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ARTICLE

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Sex differences in nest defence by the red-backed shrike *Lanius collurio*: effects of offspring age, brood size, and stage of breeding season

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Abstract The red-backed shrike *Lanius collurio* is an open-cup nesting passerine bird, which protects its nest aggressively attacking predators near the nest. The response of parents to a human observer was investigated during the nesting period 1999–2001 in Poland. The intensity of nest defence increased as the breeding cycle progressed in accordance to the offspring value hypothesis. However, we did not find an increase in the level of aggression according to the number of offspring and the time of season. Contrary to previous predictions, we did not find gender differences in nest defence. More aggressive parents, both females and males, have significantly better breeding success than quieter individuals.

Key words Red-backed shrike · *Lanius collurio* · Nest defence · Breeding success · Predation

Introduction

Nest predation belongs to the major causes of nesting failure in birds (review in Martin 1993). One of the tactics of avoiding nest predation is vigorous nest defence (Edmunds 1974). The parents may increase the chance of survival of their offspring by nest or youngster defence (Montgomerie and Weatherhead 1988). However, defence behaviour may be costly, because parents risk injury caused by predators (Sordahl 1990). In addition, it may help predators localise the nest (McLean et al. 1986) as well as significantly reducing the time of foraging and parental care (Ueta 1999).

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The costs of defence may differ between the sexes; for example, one of them may be exposed to higher risks of being injured than the other or one may lose more time on defence than the other (Slagsold 1985, Kis et al. 2000).

In the present study we examine the effect of brood characteristics on nest defence behaviour in a small passerine bird, the red-backed shrike *Lanius collurio*. The species is extremely suitable for such a study because of its highly aggressive nest defence behaviour towards potential predators, including humans (Gotzman 1967, Ullrich 1993). Male red-backed shrikes tend to be larger than females (review in Kuźniak and Tryjanowski 2003). If size relates to the success of driving predators away from the nest, then males are expected to defend their nest more intensively than females (Montgomerie and Weatherhead 1988).

Therefore, the main aim of the study was to test the strength of the antipredator behaviour of red-backed shrikes during the nesting cycle, and to analyse how this behaviour influences nest success. We also analysed intersexual differences in nest defence in the red-backed shrike.

Methods

The red-backed shrike is a small passerine species that breeds in shrubs of semi-open habitats in the middle latitudes of the western Palearctic. Females lay 3–7 eggs and incubate for 14 days whilst being occasionally fed by males. Nestlings are cared for and fed by both parents for 14 days in the nest and with decreasing intensity for about 1–2 weeks after fledging (Olsson 1995). Disturbed nestlings can leave the nest earlier (Olsson 1995, Tryjanowski and Kuźniak 1999).

The study was carried out in farmland of the Mazovian Lowland (CE Poland) between the years 1999 and 2001. The red-backed shrike was amongst the most numerous species with a density reaching 1.7 breeding pairs/10 ha. The most important nest predators were the magpie *Pica pica*, the jay *Garrulus glandarius* and the hooded crow *Corvus corone*. We searched the area for nests and the majority

were found during incubation. The located nests were put on a detail plan of the study area and not marked in the field. The nests were checked regularly, but due to the possibility of strong human impacts on nest success (Tryjanowski and Kuźniak 1999), only 1–5 visits (depending on nest searching time) were made every 4–5 days. The age of nestlings was determined according to either the day of hatching (day when the last egg was laid is day 0, hatching day is day 14; Kuźniak 1991; Olsson 1995). Distraction displays were recorded in response to the brood disturbance caused by an approaching researcher. The observer directly approached the nest entrance until the female departed. Female red-backed shrikes incubate eggs and rear nestlings (Panow 1996, Kuźniak and Tryjanowski 2003) while males generally spend time in the close surroundings of their nests and sometimes alarm the incubating female. Therefore, in this study we recorded alarm behaviour of both genders.

The antipredator mechanism was studied one to five times on different days at each nest (mean ± SE = 2.6 ± 1.3). Knight and Temple (1986) argued that the number of presentations (in this context visits to the nest) may influence the intensity of nest defence. We investigated this idea, but none of our findings supported the argument of Knight and Temple (1986). We found no evidence that the number of nest visits was related to the intensity of mobbing ($r_s = 0.100$, $N = 235$, n.s.) and nest division behaviour. However, in accordance to statistical pseudoreplication problems in further analysis we used only data obtained during the first nest controls.

