Costly replacement: how do different stages of nest failure affect clutch replacement in the red-backed shrikes *Lanius collurio*?

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Re-nesting is costly and strongly stage- and time-related in the red-backed shrike. We tested whether failure which occurred at more costly developmental stages of the first clutches influenced the characteristics of replacement clutches in red-backed shrike *Lanius collurio*. Field work was conducted in the breeding seasons 1999-2006 at three study plots in Poland. During nest visits, standard data on breeding biology were collected, including clutch size, eggs measurements, laying date, and number of nestlings. We found significant differences in the clutch size of replaced clutches according to the failure phase of first clutches. Pairs which experienced brood failure at the nestling phase produced smaller replacement clutches than pairs whose nest was destroyed at the egg laying stage. There were no differences in the nesting success of replaced cluches relative to the stage where the first clutch was lost. However, pairs which failed during the nestling phase of the first clutch significantly more often skipped further reproduction in that season than those which failed during other phases. For breeding red-backed shrikes the best strategy is to initiate clutches as early as possible because it gives a more time for possible re-nesting.

KEY WORDS: breeding success, cost of breeding, *Lanius collurio*, red-backed shrike, replacement clutches.

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INTRODUCTION

One of the most common features of avian biology are breeding losses and several bird species produce replacement clutches after having lost previous ones (e.g. Martin 1995, Mcfarlane Tranquilla et al. 2003, Takagi 2004, Tryjanowski et al. 2004). Producing replacement clutches represent one of the classical trade offs between current reproduction and survival prospects for both adults and nestlings (Lessels 1991). First of all, each failure of a nesting attempt decreases individual productivity in a given season. Moreover, nest failure might strongly influence the adult's survival and reproductive effort in the future as well as in terms of its overall lifetime reproductive gain (Newton 1989). In one-brood species the number of young produced depends on clutch size and on the probability of nest survival (Martin 1995). If the first clutch fails, birds have the possibility of laying a replacement clutch (Newton 1989, Martin 1995, Takagi 2004). Decision rules impacting on individuals producing or not producing replacement clutches might be constrained by several factors such as the duration of the breeding season, the timing of the breeding losses, the condition of the female and, finally, potential food resources (Takagi 2004).

It is a well known pattern in avian biology that clutch size decreases with the progress of the breeding season, and late clutches, including replacement ones, are smaller than first clutches (e.g. Kuźniak 1991, Rooneen & Robertson 1997). To date two groups of hypothesis were proposed to explain this seasonal decline in clutch size. The first group states that there is a casual link between the time of breeding and reproductive success due to declining levels of food resources during the course of the breeding season and to the reduced parental effort of late breeders which results in lower chances of survival of the young (cf. Christians et al. 2001 and citations therein). The second group, quality hypothesis, matches the time of reproduction with several components of individual quality. In general high quality individuals start breeding early, are more competitive over high quality territories and potential mates which results in larger clutch sizes (Nilsson 2000, Christians et al. 2001 and citations therein). Early arrival and start of breeding results in a higher reproductive output in several bird species. Also early hatched young have higher survival prospects than later ones due to differences in condition, body mass and immunocompetence (Sorci et al. 1997).

However, this general pattern does not occur in some species (Takagi 2004). Despite that fact, ecological factors affecting re-nesting (Arnold 1993) are rarely investigated. Nesting failures might take place at different stages

of the breeding cycle, and this implies differences in the potential costs for parents and therefore different chances for replacement. Ideally, it would be most accurate to study the cost of failure at particular nesting stages; however any proper experiments were done only during the incubation stage (ARNOLD 1993, ROONEEN & ROBERTSON 1997, NILSSON 2000, CHRISTIANS et al. 2001, DOUTRELANT et al. 2008, MORALES et al. 2008). Moreover, studies of this type raise ethical questions as well, because, to reduce breeding success, nests with developed nestlings must be destroyed (TRYJANOWSKI et al. 2004). Among the studies dealing with the re-nesting behaviour of birds, there is a great skew towards wildfowl (ducks, grouses and waders), whereas passerines are a rare models for such studies (but see HOWLETT & STUTCHBURY 1997, ROONEEN & ROBERTSON 1997, TRYJANOWSKI et al. 2004).

In the present study, we investigated differences in the cost of re-nesting after failure at different stages of first clutches in a small passerine bird, the red-backed shrike *Lanius collurio*. We tested the hypothesis that failure at more costly developmental stages of first clutches would influence the breeding parameters of replacement clutches. We predicted that pairs which failed during the nestling stage (the most costly stage) should produce smaller replacement clutches than in the cases where loss occurs at the laying or incubation stages (less energetically expensive stages). Also, we asked whether there were any emergent patterns in egg measurements between the different classes of the replacement clutches. Finally, one of the common patterns of avian reproduction is to skip further reproduction in that year after experiencing failure at nestling stages; we therefore asked whether there were any differences in the frequency in re-nesting behaviour relative to the time of failure of the first clutch.

