

The timing of clutch initiation in Bull-headed Shrikes (*Lanius bucephalus*) in relation to re-nesting or second nesting

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The date of initiation of reproduction was studied in Bull-headed Shrikes (*Lanius bucephalus*) to test whether this date allows time for re-nesting and successfully laying a second clutch, and whether nest predation influences chances of re-nesting. The study was conducted during the breeding season (April–July) from 1994 to 1996 in northern Japan. Only breeders that started laying eggs in April or in early May bred twice in one season. However, not all pairs with a first nest within this period necessarily breed twice. Of the 39 pairs that bred successfully in the first breeding attempt, only four pairs (10%) initiated a second nesting attempt. The timing of laying eggs in the first nesting attempt is a necessary, but not sufficient condition for the second nesting attempt. The probability of re-nesting after nest predation decreased at 3% day⁻¹ as the date of clutch initiation progressed. Predation during the nestling stage reduces the probability of re-nesting much more than predation during egg-laying or incubation. It is likely that the degree of investment in the first nest determines whether or not shrikes re-nest after nest failure. To ensure the chance to re-nest after failure in the first nesting attempt, Bull-headed Shrikes need to start laying as early as possible.



1. Introduction

In multi-brooded species the number of young produced depends on the number of broods (Crick *et al.* 1993, Svensson 1995), which will determine annual reproductive success. The number of broods per breeding season is possibly limited by the time period when enough food is available (Lack 1954, Svensson 1995). It is suggested that multi-brooded species start laying eggs as soon as the female can store the energy needed to form a clutch (Schoech 1996). To breed successfully

more than once per year, birds must initiate their first nests prior to a certain date (Geupel & DeSante 1990, Stouffer 1991, Verboven & Verhulst 1996). Westneat (1992) suggested that, if the rate of nest predation is high, it would be advantageous to start breeding as early as possible in order to have time available for re-nesting if the first fails due to predation. In addition, the timing when nest predation occurs will influence whether re-nesting is possible because progress in the breeding stages will shorten the period available for re-nesting and also add additional costs of

reproduction (Martin 1987). Thus, when nests fail later, pairs are less likely to initiate new nesting attempts. Re-nesting should depend on the timing of egg-laying in the prior clutch and the breeding stage when the nest was preyed upon.

In this paper, I selected Bull-headed Shrikes (*Lanius bucephalus*) as the study material. Bull-headed Shrikes can re-nest after nest predation, and if Bull-headed Shrikes can fledge nestlings early in the breeding season, they will have a chance to breed twice per season. I wished to answer the following two questions concerning Bull-headed Shrikes. Does the calendar date and breeding stage when nest predation occurs influence the probability of re-nesting? What is the limiting date for first nest initiation that will permit pairs to successfully nest more than once in any given year? Then, based on the answers to the questions, I examined the timing of breeding in Bull-headed Shrikes.

2. Material and methods

2.1. Study species

The Bull-headed Shrike is a medium-sized, monogamous bird weighing about 40 g. The female lays one egg every day, and modal clutch size is six. The female incubates in an open-cup nest for about 15 days. The male feeds its mate and the nestlings and both parents feed the nestlings and fledglings for about 15 days (Takagi & Abe 1996, Lefranc & Worfolk 1997, Takagi 2001).

The Bull-headed Shrike is a summer migrant in northern Japan, and starts arriving there in the middle of April when snow remains on the ground (Takagi 2003). Their arrival in the area is about a month and a half earlier than that of other summer migrants: a congeneric Brown Shrike (*L. cristatus*), Stonechat (*Saxicola torquata*), Chestnut-eared Bunting (*Emberiza fucata*), Daurian Starling (*Sturnus sturninus*) and Wryneck (*Jynx torquilla*) (Takagi 2002, unpublished data). Bull-headed Shrikes build open-cup nests on sites concealed by leaves or twigs, most likely in order to be safe from predators (Takagi & Abe 1996). But, when the earliest breeders start breeding in the area, dwarf bamboo with dense foliage is the only available site for nesting, because deciduous shrub

species have not yet leafed out. Since dwarf bamboo does not provide a higher position, it is not as safe a site for nesting as are the deciduous shrubs later in the season. About 70% of all nests fail to result in fledging because of predation by terrestrial mammalian species early in the breeding season (Takagi & Abe 1996).

