd Trnka, Department of Biology, University of Trnava, Priemyselná 4, SK-918 43 Trnava, Slovakia.

E-mail: atrnka@truni.sk

Abstract

In birds with biparental care, males and females often conflict over how much care to provide to their offspring and it may be substantially influenced by increased level of polygamy. In accordance with sexual conflict theory, males of socially polygynous bird species provide much less care to their nestlings than do males of most socially monogamous species. Most of previous studies, however, have used feeding behaviour as an index for variations in male parental care only. However, this may be skewed if polygynous males compensate for lower feeding assistance through the provision of other parental care such as protection of nests from predators. In this paper, we examine nest defence behaviour in the facultatively polygynous great reed warbler with respect to sex and type of social mating system. We recorded latency to the first arrival, distance from the predator and defensive reaction of each parent towards a human intruder. Socially polygynous males with two simultaneously active nests defended primary females' nests less vigorously than socially monogamous males, whereas no differences were found between monogamous and primary females. Generally, however, they took a bigger role in nest defence than males in all cases. Our results support an idea that sexual conflict is driven by polygamy and that type of social mating system can influence nest defence behaviour of facultatively polygynous birds. This finding should be taken into consideration when studying nest defence parental care in polygynous mating systems.

Introduction

In the vast majority of altricial birds, both parents participate in the rearing of their offspring. However, because of different evolutionary interests, males and females often conflict over how much care to provide to their offspring (Parker 1979; Chapman et al. 2003; Arnqvist & Rowe 2005; Olson et al. 2008). As parental care is costly in terms of reduced parental survival and loss of mating opportunities, males of many species invest less when they have more opportunities to reproduce (Møller & Thornhill 1998; Von Hippel 2000). This suggests that intensity

of sexual conflict may be substantially influenced by increased level of polygamy (Walter & Trillmich 1994; Sejberg et al. 2000; Arnqvist & Rowe 2005). In accordance with this sexual conflict theory, males of socially polygynous bird species provide much less care to their nestlings than do males of most socially monogamous species (Verner & Willson 1966; Orians 1969, Wiktander et al. 2000; but see Hartley & Shepherd 1994). The other reason is that socially polygynous males with two or more simultaneously active nests are not capable of providing each female with as much parental assistance as they would if only one active nest existed on their territory. In

contrast to this prediction, however, socially polygynous males of some facultatively polygynous species with overlapping broods are known to give assistance to their primary females similarly to that provided by socially monogamous males to their females (Sejberg et al. 2000), suggesting that there should be selection for a socially polygynous male to provide total parental care to first mated female (comparable to socially monogamous males) at the expense of other females.

To test this, previous studies have mainly used nestling provisioning behaviour as an index for variations in paternal effort (e.g. Dyrcz 1986; Urano 1990; Sandell et al. 1996; Westerdahl et al. 2000; Sejberg et al. 2000; Kleindorfer et al. 2001), thereby ignoring other components of realised male assistance. Socially polygynous males, however, may compensate for lower feeding assistance through the provision of high-level protection of nests from predators, which may be more costly than nestling provisioning, because defenders risk attracting other predators and they risk injury and the chance that they will not survive to breed again (e.g. Regelmann & Curio 1986; Brunton 1986; Montgomerie & Weatherhead 1988; Hogstad 1993; Ueta 1999). On the other hand, several studies have shown that the nests of pairs that showed higher nest defence intensity have also better fledging success (Knight & Temple 1986; Tryjanowski & Golawski 2004; but see Hatch 1997). Thus, the degree to which males will engage in nest defence should balance in terms of the cost/benefit ratio. Most studies on nest and brood defence, however, have examined defensive behaviour in socially monogamous species (Montgomerie & Weatherhead 1988; Weatherhead 1989; Carrillo & Aparicio 2001; Pavel & Bureš 2001; Rytkönen 2002; Tryjanowski & Golawski 2004; Hogstad 2005), and little or no attention has been paid to this pattern of behaviour in socially polygynous birds (Knight & Temple 1988; Johnson & Albrecht 1993; Kleindorfer et al. 1997).

Facultatively polygynous species such as the great reed warbler *Acrocephalus arundinaceus* serve as a good model for studying associations between nest defence and cost of polygyny. However, because males and females show little difference in their morphology, examination of the differences in nest defence by gender in this species has not been undertaken to date (see Kleindorfer et al. 2005). We are only aware of studies on sex-specific defence behaviour by the great reed warbler against a brood parasite, the common cuckoo *Cuculus canorus* (Požgayová et al. 2009).