METHODS

Study species

The red-backed shrike is a small passerine species widely distributed in the Western Palearctic. It is a long distance migrant which belongs to one of the latest arriving passerines in Central Europe (TRYJANOWSKI & SPARKS 2001). This species is single brooded, and the majority of clutches is completed by the end of May. When nest failure occurs, replacement clutches are laid regularly. Therefore, the study species, the red-backed shrike, seems to be ideal for the purpose — it is a long distance migrant, strongly constrained by time; additionally, it is single brooded with a high level of breeding losses (TRYJANOWSKI et al. 2000) and frequent replacement nesting attempts.

Study areas

Field work was conducted in the breeding seasons 1999-2006 at three study plots in Poland. The first study plot, with an area of ca 20 km² near Leszno (51°51'N, 16°35'E) in western Poland, has typical breeding densities of the red-backed shrike in Poland: ca 4.7 breeding pairs/1 km² (KUŹNIAK & TRYJANOWSKI 2000 and unpublished data). From 1999 to 2003, another study plot (9 km²) was also established in the farm-

land of the Mazovian Lowland (CE Poland, 52°12′N, 22°17′E). The latter had breeding densities of up to 19 breeding pairs/1 km², and the red-backed shrike was among the most numerous species breeding in that area (GOŁAWSKI 2006). The third plot (10 km²) was located in western Poland near Odolanów (51°34′N, 17°40′E, 10 km², years 2004-2006), and densities there reached up to 10 pairs/1 km². The study plots were regularly surveyed for breeding pairs and nests. Found nests were checked regularly, but due to the possible strong human impact on nest success (TRYJANOWSKI & KUŹNIAK 1999) only 1-5 visits (depend on nest searching time) were conducted, every 4-5 days.

During nest visits, standard data on breeding biology were collected, including clutch size, laying date, and number of nestlings. In some cases, measurements of the breadth and length of eggs were taken by callipers to nearest 0.1 mm. When nest failure occurred, we searched for replacement clutches, where the same protocol was applied. We divided nestling failures of first clutches into the following phases: egg laying, incubation, nestling. Failure at the egg laying phase was assessed when the nest was destroyed before the clutch was completed. The most important reasons for nest losses were predation and abandonment of clutches, mainly during egg laying (TRYJANOWSKI et al. 2000, GOŁAWSKI 2006). The nest was considered as successful when at least one offspring fledged. Some breeding birds were colour marked (30%), additionally several pairs were recognised by specific plumage features (e.g. presence of white mirrors in the wing, grey feathers on the head of females — see KUŹNIAK & TRYJANOWSKI 2003).

Statistical analyses

Because we did not find any significant differences in breeding parameters between the study seasons and the plots (ANOVA, $P > 0.05$ in all cases), the data were pooled to improve sample size. Moreover, at some nests, full data on egg measurements and some patterns of the breeding biology were not available in the field resulting in variation in sample sizes. We used the chi square test, paired t-test, one-way ANOVA and analysis of covariance (ANCOVA). The last test was used to assess variation in the clutch size of replacement clutches in relation to the phase when the first clutch failed. We also added a variable describing the date of loss of the first clutch. We observed a decrease in clutch size as the season progressed ("calendar effect") in the studied population of the red-backed shrike (KUŹNIAK & TRYJANOWSKI 2003, GOŁAWSKI 2006). Throughout the text, values are reported as means ± SD. Analyses were conducted using Statistica 6.0 (STATSOFT 2003). All basic statistical analyses were applied according to the recommendations of ZAR (1999).