2.2. Study area

The study was conducted during the breeding season, April–July, in 1994–1996 at Oyafuru in Ishikari, which is approximately 15 km north of Sapporo (43° 13'N, 141° 20'E) in northern Japan. The study area is about 900 ha, and consists of pastures and crop fields with wind shelter-belts composed of 15 m tall trees (56%), grassland with small shrub patches (33%) and other areas that include roads and houses (see also Takagi & Abe 1996).

2.3. General method

The date of clutch initiation, clutch size, and nesting fate were determined by nest inspections at a maximum interval of four days. Nesting fate was broken down into five categories: (1) successful, (2) predation during nestling stage, (3) predation during egg-laying or incubation stage, (4) desertion during egg-laying or incubation stage, and (5) parasitization by cuckoos (*Cuculus canorus*). If one nestling fledged from a nest, nesting fate was defined as successful. If all eggs or all nestlings disappeared from a nest, it was defined as predation (Takagi & Abe 1996). Breeding birds were captured with mist nets during the nestling period and were marked individually by using colour rings to determine whether the birds had subsequent nesting attempts after fledging young from the first brood.

When a nesting attempt failed during the egg-laying or incubation period in a territory, I inspected the territory thoroughly every day after the failure to observe whether the pairs stayed in their territory. It was observed that after nesting failure not all pairs stayed in their territories and attempted re-nesting. On the other hand, I did observe that territories where pairs stayed were sta-

Table 1. Nest success in each period during 1994–1996.

	1994	1995	1996	Total
A	27.3% (6/22)	31.6% (6/19)	17.6% (3/17)	25.9% (15/58)
B	22.7% (5/22)	38.1% (8/21)	36.4% (4/11)	31.5% (17/54)
C	43.8% (7/16)	33.3% (3/9)	40% (6/17)	38.1% (16/42)
D	14.3% (1/7)	0% (0/3)	0% (0/5)	6.7% (1/15)
Total	28.4% (19/67)	32.7% (17/52)	26% (13/50)	30% (49/169)

A: April 21–May 10, B: May 11–31, C: June 1–20, D: June 21–July 10. Parentheses show the number of successful nests/total number of nests.

ble, and the pairs attempted re-nesting without exception. In these cases, I assumed that these territories were occupied by the same pairs.

2.4. Data analysis

To examine the seasonal change in nesting fate, the breeding season was divided into four periods of 20-day intervals. Periods A, B, C and D are April 21–May 10, May 11–31, June 1–20, and June 21–July 10, respectively. The total number of nests in 1994, 1995 and 1996 were 67, 52 and 50, respectively.

I used multiple nominal logistic regression to analyse the annual (years: 1994, 1995 and 1996) and seasonal changes (the four periods) in nesting fate. A multiple nominal logistic regression analysis was also used to show whether pairs re-nest after nest failure. The number of the first nesting at-

tempts in 1994, 1995 and 1996 were 40, 30 and 30, respectively. The analysis tested the importance of three variables, year (1994, 95, and 96), clutch initiation date (calendar date) and breeding stage at nesting failure (egg-laying, incubation or nestling stage) for re-nesting. In the analyses, I adopted the method of all possible combinations (SAS Institute Inc. 1998), and P -value for input of variable was set as $P < 0.05$. Statistical analyses were performed with a statistical package (StatView Ver. 5.0, SAS Institute Inc. 1998).

3. Results

Nest success was not significantly different between years, or between periods (Table 1, nominal logistic regression model, likelihood ratio test, $\chi^2_5 = 7.39$, $P = 0.19$, proportion of deviance explained = 4%).

