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Original Article

To compensate or not to compensate: testing the negotiation model in the context of nest defense

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Theory of parental care in biparental species predicts that a decrease in 1 mate's parental effort should trigger a partial increase of care by the other mate. Previous studies investigating compensatory behavior used nestling provisioning as the measure of parental effort. However, nest defense is also a costly component of parental care because defenders risk injury or death caused by predators. Here for the first time, we test the compensation hypothesis in the context of nest defense. We experimentally widowed (by temporarily removing the other mate) female or male great reed warblers *Acrocephalus arundinaceus* and faced them with a predator near the nest (the stuffed Eurasian sparrowhawk *Accipiter nisus*). Female responses were independent of their partner's presence or absence. In contrast, lone males did not compensate for the absence of their mates; they even behaved more aggressively when their partner was present, contradicting the partial compensation hypothesis. We discuss potential determinants of between-species variation in sex-specific compensatory behavior. We predict that a lack of compensation might be found in species with different renesting and remating potentials between males and females, for example, where males are unwilling/unable to raise the brood when unassisted by females and therefore, avoid an investment that cannot increase their fitness. *Key words:* negotiation model, nest defense, partial compensation. *[Behav Ecol]*

INTRODUCTION

Parental care theory predicts that parents should invest in rearing their offspring when the benefits of care outweigh the costs (Trivers 1972; Clutton-Brock 1991). In biparental species, where both parents contribute to parental care, the benefits (if both parents are genetically related to the young they care for) are shared between them, whereas the costs of care are paid by each parent individually (Smiseth et al. 2005; Kosztolányi et al. 2009; Lessells and McNamara 2012). Therefore, it is in each parent's best interest that the other parent invests more resources in raising the young, resulting in a sexual conflict over levels of parental care (Clutton-Brock 1991; Houston et al. 2005).

If 1 pair member decreases its parental effort, its partner may then respond in 4 ways: continue caring at the same level, increase its own effort, decrease its own effort, or abandon the nest (Harrison et al. 2009). According to theoretical models, the optimal response to a reduction in parental investment by 1 partner is for the other to increase his/her effort (Wright and Cuthill 1989; Whittingham et al. 1994). However, given that full compensation for decreased mate effort would leave the parent open to exploitation, it should only partially redress a shortfall in care by its partner (Hinde 2006). Therefore, biparental care is predicted to be an evolutionarily stable strategy if a change in 1 parent's effort selects for change of smaller magnitude in the opposite direction by the other partner ("partial compensation hypothesis," Houston and Davies 1985; Wright and Cuthill 1989; McNamara et al. 1999; Johnstone and Hinde 2006).

Empirical studies, on the other hand, have revealed a much wider range of compensatory responses, from the lack of any response (Saether et al. 1993; Schwagmeyer et al. 2002) through partial compensation (Wright and Cuthill 1989, 1990; Whittingham et al. 1994; Markman et al. 1995) to full compensation (Jones et al 2002; Paredes et al. 2005). Moreover, some studies have also found sex differences in compensatory behavior (Sanz et al. 2000; Rauter and Moore 2004; Smiseth et al. 2005; Harrison et al. 2009; but see Paredes et al. 2005).

Most empirical studies investigating the compensatory hypothesis in animals have used nestling provisioning by birds as the proxy for variation in parental effort (for reviews see Paredes et al. 2005; Hinde 2006; Harrison et al. 2009). However, given that nest predation is a major cause of nesting failure in birds, nest defense is also important to parental fitness (Ricklefs 1969; Martin 1993). As defenders also risk their injury or death caused by predators (Regelmann and Curio 1986; Montgomerie and Weatherhead 1988), parents might respond differently to changes in a partners' nestling provisioning versus changes in its nest defense effort. Thus, nest defense may provide a strong, novel test of the partial compensation hypothesis.