The aim of the present study was, therefore, to make a detailed analysis of parental nest defence in the great reed warbler with respect to gender and whether females are mated to monogamous or polygynous males. Based on previous assumptions, we predicted that (i) socially polygynous males with two simultaneously active nests will defend primary nests less aggressively compared to their monogamous counterparts and that (ii) sex differences in nest defence will be more pronounced in socially polygynous pairs, where the intensity of sexual conflict should be higher than in socially monogamous pairs. Specifically, socially polygynous males will defend their nests less than primary females, but socially monogamous males and females will take an equal share in defending of their offspring. Finally, if primary females receive less male parental assistance in defending their offspring than do monogamously mated females, we might expect behavioural compensation from primary polygynously mated females in the form of higher nest defence responses. Thus, primary females should defence their nests more intensively than monogamous females.

Methods

Study Site and Species

We conducted this study in 2008 at three fishponds near Štúrovo, south-western Slovakia (47°51′N, 18°36′E, 115 m a. s. l.) over a total study area exceeding 45 ha. The great reed warbler breeds at this site in narrow (approximately 5–10 m wide) strips of the reed, *Phragmites australis*, bordering the ponds. This species is the most abundant passerine observed in the area.

This is an altricial, relatively large and aggressive passerine that builds open, conspicuous nests in reeds. The rate of polygyny in this species varies between 8–43% (Hasselquist 1998; Leisler & Wink 2000; A. Trnka, pers. comm.), and in our study populations, it reached 20.8–43% of mated males (Trnka et al. 2010; Trnka, pers. comm.). Because nestling periods of primary and secondary broods of polygynous males often overlap, females mating with socially monogamous males usually receive significantly more male assistance during the nestling stage than females mating with polygynous males, with the latter having to share the parental activities of their mate with another female (or females) (Catchpole et al. 1985; Dyrcz 1986; Urano 1990; Bensch & Hasselquist 1994; Sejberg et al. 2000). In our study population, primary females start breeding

on average 9.2 d before secondary females. Only females build the nests and incubate the eggs, but both sexes feed and defend the young. Because of the short breeding period of this species in the study area (the earliest known laying date of the first egg is 11 May, the latest is 4 July), great reed warbler females have usually a single clutch per year. Two broods in one season are very uncommon. In the study population, males were significantly heavier and had longer wings than females (weight, mean ± SE: 32.7 g ± 0.36 vs. 30.4 g ± 0.32, n = 31 and 39, respectively, $t = 4.84$, df = 68, p < 0.001; wing length: 95.7 mm ± 0.34 vs. 91.1 mm ± 0.37, n = 31 and 39, respectively, $t = 8.84$, df = 68, p < 0.001).

The species suffers relatively high rates of nest predation (Bensch & Hasselquist 1994; Hasselquist 1998; Batáry & Báldi 2005; Trnka et al. 2009). Although there are plenty of opportunities for females to lay replacement clutches, renesting is highly costly (Bensch 1996; Hansson et al. 2000b). Great reed warbler nest predation ranged from 20% to 43% (Bensch & Hasselquist 1994; Batáry & Báldi 2005; Trnka et al. 2009), with slightly higher frequency of predation on nests located in monogamous compared with polygynous territories (Hansson et al. 2000a). Moreover, spatial distribution of nest predation is known to contribute to polygyny in the great reed warbler (Bensch & Hasselquist 1991; Hansson et al. 2000a).

The main avian nest predators known in this species are little bittern *Ixobrychus minutus*, bittern *Botaurus stellaris*, marsh harrier *Circus aeruginosus*, and occasionally water rail *Rallus aquaticus* and coot *Fulica atra* (Bensch & Hasselquist 1994; Hansson et al. 2000a; Trnka et al. 2009). As the great reed warbler suffers relatively high rates of cuckoo *Cuculus canorus* parasitism (Moskát & Honza 2002; Kleven et al. 2004) in some parts of its breeding range, the cuckoo is also considered to be severe nest predator of great reed warbler nests. Moreover, there is known intraspecific nest predation (infanticide) in this species where secondary females destroy eggs of primary females to gain increased paternal investment (Bensch & Hasselquist 1994). Based on experimental studies, the rate of conspecific predation on primary female nests may reach up to 40% (Hansson et al. 1997; Trnka et al. 2010). Mammalian nest predators on this species include mink *Mustela vison*, water vole *Arvicola terrestris* and other undetermined small mammals (Hansson et al. 2000a; Trnka et al. 2009).