RESULTS

Influence of stage of failure on re-nested clutch size

In total, 96 first clutches were destroyed and red-backed shrikes laid corresponding replacement clutches. Among this number, 32 nests were destroyed during egg laying, 48 nests failed during incubation and 16 in the nestling phase. The average size of the complete first clutch was 5.2 ± 1.0 eggs, and replacement clutch size was 4.2 ± 1.3 eggs ($t_{53} = 3.8$, $P < 0.001$). There were significant differences in the clutch size of replacement clutches depending on the phase when the first clutch failed ($F_{3,63} = 3.3$, $P = 0.03$). Post
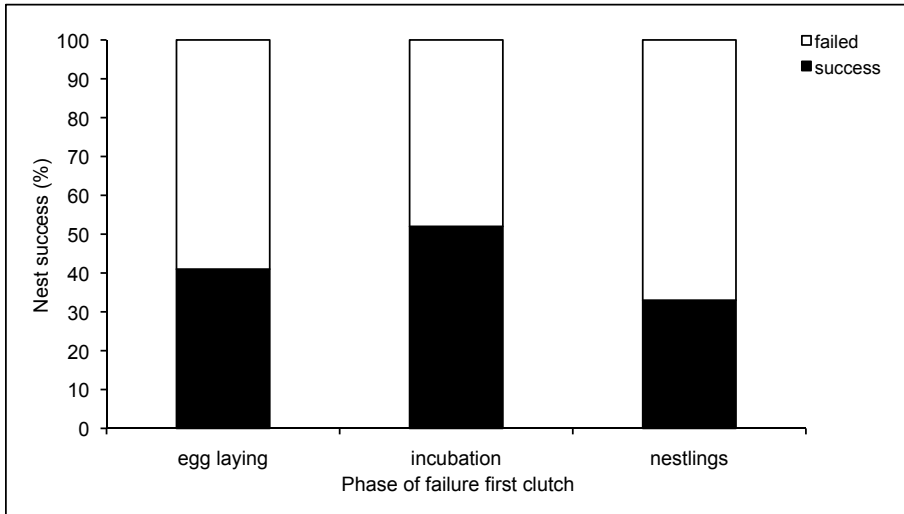
Fig. 1. — Differences in the breeding success of replacement clutches relative to the timing of nest failure in the first clutch.
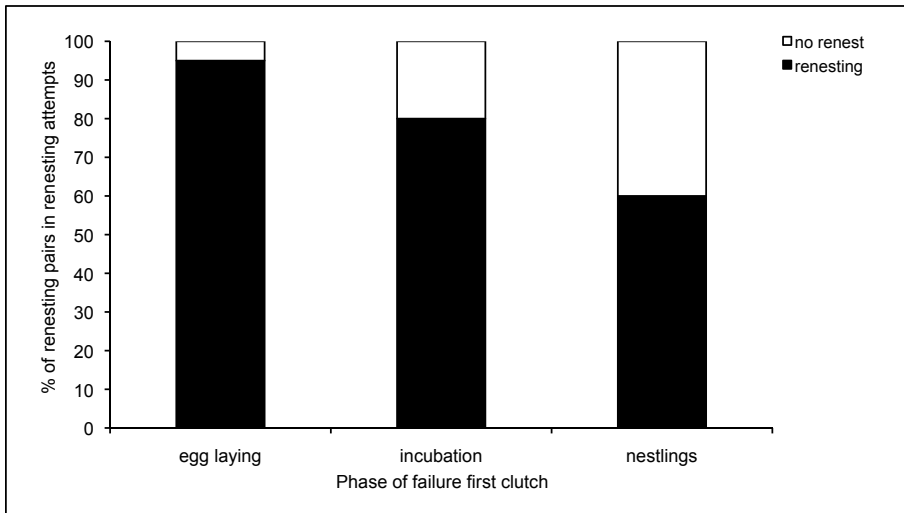

Fig. 2. — Differences between the failure phases of the first clutch in the proportions of pairs producing replacement clutches.

hoc comparisons revealed that pairs which failed at the nestling phase produced smaller replacement clutches (mean 3.6 ± 1.5, N = 13) than pairs whose nests were destroyed at egg laying (mean 4.8 ± 0.9, N = 2, Tukey post-hoc test, P = 0.03). The date of loss of the first clutch ("calendar effect") had no significant effect (P = 0.39) on the clutch size of replacement clutches.

Egg measurements

The phase at which the first clutch failed did not influence the egg dimensions of re-nested clutches, as there were no significant differences in egg length ($F_{3,44} = 0.6$, $P = 0.56$) and breadth ($F_{3,44} = 1.7$, $P = 0.20$).

Success of replacement clutches

There were no differences in the nesting success of replacement clutches relative to the phase at which the first clutch was lost ($\chi^2 = 2.9$, df = 2, $P = 0.23$, $N = 93$, Fig. 1). However, pairs of red backed shrikes which failed during the nestling phase of the first clutch significantly often skipped further reproduction in the given season (at least in their territory) than in other phases at which replacement clutches occurred ($\chi^2 = 8.0$, df = 2, $P = 0.02$, $N = 82$, Fig. 2).

<div align="center">DISCUSSION</div>

In line with the predictions of life history theory, reproduction costs are defined as costs generated by current investment in reproduction which negatively affects the chances of survival of the adults as well as their future reproductive output (HAMILTON 1966, LINDEN & MØLLER 1989). The main predictions of this theory are that adults in the course of their reproductive cycle should balance between the benefits of current reproductive attempts and the perspectives of their own survival and future reproduction. In several bird species, breeding losses are the main reasons for a reduction in annual reproductive success (LINDEN & MØLLER 1989, MARTIN 1995). After the loss of a first clutch, breeders have three main options. Firstly, they can stay in the current territory and lay a replacement clutch. Secondly, they may disperse and try to re-nest in other places. Alternatively, they may not reproduce again in the given season. Several factors may influence the re-nesting decisions of individuals, and at least in some species, individuals may apply all three strategies (ISENMANN & FRADET 1998).