The following data, which reflect the risk taken by parents (dependent variables) were recorded for each experiment: (1) the intensity of intruder's attention distraction – *intensity of display*; (2) the researcher–nest distance (accurate to the nearest 10 cm) when the female left the nest – *flushing distance*. The responses of the red-backed shrike varied from a straight-line flight away from the nest with no distraction displays to a directional attack on the observer, during which parents intensively distracted the potential predator away from the nest. The intensity of display was ranked (separately for females and males) on a subjective scale depending on the risk taken by the bird during nest control from 0 (minimum risk, no calling by parents) to 2 (maximum risk, a parent attacked an observer) (cf. Pavel et al. 2000). The sum of distraction displays for both sexes were used as the intensity of parental care of the pair.

Nest defence responses were compared at each stage of the nesting period (egg laying, incubation and nestling) between depredated nests and nests that were successful. For depredated nests only the last visit before predation occurred was used in these comparisons because nest defence behaviour changed significantly during the breeding cycle.

Because parental nest defence is sometimes related to weather conditions (e.g. Slagsvold 1985), we visited the nests only on days with good weather (no rain, temperature above 13°C).

Data were analysed using SPSS software (Norusis 1994). Since we found no significant differences (ANOVA, in all comparisons $P > 0.2$) between three study years in nest defence, data from these years were pooled. All statistical tests are two-tailed.

Results

Description of antipredator behaviour

Females of red-backed shrike incubate rather persistently and leave the nest at distances of 20–300 cm (mean ± SD 97 ± 62, $n = 44$) from a researcher. The distance to which females left the nest, incubated eggs and heated nestlings did not differ significantly [106 ± 67 ($n = 30$) vs 84 ± 51 cm ($n = 11$), $t = 0.99$, $P = 0.327$). Moreover, we found no significant difference in the nest flushing distance in nest stages with eggs and nestlings, even when we controlled the time of season (ANCOVA, $F_{1,38} = 0.67$, $P = 0.41$, with number of visits and progression of a breeding season as covariates).

Influence of offspring age, offspring number and time of season

In the presence of a human observer, intensity of nest defence significantly increased with the age of offspring (partial $r = 0.334$, $P < 0.001$, when the offspring number and season advancing are held constant, $n = 120$ observations). However, the level of aggression did not change with the number of offspring (partial $r_p = 0.055$, $P = 0.604$, when the offspring age and season advancing are held constant) and the progression of breeding season (partial $r = 0.007$, $P = 0.941$, when the offspring number and the offspring age are held constant).

Difference between the sexes

During the first controls females were aggressive due to a human observer in 14 cases (12.6%), males in 14 cases (12.6%), and both parents reacted during 7 visits (6.3%). Therefore, differences between genders were absolutely non-significant.

Did more aggressive birds have better breeding success?

Nests of pairs with at least one aggressive partner had better breeding success (at least one young fledged successfully) than nests of non-aggressive birds (72.4% vs 46.3%; $n = 29$ and 82, respectively, chi-square = 5.85, $P = 0.016$, Fig. 1). Moreover, the mean number of fledglings of aggressive parents was higher than non-aggressive individuals (mean ± SD 3.3 ± 2.1 and 2.1 ± 2.4, respectively, Z = 2.22, $P = 0.026$, Fig. 1).

Discussion

Observed antipredatory behaviours are typical in the red-backed shrikeand have also been shown by other authors