In the present study, we therefore applied a novel experimental approach to test the compensatory hypothesis. We investigated behavioral responses of parents to the loss of

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their partners' nest defense assistance in a relatively large (~30 g) and highly aggressive passerine, the great reed warbler *Acrocephalus arundinaceus* (Kleindorfer et al. 2005; Honza et al. 2010; Trnka and Prokop 2012) by temporarily removing 1 parent (male or female) from monogamous breeding pairs and exposing the remaining parent to a predator, the Eurasian sparrowhawk *Accipiter nisus* (a taxidermic mount placed near the focal nest). The great reed warbler has a facultative polygynous mating system in which polygynous males provide much less parental care to their nestlings, including nest defense, than do monogamous males (Bensch and Hasselquist 1994; Sejberg et al. 2000; Trnka and Prokop 2010). This sets the stage for the evolution of compensatory behavior in females and makes this species an ideal model for testing the compensatory hypothesis.

In the great reed warbler, both parents participate in protecting their offspring but females generally play a larger role in direct nest defense than males do (Trnka and Prokop 2010, 2012). The "relative contributions" hypothesis predicts that only the sex that contributes relatively little to parental care will adjust its behavior after removal of its mate (Møller 2000; Hunt and Simmons 2002; Rauter and Moore 2004; Smiseth et al. 2005; Harrison et al. 2009). We, therefore, predicted that females would either show no change in defense behavior after losing their mate or increase their nest defense intensity less than experimentally temporarily widowed males.

METHODS

Study site and general field procedures

We conducted the study during breeding season 2011 on a color-ringed great reed warbler population by fishponds near Štúrovo, south-western Slovakia (47°51′N, 18°36′E, 115 m asl). For a detailed description of the study site, see Trnka and Prokop (2010, 2012). Great reed warblers breed there in narrow (~5–10 m wide) strips of reeds that border the ponds. The studied population consisted of 40–60 breeding pairs. Because of the relatively short breeding period of this species in the study area, great reed warbler females usually have just a single clutch per year. The nest predation rates average 20% (Trnka and Prokop 2012). The rate of polygyny (i.e., percentage of polygynous males) varies from 21% to 43% across years (Trnka and Prokop 2010, 2011).

Great reed warbler nests were systematically searched from the end of May to late July. The social mating status of each parent was determined on the basis of direct observations of color-ringed birds defending their nests or feeding young (for details see Trnka and Prokop 2010, 2011). In the present study, we examined only monogamous pairs that were raising their first nonpredated brood of the season.

Experimental procedures

Great reed warbler pairs in our study were randomly assigned to 3 treatments: (1) a group in which only the male was removed ("female alone" group, n = 15 nests), (2) a group in which only the female was removed ("male alone" group, n = 18 nests), and (3) a group in which neither of the 2 pair members were removed ("both" group, n = 11 nests). Mate removal was done by catching the focal parent in a 10-m long mist net stretched in its territory, away from the nest so as to not disturb the other partner. The captured bird was ringed, weighed, and measured (see below) and then put carefully into a cloth bag where it was held until the experiment was finished.

There were no differences in the date of experiment (Welch's ANOVA; $F_{2,24.95}$ = 0.12, P = 0.89) and brood size ($F_{2,23.10}$ = 0.72, P = 0.50) among the 3 treatments. Thus, our experiments were successfully randomized for timing within the breeding season and reproductive value of the brood, which might otherwise affect avian nest defense behavior.

Previous studies of great reed warbler nest defense behavior have shown that great reed warblers clearly considered the mount of the sparrowhawk a threat to their nests and/or themselves and attacked them aggressively (Honza et al. 2010; Trnka and Prokop 2012). Therefore we also used this avian predator (a male) in the present work. To reduce the probability that differences between treatments could be caused by a particular mount, we used 3 different mounts of the sparrowhawk and presented them in random order across nests (see Hurlbert 1984).

We followed previously established protocols recommended for nest defense studies (Sealy et al. 1998). The mounts were in life-like positions with folded wings and head pointing forward. In each experiment, the mount was placed 0.5 m from the focal nest at the same height as the nest. The experiment started when the nest owner(s) appeared in the immediate vicinity of the nest and spotted the mount. The response of the focal bird(s) was measured as the number of contact attacks per 1 min from the first physical contact between the focal nest owner(s) and the mount (see also Trnka and Prokop 2012). The experiment was finished after 5 min at nests where nest owner(s) did not attack the mount. Observations were made by the first author from a blind placed 5 m from the focal nest and double checked by the other observer from a distance of approximately 10 m (these distances are enough to avoid disturbing warblers in the study population, see Trnka and Prokop 2010, 2012).