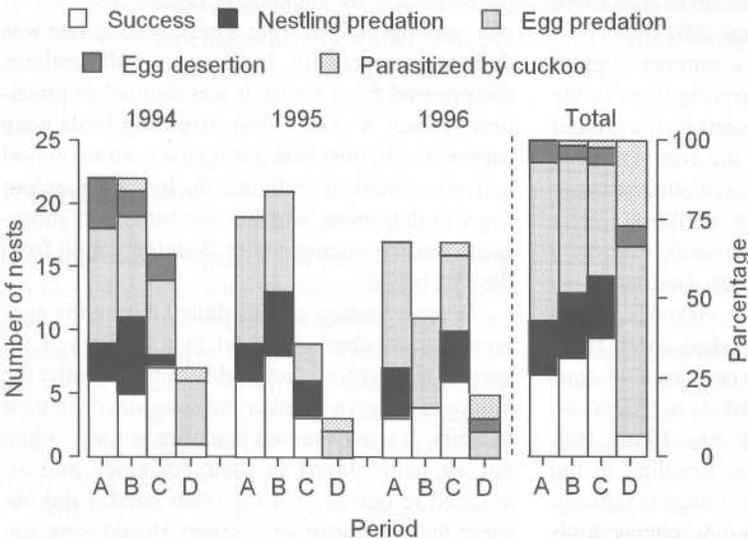


Figure 1. Seasonal change in nesting fate in 1994–96, and total of the three years. Periods A, B, C and D are April 21–May 10, May 11–31, June 1–20 and June 21–July 10, respectively.

Table 2. Parameter estimates (point estimate and 95% confidence limits) for the logistic regression equation for repeat nesting attempts in relation to timing of the first nesting failures.

	Coefficient (SE)	χ^2	P	Exp(coeff)	95% confidence	
					Lower	Upper
Constant	-0.43 (0.78)	0.3	0.59	0.65	0.14	3.04
Date	-0.03 (0.01)	5.62	0.02	0.97	0.95	1
Stage						
egg predation	1.35 (0.61)	4.93	0.03	3.85	1.17	12.64
egg desertion	1.69 (0.89)	3.57	0.06	5.41	0.94	31.23

Egg- and nestling-predation were the highest components of nesting fate in each period (Fig. 1). Desertion mainly occurred in period A in 1994, generally during the egg-laying or incubation period (Fig. 1). Parasitization by Cuckoos predominantly occurred in period D (Fig. 1). The mean date of the first clutch initiation in 1994 was May $20.5 \pm \text{SD } 19.0$, $n = 40$ in 1994; in 1995, May $20.2 \pm \text{SD } 18.0$, $n = 30$; and in 1996, May $20.8 \pm \text{SD } 16.7$, $n = 30$. Clutch initiation dates did not differ among years (Kruskal-Wallis test, $H = 0.10$, $P = 0.95$).

In re-nesting after nest failure, the nominal logistic regression model was significant with the three variables (Likelihood ratio test: $\chi^2_5 = 13.65$, $P = 0.018$), but year did not significantly contribute to the model ($\chi^2_2 = 1.16$, $P = 0.56$). The goodness-of-fit test of the new model was significant with date and breeding stage ($\chi^2_3 = 12.5$, $P = 0.006$). Date of clutch initiation affects the probability of re-nesting ($\chi^2_1 = 6.26$, $P = 0.012$), and the odds ratio of re-nesting increased 0.97 times day by day

(Table 2). The breeding stage during nest failure significantly influenced probability of re-nesting ($\chi^2_2 = 6.67$, $P = 0.036$). Re-nesting by pairs whose nests were preyed on, or who deserted their nests, during the egg-laying stage was more frequent than that by pairs whose nestlings were preyed on (Table 2). Clutch size in the first nesting (5.5 ± 0.2 , 4–6, $n = 12$) did not decline in the re-nesting (5.2 ± 0.2 , 4–6, $n = 12$, Wilcoxon signed-rank test, $z = -0.98$, $P = 0.29$, Fig. 2).