In our study area, most frequent nest predator species of great reed warbler nests are, besides conspecifics, little bittern and marsh harrier. The rate of interspecific nest parasitism reaches 16–20% (Trnka, pers. comm.).

We captured most of the males in April, soon after their arrival from African wintering grounds. We used tape recordings of conspecific song to attract them to 12- m-long nets in their vicinity. Females were captured at or near nests during their egg-incubating period. Each bird was marked with one aluminium ring and a unique combination of two or three coloured plastic rings. Birds were sexed, and body mass and the length of their right wing were recorded. The physical condition of each bird was calculated using the residuals of the regression of body weight against wing length (as a body size indicator), as described previously (Yong & Moore 1997). Great reed warbler nests were searched for systematically at 4- to 5- d intervals between early May and late July. We believe that we located all (or at least 95%) active nests. The social status of males (monogamous or polygynous) and the status of nests and females (monogamous, primary, secondary or possibly tertiary) were determined on the basis of direct observations of colour-ringed males and females defending their nests and/or captures/recaptures of birds at or near their nests. The both male and female parents were determined for each active nest in the study area. Of 61 active nests found in the study area in 2008, 34 nests were of monogamous status, 14 nests were of primary status, 12 of secondary status, and only one nest was of tertiary status.

Nest Site and Breeding Characteristics

Because there are known relationships between nest concealment, nest location and parental behaviour (Cresswell 1997; Weidinger 2002; Trnka et al. 2009), we measured the following nest site characteristics at the end of each experiment: distance from the nest to the open reed-water edge; number of reed stems within a square of 0.5 m × 0.5 m with the nest in the centre; height and diameter of ten randomly chosen stems in each square; and distance from the territory to the nearest active territory of another male.

Previous studies have also shown that nest defence increases with the number and age of offspring, parental condition and with the decline of renesting potential (reviewed by Montgomerie & Weatherhead 1988; Pavel & Bureš 2001, 2008). At the time of each experiment, we therefore recorded the number of nestlings and the date during the

breeding season. As we checked the study area every 4–5 d, we were confident that we had found almost all nests during the nest-building or egg-laying periods. Based on these data, we calculated the laying and hatching days of each clutch.

Nest Defence Experiment

The nest defence behaviour of great reed warblers during their brood provisioning period was studied in a response to a human (first author) nest predator/intruder. This approach has also been used successfully in other studies of nest defence behaviours in passerines (Knight & Temple 1986; Radford & Blakey 2000; Pavel et al. 2000; Tryjanowski & Golawski 2004; Hogstad 2005; Hollander et al. 2008). Similarly, according to our prior study with taxidermic mounts and living individuals of main great reed warbler nest predators, marsh harrier and little bittern, and human (A. Trnka and P. Prokop in prep.), great reed warblers perceive a human as potential threats to their nestlings and behave towards him in a similar way to how they behave towards other nest predators. In our 'human' experiment, the procedure was as follows: human (first author) approached the experimental nests from open water, leaned slightly over nest and after 1 min, he was alternately shaking with surrounding reeds and taking the excitedly calling chicks out of nest to simulate a real nest predation event. During this procedure, the nestlings were also ringed. The time taken for the arrival of the parents was recorded, and their behaviour was then observed for 5 min. All observations were made by the first author and controlled (videotaped) by the second author from a distance of approximately 10 m. The identity and sex of each bird were determined by reading the coloured rings.

Because of possible age gaps between the broods of females mated with the same polygynous male and different male assistance provided by polygynous male to their mates (Bensch & Hasselquist 1994; Leisler et al. 1995, A. Trnka, pers. comm.), to standardise the experimental treatment, we performed all tests in this experiment at nests of monogamous and primary polygynous females only.