All experiments were conducted in the late nestling stage when the chicks were 8–10 days old and under good weather conditions (no rain or strong wind). Based on our preliminary study (Trnka A, unpublished data), in the treatments of "female alone" and "male alone," the nest defense experiment was performed 2 h after the focal bird's mate removal so that the widowed pair member had enough time to adjust to the novel situation (as also evidenced by significant effects we found, see Results). Immediately after completing each experiment, the tested bird was mist-netted, weighed, and measured (see below) and then released back into its territory together with its removed partner. No adult or nestling died and no nest was depredated or abandoned within 2 days after the experiment.

Measurements of behavior, morphology, and condition

Following previous work (Sealy et al. 1998; Hogstad 2005; Grim 2008) including studies of the great reed warbler nest defense (Požgayová et al. 2009; Honza et al. 2010; Trnka and Prokop 2010, 2012), the responses of parents toward the mount of the sparrowhawk were evaluated as 3 variables that are established as standard measures of parental behavior in nest defense studies (Sealy et al. 1998 and references therein).

Contact "Attacks" (continual, count) quantified the number of strikes and pecks delivered to the mount per 1 min. Attacks represent probably the most energetically costly nest defense activity (Sealy et al. 1998) and also the highest risk to parents (Regelmann and Curio 1986).

General "Aggression" (ordinal, ranks) was measured using the following predetermined scale: 0 = the bird watched the nest silently from a safe distance, 1 = the bird approached the mount at a distance of 0.5–1 m giving short warning calls, 2 = the bird jumped closely around the mount giving alarm calls and rarely attacked it (less than 8 strikes or pecks per 1 min; median = 6 attacks), 3 = the bird flew around the

mount giving alarm and distress calls and more frequently attacked it (9–15 strikes or pecks per 1 min; median = 11 attacks), and 4 = the bird persistently gave distress calls and frequently attacked the mount (more than 16 strikes or pecks per 1 min; median = 18 attacks). We used general "aggression" to measure the willingness of parents to engage in direct nest defense. More aggressive defenders are more likely to be successful in fighting predators, but they also face a higher risk of being injured or killed and may attract other nest predators (Montgomerie and Weatherhead 1988; Grim 2008).

Latency to "Arrival" (continual, s) quantified the time lag from the moment when the observer retreated to the blind to the focal individual's arrival to the immediate vicinity of the focal nest. Latency to arrival reflects time spent by parents near nest (i.e., nest guarding behavior) as it can also be costly because it reduces time available for feeding and other activities (Komdeur and Kats 1999).

As nest defense intensity can be affected by the size and body condition of defenders (Montgomerie and Weatherhead 1988; Hogstad 2005), we measured all tested birds for the following morphological variables: the length of their left wing and tarsus (measured with a ruler to the nearest 1 and 0.1 mm, respectively) and body mass (with a Pesola scale to the nearest 0.1 g). We then calculated their body condition as residuals from the regression of mass on tarsus length (relationship was nonlinear: $F_{2,52} = 15.54$, $P < 0.0001$; quadratic term: $t = 2.40$, $P = 0.02$; mass = 0.41 + 1.10 × tarsus − 0.46 × [tarsus]^2).

Females ($n = 26$) were smaller than males ($n = 29$) in all measured morphological traits (data pooled across treatments, wing length: $t_{49.27} = 5.89$, $P < 0.0001$; tarsus length: $t_{52.92} = 4.21$, $P < 0.0001$; mass: $t_{47.45} = 4.33$, $P < 0.0001$; condition: $t_{51.90} = 2.48$, $P = 0.02$). Trends remained the same but some differences failed to show statistical significance when data were analyzed separately by experimental treatments (Table 1). We note that these differences and/or trends are opposite to those that would be expected if morphological traits of the 2 sexes biased or explained our findings.

Most importantly, females assigned to the 2 treatments (mate removal "alone" and control "both") did not differ in their phenotype and body condition (Table 2). Also, males did not vary in most of their morphological traits between the treatments (Table 2). In a single case where there was a statistically significant difference in morphological traits in males assigned to "alone" and "both" treatments (wing length), the effect size was very small (2 mm, longer in "both" treatment, Table 1). This was most likely biologically irrelevant as evidenced by the nonsignificant correlation between number of contact attacks and wing length (see above).

