BREEDING ECOLOGY OF A BURROW-NESTING PASSERINE, THE WHITE-RUMPED SNOWFINCH
MONTIFRINGILLA TACZANOWSKII

ECOLOGÍA REPRODUCTIVA DE UN PASERIFORME NIDIFICANTE EN MADRIGUERAS, EL GORRIÓN ALPINO DE MANDELLI
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Xianhai ZENG* and Xin LU* 1

Summary.—Breeding ecology of a burrow-nesting passerine, the white-rumped snowfinch Montifringilla taczanowskii.

This work provides reproductive data about the white-rumped snowfinch Montifringilla taczanowskii and learn how avian life history respond to cavity-nesting and altitudinal gradients. The study was carried out in an alpine meadow in the northeastern Tibetan plateau, in Gahai National Nature Reserve (34° 14’ N, 102° 20’ E). During two breeding seasons individuals were marked and their nests contents were monitored. Nests were placed in pika Ochotona curziona burrows and constructed by females only. Egg-laying occurred between late April and early June. Some pairs (9 %) made two breeding attempts in a single year. Clutch size averaged 4.7 (2 - 6) and brood size at fledgling average was 3.5 (2 - 6). Females incubation lasts 9 to 15 days (13) and both sexes provide parental care until nestlings fledged at 18 to 24 days (21). Overall, 69 % of the nesting attempts produced at least one fledgling. The habit of cavity-nesting might allow the snowfinches to start breeding earlier, produce larger clutches, reduce nest attention and enjoy a higher reproductive success than several local open-nesting passerines. Compared to their higher-altitude conspecifics, the lower-altitude snowfinches reach a greater annual productivity mainly through rearing larger broods.

Keywords: alpine meadow, cavity-nesting, life history, Montifringilla taczanowskii, reproduction, Tibetan plateau.

Resumen.—Ecología reproductiva de un paseriforme nidificante en madrigueras, el gorrión alpino de Mandelli Montifringilla taczanowskii.

El trabajo ofrece una serie de registros reproductivos de una especie poco conocida, proporcionando información sobre cómo un nidificante en madrigueras responde a los gradientes altitudinales. Se realizó en praderas alpinas del noreste de la altiplanicie tibetana, en la Reserva Natural de Gahai (34° 14’ N, 102° 12’ E). Durante dos estaciones reproductoras se marcaron los individuos e inspeccionó el contenido de los nidos. Los nidos se ubicaron en madrigueras de pika Ochotona curziona y son construidos exclusivamente por la hembra. La puesta acontece a finales de abril y principios de junio. Algunas parejas (9 %) realizan dos intentos de cría en una misma estación reproductora. El tamaño medio de la puesta es de 4,7 huevos (2 - 6) y el de pollos de 3,5 (2 - 6). La incubación corre a cargo de la hembra durante 9 - 15 días.

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INTRODUCTION

The genus *Montifringilla* contains seven species all well adapted to treeless alpine meadow or rocky environments in the Tibetan plateau (Vaurie, 1959; Sibley and Monroe, 1990; Cramp and Perrins, 1994; Zheng, 2000). Occupying altitudes ranging from 3,000 to 5,000 m, the snowfinches represent the highest altitude distributed passerine birds in the world. Adaptive radiation of the avian genus is thought to have occurred 2 - 2.25 mya with dramatic climatic changes resulting from the uplift of the Tibetan plateau (Qu et al., 2006).

Snowfinches are secondary cavity breeders, nesting in burrows of small mammals, rock crevices or building holes. The harsh high altitude environments in terms of climate and vegetation structure (Landmann and Winding, 1993, 1995a, b) provide limited spaces for recourse partitioning among the snowfinch species. As a result of interspecific competition, most *Montifringilla* snowfinches are separated by altitudes or microhabitats although they may overlap in overall geographical distribution (Zheng, 1983; Qu et al., 2002). The white-rumped snowfinch *M. taczanowskii* (40 g in body mass) is one of the largest species among its genus and occurs across much of the Tibetan plateau. Being dominant over other small-sized congeners, white-rumped snowfinches occupy lower altitudes where ecological conditions are relatively good, excluding other symmetrically-breeding snowfinch species to higher altitudes or poor-quality habitats (Zeng and Lu, 2009).