Of the 39 pairs that bred successfully in the first breeding attempt, four pairs (10%) initiated a second nesting attempt. The mean date of the first clutch initiation in pairs with second attempts (April $28 \pm \text{SE } 2.8$, range April 10–May 3, $n = 4$) was significantly earlier than for other pairs (May $20 \pm \text{SE } 2.9$, range April 26–June 26, $n = 35$, Mann-Whitney U-test, $z = -2.5$, $P = 0.013$, Fig. 3 (A)). For pairs that start laying eggs before 3 May, the probability of second nesting is 23% (4/17). The mean duration between the first and second clutch initiation dates was $56.8 \pm \text{SE } 1.0$ days (range 54–59, $n = 4$). When pairs constructed the second nests, fledglings from the first broods remained within their natal territories. Mean clutch size in the second attempts ($4.8 \pm \text{SE } 0.3$, $n = 3$) was smaller than that in the first attempts ($5.8 \pm \text{SE } 0.3$, $n = 4$, Fig. 3 (B)).

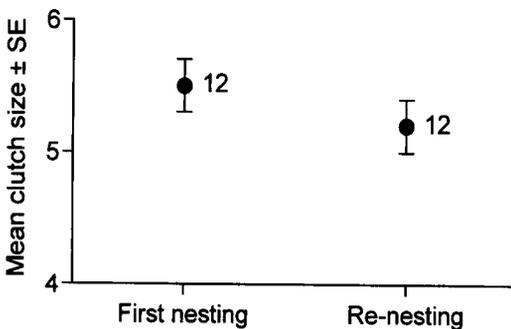


Figure 2. Clutch size in the first and re-nesting attempts. Number of nests shown in figures.

4. Discussion

The probability of re-nesting after nest predation decreased at 3% per day with clutch initiation date as the time of first nesting advanced in the breeding season. Westneat (1992) suggested in relation to nest predation that early breeders have a higher

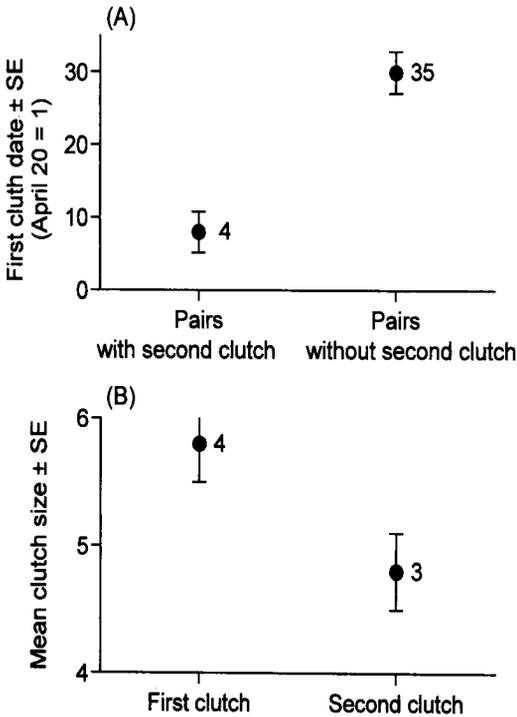


Figure 3. (A) Clutch initiation date of the first clutches in pairs with and without second clutches. (B) Clutch size in the first and second clutches. Number of nests shown in figures.

probability to produce a replacement clutch than late breeders do. The probability of re-nesting is about five times lower if predation occurs during the nestling stage than during the egg-laying or incubation period. In addition, although clutch size after failure in the first nest is generally smaller than in the first clutch (Bańbura & Ziełiński 1998, Nilsson 2000, see also Sockman & Schwabl 2001), Bull-headed Shrike females could lay as large a clutch in the re-nesting attempt as in the first clutch size. It is likely that a degree of investment in the first nesting determines whether or not shrikes re-nest after nest failure, and that Bull-headed Shrike females in good condition are able to lay eggs again after failure in the first nesting.