The defensive reaction of parent birds was scored using the following predetermined scale: 0 – the bird was not observed at or in the vicinity of the nest; 1 – the bird watched the nest silently from a safe distance; 2 – the bird approached the nest (hopped on the reed stems) and gave short warning calls; 3 – the bird jumped or flew around/over the intruder, per-

sistently giving alarm and distress calls; and 4 – the bird dived repeatedly at the intruder or attacked him. In each case, the maximum reaction of each parent was taken into account. We also recorded latency to the first arrival (in seconds) and the distance from the predator, i.e. the shortest direct distance between defender and human intruder (in metres) for each parent. As it is generally accepted that risk to parents increases with decreasing distance to the predator and with increasing intensity of display (defensive) behaviour (Montgomerie & Weatherhead 1988; Brunton 1990, Pavel & Bureš 2001, 2008), we used minimum distances to the intruder and maximum aggression scores (defensive reactions) as measures of risk-taking. Based on previous experience, we decided not to evaluate the intensity of vocalisation separately because of the difficulties in identifying (sexing) the birds producing calls further away from the nest (because of dense vegetation). Moreover, we observed that birds more active in terms of display movements also produced more alarm calls.

As nest defence is known to increase with nestling age (Montgomerie & Weatherhead 1988), we assessed the behaviour of the parents when nestlings were 8- to 10- d old. Similarly, nest defence may be affected by weather conditions (Tryjanowski & Golawski 2004; Fisher et al. 2004). To minimise the influence of weather, we conducted observations between 7 and 11 am only on days when conditions were good (warm days with no rain or strong wind). Each nest was visited only once. Eight nests that were successfully parasited by the common cuckoo were excluded from analyses. In total, we used data from 31 monogamous and 14 polygynous (primary female) pairs.

Statistical Analysis

Data were analysed using SPSS software v.15 (SPSS Inc., Chicago, IL, USA). Normality of data was checked using the Shapiro–Wilks normality test. When data were non-normally distributed, they were log $(y + 1)$ transformed. Wing lengths of females were square-root transformed. After transformations, the normality of all data was achieved (Shapiro–Wilks test, all p's >0.05). Therefore, we used parametric statistical tests. Means $\pm$ SE are given throughout.

Three nest defence variables (latency time, distance from the predator and defensive reaction) were also log $(y + 1)$ transformed and submitted to Principal Component Analysis (PCA). Data loaded to a single factor with eigenvalue 1.69 were derived. This factor accounted for 56% of the total variance

of results. This single composite variable was then defined as dependent variable in subsequent analysis of covariance (ANCOVA). Sex of birds and social status (monogamous vs. polygynous pairs) were categorical predictors, and the time of season and brood size (number of young per nest) were continuous predictors to control the analysis for these potentially confounding variables. Relationship between nearest-neighbour distance of nest, and male and female nest defence behaviour was analysed with Pearson correlation coefficient for each sex separately. For this analysis, a single composite variable of nest defence behaviour as well as nearest-neighbour distance was regressed against the effect of social system.

Results

Nest Site and Breeding Characteristics

There were no apparent differences in vegetation structure and nest placement between monogamous females and polygynous primary females of this species (Table 1). The distance of monogamous nests from open water was slightly shorter than observed with those of primary females. However, this variable did not correlate with any nest defence components of males or females (partial correlations controlled for the effect of social system, all p's > 0.13, n = 45). Similarly, no differences were found in brood sizes or point in the breeding season between the two types of nests.

Finally, there were no differences in clutch sizes and brood sizes between polygynous and monogamous great reed warbler pairs (clutch size: 4.70 ± 0.11 vs. 4.53 ± 0.10; brood size: 2.48 ± 0.34 vs. 3.12 ± 0.30, $n_1 = 27$, $n_2 = 34$, Mann–Whitney

U-tests, $U = 367.0$ and 356.0, p = 0.18 and 0.14, respectively).

Nest Defence

Great reed warblers showed relatively high levels of aggression towards a human intruder. However, while most of females at both monogamous (20 of 31) and primary nests (10 of 14) detected the intruder immediately (within 30 s), they approached the human very closely (up to 1 m, 23/31 and 14/14, respectively) and repeatedly dived at intruder or even directly attacked him (19/31 and 10/14), responses of males were markedly poorer. Only 11 of 31 monogamous males and 1 of 14 polygynous males attacked the intruder and 20 of 31 monogamous males and 5 of 14 polygynous males approached him more closely. In contrast, only half of the monogamous and polygynous males detected the intruder within 30 s (15/31 and 8/14, respectively).