Breeding of the white-rumped snowfinch is poorly known so far. Zhang (1982) only provides a sample list of breeding season, clutch size and egg size of this species occurring in a 3,300 m alpine meadow in northern Qinghai. We also collected a few data on nesting ecology of the birds at a higher site in north Tibet (4,300 m; Lu et al., 2009). In this paper, we report a two-year study on an individually marked population in the northeastern Tibetan plateau. The knowledge will contribute to our understanding of how birds, in general, cope with extreme environments (Martin and Wiebe, 2004; Bears et al., 2009). Moreover, alpine animals well adapted to extreme conditions are more vulnerable to human activities, especially global climate change (Smith and Foggin, 1999; Wu et al., 2005). Thus, the current data may aid conservation of the alpine ecosystem.

METHODS

Study site and species

This study occurred in Gahai National Nature Reserve (34° 14’ N, 102° 20’ E) in the northeastern Tibetan plateau from April to September in 2006 and 2007. The study area is rounded by relatively low mountains (3,450 -
3,800 m) covered with alpine Kobersia steppe meadow. Detailed information on climate and vegetation can be found in Wang et al., 2007 and Zeng and Lu, 2009.

White-rumped snowfinches are sexually monomorphic in size and plumage. They nest in burrows of the black-lipped pikas Ochotona curzoniae, the most dominant small mammals in the area (mean density of pika burrow = 90 per 100 ha; Zeng, 2008). Pika burrows are 10 - 80 cm under the ground and a burrow system consists of branched tunnels which lead to one chamber at the end and one open on soil surface. Active burrows currently used by the pikas are preferred over inactive ones previously used (Zeng and Lu, 2009). Distance of the nearest snowfinch nest neighbours varies from 2 to 1,400 m (averaged 65 m) and territory size from 1,029 to 5,131 m² (average 1,715 m²) in which the birds displayed most foraging activities. Within the study plot, the densities of breeding snowfinches were 13 pairs per 100 ha in 2006 and 17 pairs per 100 ha in 2007. Moderately-steep slopes, abundant burrow openings and large bare-patches around the nest burrow entrance character snowfinch nest burrows in comparison to random-sampled burrows.

Another snowfinch species sympatrically breeding in the alpine meadow is the rufous-necked snowfinch M. ruficollis (30 g). Being smaller in size and thus lower in social rank than the white-rumped snowfinch, this species exhibits no territoriality, nests in deserted pika burrows located in marginal habitats, and has a much low breeding density (2 pairs per 100 ha) compared with the white-rumped snowfinches (Zeng and Lu, 2009).

Data collection

A study plot of 390 ha extending between 3,400 and 3,650 m was set in the alpine meadow. Nests were systematically searched over the plot by following nesting-related activities. Nests located were checked every day or every other day to monitor their breeding progress and fate. Around the expected time of hatching and fledging nest visits were made daily. Adult snowfinches were mist-netted at their burrow entrance during the incubation (mainly females) and or nestling period (mainly males). For each individual captured, we measured its body mass (with an electronic balance to the nearest 0.1 g) and linear dimension (body, bill, wing, tail and tarsus length, with a calipers to nearest 0.1 mm) and marked it with colour leg rings and an aluminum ring. Adults were sexed by behaviour and incubation patches and further by DNA analysis using the brood samples taken upon capture (Zeng, 2008). Behavioural data, including nest selecting, nest building, mate guarding (pair distances and the sex initiating a movement), copulation, incubating and young-caring, were collected for randomly-selected focal pairs or nests from a distance of 40 - 50 m at which the birds behaved normally. Through locating all nesting attempts in the study plot throughout the breeding season, we may determine how many broods a pair produced per year.

To check nest contents, we dug a vertical hole at the end of the snowfinch nest placement. The hole then was re-covered with soil-filled bags to facilitate subsequent inspection. These operations were made for a few nests and did not lead to burrow collapse or other adverse effects on breeding activities of the birds. Nest dimension measured include: external diameter (the widest part of the nest outside wall), internal diameter (the widest part of the nest inside wall), cup depth (the vertical distance from the entrance rim to the bottom of the inner cup) and cup height (the distance from the entrance rim to the bottom of the outside of the nest). Eggs were measured for their fresh mass (using an electronic balance to the nearest 0.1 g), and maximum length and width (using a calipers to nearest 0.1 mm). Nestling development was regularly monitored through measuring their body mass and linear dimensions.
Nestlings near fledging received food from parents at the burrow entrances. The behaviours allowed us to count brood size, captured, marked and measured the young (with the same method as taken in adults). The sex of young was molecularly analyzed using blood samples collected at capture. We considered the egg-laying date to be when a female frequently made brief visits to the nest with her mate, which occurred a few days after the female ceased carrying soft nest materials. Incubation was thought to start when we failed to observe the female around her nest for at least one day, and hatching date was determined when the female came back the nest with food for the first time (this usually corresponded to the time egg shells were found nearby the burrow). The nestling period was the span from the hatching to fledging date, the day on which the nestlings firstly appeared in the burrow entrance (in some cases this was confirmed by the fresh droppings of nestlings). Food items delivered to nearly fledged young were collected by neck-collaring. Each nestling was neck collared once for 15 - 20 min, leading no effect on its survival although no food was fed after the operation. We identified the possible causes of nesting failure based on direct observations or analyzing the remains within or near the nests.