Statistical analyses

The unpaired continuous data (Arrival, Attacks) from "female alone" and "male alone" treatments were analyzed with the unequal variance *t*-test (i.e., Welch's *t*-tests), which performs better than both the equal variance *t*-test and Mann–Whitney test (see Ruxton 2006). The unpaired ordinal data (Aggression) from the "alone" treatments were analyzed with the Mann–Whitney test. The paired data (Arrival, Attacks, Aggression) from the control "both" treatment were analyzed with Wilcoxon sign-rank tests for paired data.

We employed Spearman rank correlations (r_s) for examining relationships between responses of partners within a pair (the control treatment). Differences in date of experiment and brood size among the 3 groups of nests were tested by Welch's ANOVAs assuming unequal variances (Ruxton 2006). All calculations were performed in JMP 8.0.1.

Table 1

Differences in phenotypic parameters (mean ± SE) of female and male great reed warblers at nests where only 1 sex was present at the nest (unpaired "alone" treatment, analyzed with Welch's *t*-tests) or both parents were present (paired "both" treatment, analyzed with Wilcoxon sign-rank tests)

	Alone				Both			
Parameter	Female ($n = 15$)	Male ($n = 18$)	t	P	Female ($n = 11$)	Male ($n = 11$)	Z	P
Wing	91.3 ± 0.7	95.3 ± 0.6	4.48	0.0001	93.1 ± 0.7	97.3 ± 0.5	27.5	0.002
Tarsus	27.7 ± 0.2	28.8 ± 0.2	4.30	0.0002	28.3 ± 0.2	29.1 ± 0.3	18.5	0.07
Mass	30.1 ± 0.5	32.5 ± 0.3	3.74	0.001	30.4 ± 0.5	31.8 ± 0.4	21.0	0.06
Condition	–0.31 ± 0.4	0.67 ± 0.4	1.87	0.07	–0.81 ± 0.5	0.1 ± 0.4	13.0	0.28

For a definition of terms and calculation of condition, see Methods.

Table 2

Within-sex comparisons of behavioral and phenotypic traits between "alone" and "both" treatments

Parameter	Female			Male		
	t	ddf	P	t	ddf	P
Arrival	0.47	15.97	0.65	1.35	26.15	0.19
Attacks	0.21	23.95	0.84	2.00	17.56	0.06
Aggression	0.68	24	0.49	3.23	27	0.001
Wing	1.73	22.71	0.10	2.66	26.80	0.01
Tarsus	1.89	19.97	0.07	0.64	16.06	0.53
Mass	0.46	23.74	0.65	1.15	21.11	0.26
Condition	0.84	21.83	0.41	1.01	22.82	0.32

For effect sizes, see Table 1 (phenotypes) and Figure 1 (behavior). Differences tested with Welch's *t*-tests except for "aggression" (ordinal variable), tested with a Mann–Whitney test. ddf, denominator degree of freedom.

RESULTS

General responses

Females were more aggressive and attacked sparrowhawk mounts much more frequently than males (Figure 1) in both male removal "alone" treatment ($t_{24.29}$ = 5.38, P < 0.0001) and control "both" treatment (Z = 33.0, degrees of freedom [df] = 10, P = 0.001). When data were analyzed on an ordinal scale (see Methods) we again found significantly stronger response of females in "alone" treatment ($U_{15,18}$ = 4.08, P < 0.0001) and the control "both" treatment (Z = 10.5, df = 10, P = 0.03; Figure 1).

Latency to arrival did not differ between sexes when each was "alone" ($t_{23.25}$ = 1.22, P = 0.24) but females arrived at their nests slightly later than males when "both" parents were allowed to respond to the enemy near their nest (Z = 18.0, df = 10, P = 0.04). However, in the latter experiments where both parents participated in nest defense, males never launched the attack before their females did. Females initiated attacks at 55% of such nests (n = 11) and both sexes simultaneously at the rest of the nests.

There was no correlation between the number of attacks by males and females in the "both" treatment (r_s = 0.39, n = 11, P = 0.24). However, there was a strong positive correlation between latencies to arrival of partners at the same nest (r_s = 0.96, n = 11, P < 0.0001).