According to the parental decision rule, parents should adjust their current expenditure to prospective benefits, not past costs (Dawkins & Carlisle 1976), and parents should not abandon the current breeding attempt as the breeding stage progresses. This may be why Bull-headed Shrikes

never desert nestlings, but why it is reasonable to desert nests during the egg-laying or incubation stage early in the breeding season. In addition, it is also true that the current investment reduces the parent's capacity for further expenditure (Clutton-Brock 1991). It is inferred that Bull-headed Shrikes should desert nests rather than consume their remaining energy before the end of the breeding season.

To successfully breed twice per year, pairs must start laying the first clutch prior to mid-May. Pairs could then start the second clutch late in June and the young would fledge in the middle of August (56 days required for rearing a clutch). Since Bull-headed Shrikes are migrants in Hokkaido (Ogawa 1977), breeders in the area need to store fat after breeding (Sandberg 2003) and they must molt completely, prior to migration (Yamashina 1934). Thus, fledglings need ample time for growth and partial molt prior to migration (Yamashina 1934).

Even if pairs begin laying eggs early in May, not all pairs that do so necessarily breed again after fledging young from the first brood. The timing of egg-laying in the first nest is a necessary, but not sufficient condition for re-nesting. We need to better understand the constraints on a second nesting, e.g. environmental condition (Perdeck *et al.* 2000, Møller 2002), heritable background of breeders (Sockman & Schwabl 2001), parental age (Geupel & DeSante 1990), and body condition (Hussell 1983).

Many non-migratory passerines in temperate climates are known to regularly raise double broods each year (Mewaldt & King 1977, Geupel & DeSante 1990). Migrants generally suffer constraints that prevent egg-laying until after the date when it is possible that the reproductive success is greatest (Crick *et al.* 1993). They then do not have enough time to raise a double brood in a given year. Migrant Brown Shrikes are strictly single-brooded per year in my study area (Takagi 2002). On the other hand, in spite of being migrants, Bull-headed Shrikes were potentially double-brooded per year but the frequency of a double brood was very low. In conclusion, I should note that to ensure the chance to produce a double brood per year by re-nesting after failure in the first nesting attempt, Bull-headed Shrikes need to start laying as early as possible.

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Härkälepinkäisen muninnan aloitusajankohdan vaikutus uusintapesintään tai toiseen pesintään

Artikkelin kirjoittaja tutki härkälepinkäisen pesinnän aloitusajankohdan vaikutusta mahdollisen uusintapesinnän ja toisen pesintäkerran onnistumiseen. Lisäksi kirjoittaja tutki vaikuttiko pesäpredaation ajankohta härkälepinkäisen uusintapesinnän mahdollisuuteen. Tutkimus tehtiin huhti–elokuussa vuosina 1994–1996 Japanin pohjoisosissa. Tutkimuksessa oli mukana kaikkiaan 67 pesää vuonna 1994, 52 pesää vuonna 1995 ja 50 pesää vuonna 1996.

Ensimmäisiä pesintäyrityksiä oli tutkimusvuosina kaikkiaan 40, 30 ja 30. Ainoastaan huhtikuussa tai toukokuun alussa pesintänsä aloittaneet yksilöt pesivät kaksi kertaa pesimäkauden aikana. Kaikki tuona aikana pesintänsä aloittaneet parit eivät kuitenkaan pesineet toista kertaa. Ensimmäisessä pesinnässään onnistuneesta 39 parista ainoastaan neljä paria (10 %) aloitti toisen pesinnän. Uusintapesinnän todennäköisyys pesäpredaation jälkeen laski 3 % per päivä pesinnän aloituspäivän myöhentyessä. Pesäpoikasaikainen predaatio vähensi pesinnän uudelleen aloittamisen todennäköisyyttä enemmän kuin muninta-aikana tai haudonta-aikana tapahtunut predaatio.

Tutkijan mukaan on todennäköistä, että ensimmäiseen pesyeseen laitetun panoksen suuruus määrää sen, pesivätkö lepinkäiset uudelleen saman pesimäkauden aikana ensimmäisen pesinnän epäonnistuttua. Härkälepinkäisen tulisi siis aloittaa munintansa mahdollisimman varhain varmistakseen mahdollisuuden uusintapesintään ensimmäisen pesinnän epäonnistuttua.

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