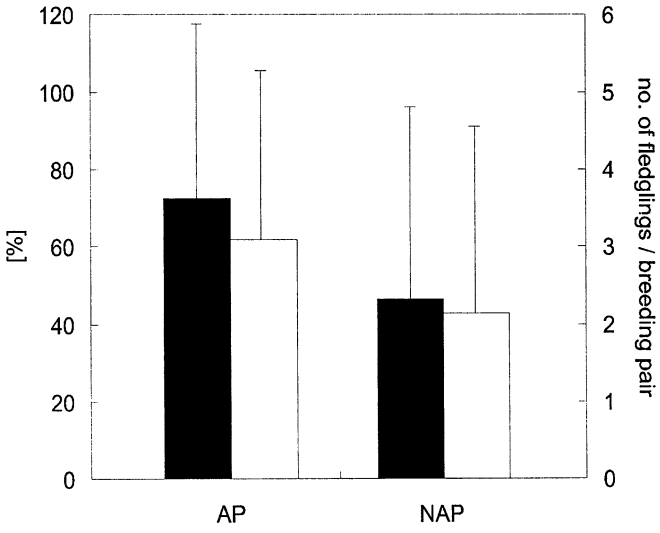

Fig. 1. Differences in breeding success (*black bars*, left scale) and number of fledglings/breeding pair (*white bars*, right scale) between aggressive (*AP*) and non-aggressive (*NAP*) pairs of the red-backed shrike. Error bars are 1 SD. Statistics, see text

(review in Panow 1996; Kuźniak and Tryjanowski 2003). Ash (1970) and Ullrich (1993) experimentally indicated that shrikes are very aggressive against potential predators. These include birds, for example the jay *Garrulus glandarius*, the barn owl *Tyto alba* and the great grey owl *Strix nebulosa*; mammals, for example, the domestic cat *Felis catus*and the red fox *Vulpes vulpes*; and humans *Homo sapiens* (Gotzman 1967, our own observations). Sometimes they might even mob a predator socially, in a group of up to four birds (cf. Beaud 2000).

The pattern of increase in nest defence intensity over the nesting stages found in this study supports the hypothesis of the brood's increasing value to the parents (e.g. Greig-Smith 1980; Montgomerie and Weatherhead 1988; Halupka 1999). Intensity of nest defence agrees with the findings of Gotzman (1967). He found that females of the red-backed shrike more frequently deserted the nest earlier and defended the nest more intensively with increasing offspring value.

However, Knight and Temple (1986) questioned this explanation and interpreted increased defence intensity as an effect of revisitations. Although, we found no evidence of habituation, similar to many other authors (e.g. Kis et al. 2000; Sergio and Bogliani 2001), we used only data for first nest control. We performed this kind of analysis to avoid the problem of statistical independence of data (pseudoreplication), because the nest is not an independent statistical point.

In opposition to some predictions, we did not find changes in nest defence due to offspring number and season advancing. However, the only way to advance research of this problem is the experimental manipulation of brood size (e.g. Redondo 1989; Halupka 1999). Similarly, our results do not support the prediction that diminishing renesting potential should enhance nest defence during the season (Halupka and Halupka 1997 and literature cited there). The influence of this factor, however, may have been balanced by the decrease in offspring value due to diminishing survival prospects. As the season progressed, the offspring mortality increased as a result of adverse weather and decline in food abundance, especially insufficient food delivery (Leugger-Eggimann 1997).

The level of aggression between sexes was similar in our study. It was contrary to the prediction that the bigger sex (males) should have attacked predators more intensively than the smaller sex (females). Moreover, mobbing of predators may be a part of self-advertisement and evidence of male condition (cf. Slagsvold 1985; Redondo 1989). On the other hand, females are more sure of parentage than males, especially because EPC occurs in the red-backed shrike populations (Jakober and Stauber 1994). These two different selection pressures can modify patterns of nest defence according to sex; hence a clear pattern in non-experimental studies is not easy to detect.

Results clearly show nest defence against potential predators (human observer) improved the chances of offspring survival. This is supported by studies in which successful pairs showed higher nest defence intensity than those suffering nest predation (Greig-Smith 1980, Knight and Tample 1986).

Aggression of parents can be considered an equivalent of parental quality, for example physiological condition due to blood parasites (Hakkarainen et al. 1998). Hence, better breeding success might be connected not only with parental aggression to predators, but simply with parental condition. However, one of the possible conditions of parental quality used in our studies (clutch size) does not affect their nest defence.

However, not all red-backed shrike individuals are very aggressive. Sometimes birds, mainly females, act as dead birds during nest control (S. Kuźniak and P. Tryjanowski, unpublished data). Ash (1956) and Hernandez (1993) found that mimetic reaction against predators is more effective than aggressive behaviour. Maybe in specifically poor environmental conditions (e.g. with very high predation pressure, unfavourable weather, and poor food conditions) when aggression is very costly the more efficient strategy is mimetic posturing. Future studies should focus on this problem.

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