Across all tested individuals (n = 55) the correlation between latency to arrival and number of attacks was nonsignificant (r_s = –0.23, P = 0.09). The number of contact attacks did not correlate with body mass, tarsus length, wing length, or condition in both females (r_s from –0.36 to 0.07, n = 26, P from 0.07 to 0.68) and males (r_s from –0.17 to 0.07, n = 29, P from 0.37 to 0.97).

Male and female responses to mate removal

Males and females showed significantly differential responses to the experimental removal of their mate. There were no detectable differences in nest defense behavior between temporarily widowed females (female "alone" treatment) and females that defended nests together with their partners (females from "both" treatment, Table 2 and Figure 1). In contrast, experimentally widowed males (male "alone" treatment) defended their nests significantly less aggressively than males accompanied by their partners (males from "both" treatment, Table 2 and Figure 1).

DISCUSSION

The present study tested whether parents of altricial birds adjust their nest defense behavior in response to the experimental temporal removal of their partner. This represents a novel experimental approach as previous studies investigating the compensatory hypothesis in birds have used nestling provisioning as the proxy for variation in their parental effort (for reviews see Paredes et al. 2005; Hinde 2006; Harrison et al. 2009). The negotiation model (Houston and McNamara 1999) predicts that both sexes should compensate for the loss of help from their mates. In the present study, however, neither male nor female great reed warblers behaved consistently with this critical prediction. Females defended their nests similarly, regardless of the presence or absence of their partners. Responses of lone males to a mounted sparrowhawk were significantly lower than those of males defending the nest in the presence of their mate. Thus, the direction of the difference between lone versus accompanied males was opposite to that predicted by the compensation hypothesis. This seems to be a unique finding as previous studies have reported a wide range of parental responses to the loss of or reduction in their partner's parental care, from no response to full compensation (Wright and Cuthill 1990; Saether et al. 1993; Whittingham et al. 1994; Markman et al. 1995; Sanz et al. 2000; Schwagmeyer et al. 2002; Paredes et al. 2005; Harrison et al. 2009). However, in contrast to the present study, no other research has found birds to respond negatively

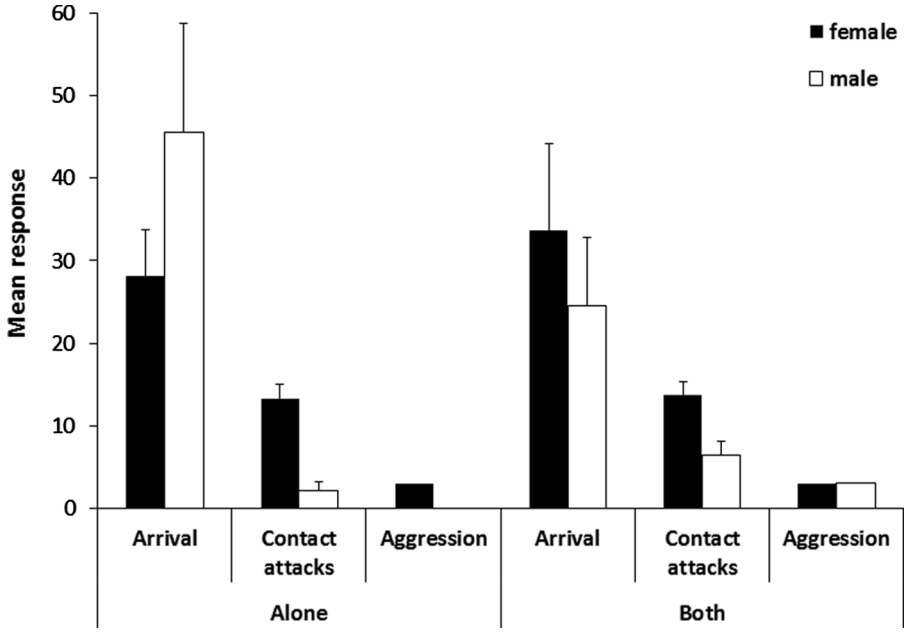

Figure 1
Great reed warbler responses (mean + standard error [SE] for Arrival and Contact attacks, median for Aggression) to sparrowhawk dummy near their nests measured as latency to arrival (s), contact attacks (number of attacks per 1 min), and aggression (ordinal scale; see Methods for details). During experiments, either only 1 parent was allowed to respond (the other sex was temporarily removed for the experimental period; "alone" treatment) or both parents were present near the nest ("both" treatment).

to a mate's reduced effort (but see retaliatory behavior in a long-lived species; Dearborn 2001).