PCA factor loadings of time, distance and response were as follows: 0.25, 0.90 and −0.90, respectively. This suggests that strong responses were typical for birds responding from close distances from the human predator. More aggressive birds also tended to respond quicker than their less aggressive counterparts.

ANCOVA showed significant effects of sex and social status on nest defence behaviour ($F_{1,84}$ = 45.20 and 5.75, p < 0.001 and p = 0.02, respectively). The interaction between variables was also significant ($F_{1,84}$ = 18.83, p < 0.001). Time of season showed no effect on nest defence, but the effect of brood size was significant ($F_{1,84}$ = 0.83 and 10.17, p = 0.36 and p = 0.002, respectively). The results imply that monogamous birds defended their nests more strongly than polygynous birds and that

Table 1: Nest characteristics of monogamous and primary females

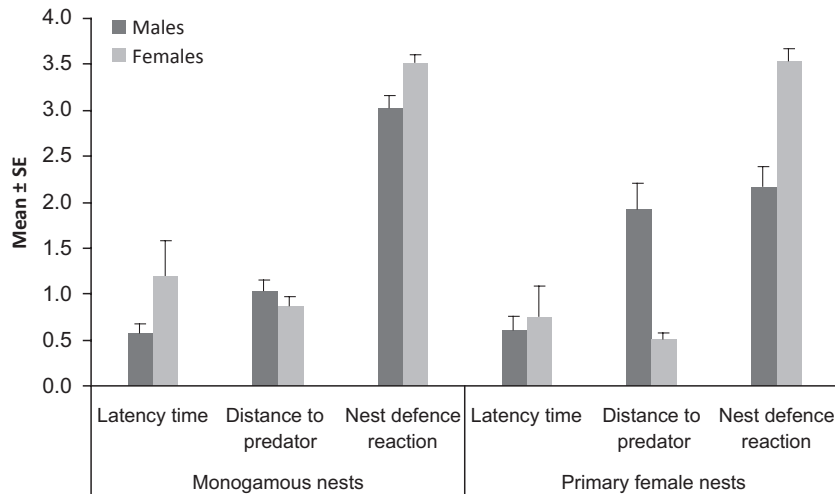|	Monogamous nests (n = 31)		Primary female nests (n = 14)				
	mean	±SE	mean	±SE	t	df	p
Vegetation structure							
Density of stems (n)	59.97	3.74	55.29	5.32	0.76	43	0.45
Height of stems (m)	1.96	0.05	1.99	0.09	−0.38	43	0.71
Diameter of stems (cm)	0.89	0.01	0.88	0.02	0.86	43	0.39
Nest placement							
Distance from open water (m)	0.94	0.11	1.51	0.27	−2.43	43	0.02
Distance from nearest nest (m)	68.06	7.28	78.57	23.44	0.45	43	0.65
Other variables							
Brood size (n)	3.61	0.18	3.71	0.30	−0.25	43	0.80
Point in breeding season (1 = 1.6. 2008)	22.00	1.23	18.79	1.75	1.59	43	0.12

Fig. 1: Male and female great reed warbler defensive behaviour under two social systems.

females defended nests more intensively than males. Interaction between variables suggests that polygynous males defended their nests less vigorously than their monogamous counterparts (Scheffe's *post hoc* test, p < 0.001, Fig. 1) supporting prediction 1, but contrary to prediction 3, there were no differences in the intensity of nest defence between monogamous and polygynous females (Scheffe's *post hoc* test, p = 0.59). In agreement with our second prediction, polygynous males defended nests less intensively than primary females (Scheffe's *post hoc* test, p < 0.001), but monogamous males showed similar intensity of nest defence behaviour to monogamous females (Scheffe's *post hoc* test, p = 0.22). Interestingly, birds with lower numbers of young defended their nests more intensively than birds with greater brood size. However, an additional linear regression revealed that this effect was significant only for males but not for females (r^2 = 0.14 and 0.03, p < 0.01 and 0.25, respectively). Distance to the nearest neighbouring nest did not influence male or female nest defence behaviour (r = −0.13 and −0.14, both p > 0.36, $n_1 = n_2 = 45$, respectively).

Discussion

Our results show a clear relationship between nest defence intensity and social mating system in the great reed warbler males. In agreement with sexual selection theory, sexual conflict over parental care was more intensive in polygynous pairs relative to monogamous pairs. As far as we know, this is the first study examining the role of social systems and sexual differences in nest defence in this species.