The results presented in the present paper, as well as other studies performed on the red-backed shrike, show that this species regularly re-nests after failure (see review in KUŹNIAK & TRYJANOWSKI 2003). Similarly, the decrease in clutch size during the breeding season, called a "calendar effect", is a common pattern of shrike breeding biology, and has been recorded in numerous studies (JAKOBER & STAUBER 1983, KUŹNIAK 1991, CRICK et al. 1993, GOŁAWSKI 2006). However, the most important finding of the present study is that there are differences in the prospect of producing replacement clutches, which are dependent on the timing of the failure in the first clutch. Although the proportion of re-nesting pairs is high, losing the first clutch at different stages of nesting significantly modifies the size of the replacement clutches. These results imply that the cost of raising nestlings is high, and that if failure occurs at this stage, the re-nested clutches are significantly smaller than when

failure occurs at the egg laying stage. One of the possible underlying explanations for these results might be the decrease in the body condition (and therefore in body materials needed for egg production) of red-backed shrike females during the progress of the breeding season (ŠIMEK 2001). Indeed, the changes in body mass of females shrikes throughout the breeding season shows the following pattern: we first observe an increase in body mass before clutch initiation, which decreases during egg laying, does not vary during the first 10 days of incubation, slightly decreases during the last period of incubation, and finally markedly decreases during the nestling stage (ŠIMEK 2001). Hence, females that experience a nesting failure at varying breeding stages start the initiation of replacement clutches in a different body condition, and consequently strongly differ in their possibilities of re-nesting. The most pronounced differences, in other words the most costly for females, is to lay replacement clutches after experiencing failure during brood raising. The proportion of females of the red-backed shrike in the studied population which produced a replacement clutch after the first clutch was destroyed at the phase of egg laying and incubation, was high and comparable to both natural and experimental studies performed on other passerine species (NILSSON 2000, LIFJELD et al. 2005). This proportion of females cannot be connected with the post-breeding moult of females because they moult on non-breeding ground in Africa (LEFRANC & WORFOLK 1997). In other species, e.g. the pied flycatcher *Ficedula hypoleuca*, females with a moult/breeding overlap laid smaller clutches than non-moulting females (HEMBORG 1999).

Interestingly our data show no differences between first and replaced clutches in egg measurements. Females of the bluethroat *Luscinia svecica* which experienced experimental removing of the first clutch laid smaller replacement clutches but showed an increased egg volume (LIFJELD et al. 2005). Re-nesting females of the Madagascar paradise flycatcher *Terpsiphone mutata* laid replacement clutches of a similar size to the first clutches but with an increased egg mass (MIZUTA 2002). These results indicate that at least some fraction of early breeding females might experience environmental constrains such as weather or food supply during egg formation of first clutch (NILSSON 2000, LIFJELD et al. 2005). Obviously, there is a strong correlation between the body condition of females and clutch size, and this pattern was recorded in several bird species (BOURGEON et al. 2006 and references therein, including the red-backed shrike — TRYJANOWSKI et al. 2004). Red-backed shrike females invest strongly in incubation and up to the first 8 days of the life of the nestlings when all brooding is done exclusively by females. However, the presence and quality of the male is essential for successful reproduction, because males intensively feed their female mates during these periods (CARLSON 1989, LEFRANC & WORFOLK 1997). In the bull-headed shrike *Lanius bucephalus* females paired with adult males laid larger clutches and there was a positive relationship between age of the male and the nestling mass (TAKAGI 2003). Thus, the quality of the male might have a positive effect on the re-nesting capacity of females.

In the studied populations, some breeders skip or change the territory after nest failure; this was observed more often after losses at the nestling stage. The change of territories was not the result of food availability because

orthopterans appear in great numbers at the end of the red-backed shrike breeding season. These insects are the main food of the red-backed shrike (KUŹNIAK & TRYJANOWSKI 2003, GOŁAWSKI 2007). The red-backed shrike is a long distance migrant with only a narrow time window for reproduction, so some birds which experience nest failure at the nestling stages have little room for current reproduction. These results are in agreement with the study of the bull-headed shrike in Japan, where pairs that failed at the egg laying and incubation phases re-nested more often in comparison to pairs which failed at the nestling stages (TAKAGI 2004). It must be noted however, that some of the breeding pairs might move to other breeding territories, and this fact may deserve further investigation. Generally however, the majority of red-backed shrikes re-nest in the same breeding territories (KUŹNIAK & TRYJANOWSKI 2003, our field observations). Our results emphasise the fact that among the ecological factors which might influence re-nesting decisions, the timing of fate of first clutch seems be important since several bird species are migratory.

To conclude, for breeding red backed shrikes the best strategy is to initiate clutches as early as possible because it gives more time for possible re-nesting.

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