There have been many variables proposed that could affect compensatory behavior by males and females, such as time of season, brood size, mating system, and others (for a review see Harrison et al. 2009). In the present study, we therefore aimed at specifically avoiding the most important confounding factors detected in previous studies. All experiments were conducted only on the first nonpredated monogamous nests and successfully randomized with respect to timing in the season and brood size (see Methods). Similarly, male and female phenotypes did not differ across the treatments (Table 2).

Given that only the female builds the nest and incubates eggs and broods in the great reed warbler, renesting is highly costly for them (Cramp 1992; Hansson et al. 2000). Moreover, it may result in the loss of their current mating status (monogamous in the case of our study; Bensch 1996; Trnka A, unpublished data). Thus, it is beneficial for them to keep the first brood of the season (that we tested in the present study) alive. We, therefore, assume that high costs of renesting are the main cause for observed female nest defense behavior. A potential explanation for the lack of female compensation in male removal experiments (female "alone" treatment) is that females were unable to respond to the absence of male assistance because they were already working at their maximum physical capacity (a "ceiling" effect, see also Markman et al. 1996; Rauter and Moore 2004; Smiseth et al. 2005; Suzuki and Nagano 2009). This was also suggested by their very high levels of aggressive behavior in all our experiments (this study; Trnka and Prokop 2010).

In contrast, great reed warbler males behaved significantly less aggressively toward predators near the nest than females in both mate removal and nonremoval treatments and were least aggressive in the male "alone" treatment. This is in stark contrast with the above-mentioned negotiation and relative contributions models (Møller 2000; Hunt and Simmons 2002; Smiseth et al. 2005) because these models predict that temporarily widowed males should attack the mount of the sparrowhawk more vigorously than nonwidowed males. Previous studies have shown that males of some species can change their parental effort in response to likelihood of paternity (Dearborn 2001). In the great reed warbler, however, males generally experience a low level of cuckoldry (Hasselquist et al. 1995; Leisler et al. 2000) and thus males' compensatory behavior seems to be less affected by certainty of their parentage, although the paternity is less than certain for males. However, given that great reed warbler males are facultatively polygynous and thus, they may attract and hold additional females in their territories for breeding, different remating opportunities may be another possible explanation for behavioral differences between the sexes in the "alone" experimental treatment groups.

Finally, we found that attacks against mounts of the sparrowhawk were generally initiated by females that were also much more aggressive than males, whereas males never launched a direct attack before their mate did ("control" treatment in this study; see also Trnka and Prokop 2012). Thus, females play a leading role in defending the nests against predators. We therefore assume that when the female is not participating in nest defense (male "alone" treatment), the male may decide not to attack the intruder, or risk less when defending the nest because he is uncertain of the necessity and efficiency of defense action. Thus, males' decisions about their nest defense strategy may depend primarily on their partners' behavior. This prediction is in agreement with the previous "information" model (Johnstone and Hinde 2006) suggesting that parents may glean extra information about the need of parental care from the behavior of their partner and behave accordingly.

In conclusion, our study shows that birds may behave inconsistently with current theoretical models of compensatory biparental care in the context of nest defense and that conclusions of previous studies using food provisioning as a metric for partner compensation do not automatically extend to all parental effort. This may provide new insights into the general problem of evolutionarily stable parental care. These results, however, do not cast doubts on previous predictions but rather suggest that the compensatory parental behavior may be context dependent and, therefore, future studies investigating compensatory hypotheses should also use other components of parental care as the proxy for variation in parental effort. Similarly, given that birds may respond differently to partner removal and partner handicapping, and do so differently in feeding and other parental efforts (McNamara et al. 2003; Harrison et al. 2009), additional studies comparing the responses to the 2 experimental manipulations and employing all types of parental effort parameters could prove to be highly valuable.

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