The risk to parents when defending their brood is known to increase with decreasing distance to the predator and with increasing intensity of display (defensive) behaviour (Montgomerie & Weatherhead 1988; Brunton 1990; Lima & Dill 1990; King 1999, Pavel & Bureš 2001, 2008). Socially monogamous great reed warbler males defended their nests more intensively than socially polygynous males defending the nest of their primary female. Thus, they seem to risk more than their polygynous counterparts. On the other hand, higher intensity of their nest defence against nest predators may improve the chances of offspring survival (Knight & Temple 1986; Tryjanowski & Golawski 2004; but see Hatch 1997). A difference in nest defence intensity between socially monogamous and socially polygynous males, therefore, may indicate the potential for higher level of sexual conflict over parental care driven by polygamy (Parker 1979; Chapman et al. 2003; Arnqvist & Rowe 2005). In our study, polygynous great reed warbler males possessed two simultaneously active nests at a particular time when our experiment was carried out. Thus, possible allocation of parental care, including nest defence, and higher reproductive potential of polygynous males may also be responsible for differences in nest defence intensity between males of two types of social systems. This is also in agreement with the reproductive value hypothesis (Montgomerie & Weatherhead 1988; Redondo 1989; Pavel & Bureš 2008). The most parsimonious explanation for our findings is that monogamous males with a single active nest may pursue different nest defence strategy than polygynous males that possess two active nests indicating that nest defence intensity of males might be influenced by the number of active nests. However, as only socially polygynous males may have two or more simultaneously active nests in a given season, it is social mating system that may, at

least indirectly, contribute to driving this pattern. Other studies comparing nest defence at sole surviving polygynous nests and monogamous nests, however, are needed to test this question.

Additional factors could also have some influence upon our results. Several studies have shown, for example, that males may defend their nests less vigorously when they contain nestlings sired by other males (Montgomerie & Weatherhead 1988; Weatherhead et al. 1994). In the great reed warbler, however, this explanation seems less likely because of low frequency of broods with extra-pair young (5.4–10.4%; Hasselquist et al. 1995; Leisler et al. 2000; Arlt et al. 2004). Similarly, variation in nest defence intensity in great reed warblers might relate to individual differences in their personality. It means that bold individuals may be more aggressive and take more risks in the presence of predators than shy individuals regardless of social mating system. Such positive relationship between personality and nest defence behaviour has been found in great tits *Parus major* (Hollander et al. 2008). Significant repeatability for both males and females in the aggression scores across years, where bold birds were bold and shy were shy, has also been found in a Swedish great reed warbler population (S. Bensch, pers. comm.). Although it seems unlikely that majority of socially monogamous males in our population were bold, the role of personality in great reed warblers in nest defence, however, should be explored in the context of social mating system as well.

Finally, nest defence intensity of great reed warblers may be influenced by habitat structure and study location. In our study site, the great reed warbler breeds in narrow strips of reed where there are limited opportunities for sheltered nest sites in contrast to large reed marches or lakes, where the birds may rely more on nest concealment and, probably, modify their nest defence behaviour accordingly. Moreover, important role may also play different nest predation pressures between study localities where natural great reed warbler nest predation may range from 24% to 43% (see Bensch and Hasselquist 1994, Hansson et al. 2000b; Batáry & Báldi 2005; Moskát et al. 2008; Trnka et al. 2009).

In contrast to males, female great reed warblers defended their nests with the same degree of intensity regardless of social system. Generally, however, they took a bigger role in nest defence than males in all cases. This finding is somewhat surprising considering that primary females experienced lower share of male nest defence assistance as monogamous females. One should expect from primary females

behavioural compensations in the form, for example, of higher nest defence responses. However, further experimental studies of sex-specific roles in great reed warbler nest defence against nest predators are needed to explain this behaviour. Different roles by great reed warbler males and females were shown in anti-parasitic nest defence by Požgayová et al. (2009). In this system, males took on the key role in fighting off cuckoo parasites and nest guarding while females were responsible for nest checking and the rejection of parasite eggs.

In conclusion, this study supports an idea that sexual conflict driven by polygamy and that type of social mating system can influence nest defence behaviour of facultatively polygynous birds, at least in case when nestling periods of primary and secondary broods of polygynous males overlap. This fact should be taken into consideration when studying nest defence parental care in polygynous mating systems.

Acknowledgements

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