Data analysis

We used the methods of Gjerdrum et al. (2005) to calculate the first-egg date according to 38 daily-monitoring nests (where the mean ± SD discovery date was 3.7 ± 2.8 days after nesting started). Comparisons were performed with parametric analyses and relationships between two variables with Pearson’s or partial correlations. Effects of nesting variables on nest fates were examined with logistic regression analysis. The significant level was set at P < 0.05 and summary statistics are presented as mean ± SD. A total 190 nests were located during the two-year study. However, sample size varied among different nesting parameters because of limited survey efforts made in collecting some of these parameters.

RESULTS

Annual turnover and recruitment of the snowfinch population

More breeders in both sexes than young marked in 2006 were rediscovered in the study plot in 2007 spring (table 1). However, the proportions of individuals that were found to nest in the plot were lower in adults (6 % of 17 males and 20 % of 15 females) than young (62 % of 13 males and 86 % of 7 females). All those adults re-mated in 2007. In additional, a 2006 breeding pair divorced in 2007, with both the male’s and female’s nests being located outside the study plot (distance from the previous nest site, the male 1 km and the female 2 km).

Breeding season

Egg-laying was initiated in mid-April (earliest 16 April) and ended in late June (latest 22

Table 1

The turnover of breeders and recruitment of young of the white-rumped snowfinch in an alpine meadow, northeastern Tibetan plateau. [Balance de reproductores y reclutamiento de jóvenes del gorrión alpino de Mandelli en una pradera alpina del noroeste de la planicie tibetana.]

<table>
<thead>
<tr>
<th>Breeder</th>
<th>Young</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>No. of birds marked in 2006</td>
<td>24</td>
</tr>
<tr>
<td>No. of birds rediscovered in 2007 (%)</td>
<td>17(71)</td>
</tr>
</tbody>
</table>

Ardeola 56(2), 2009, 173-187
June), lasting about 70 days. The average dates of the first egg were the same (27 May ± 12 days) in 2006 (N = 67) and 2007 (N = 80). Most pairs (91.2 % of 147) yearly bred one brood and a few (8.8 %) two broods. For single-brooded pairs, the laying date averaged 9 May (±11 days, N = 126). On average the first attempt of double-brooded pairs started on 5 May (±14 days, N = 12), and the second on 25 May (±13 days; fig. 1). No pairs marked after the middle of breeding period were found to produce a replacement clutch after failure (N = 13), but the possibility of re-nesting existed for those pairs that failed early in the season (N = 3).

Nest construction

Snowfinches placed their nest at the chamber or the middle of tunnel of a pika burrow, 36 cm (± 50, 15 - 60, N = 23) to the ground surface and 159 cm (± 53, 80 - 225) to the burrow entrance. Of 190 nests located, 182 were built in initially active pika burrows (the pikas were present when the birds selected nest burrows), and only 6 in inactive pika burrows (already deserted by the pikas). Nest construction was undertaken by females alone for 2 to 10 days (5.6 ± 2.7, N = 11). Double-brooded females took longer to build their first nests (7.0 ± 2.3 days, 5 - 10, N = 7) than the second ones (3.6 ± 1.3 days, 2 - 5). Nest materials, mostly grass stems, were transferred at a rate of 10.0 times per h (± 10.1, 0 - 33, 521 minutes of observations for 15 nests. The nests were cup-shaped, with external diameter being 23.7 cm (± 3.2, 17.8 - 28.0, N = 8), internal diameter 9.4 cm (± 4.4, 7.5 - 15.0), cup depth 6.3 cm (± 0.7, 5.6 - 7.5) and cup height 9.3 cm (± 2.5, 6.5 - 12.0).

Fig. 1.—Temporal distribution of the date of laying the first egg by the white-rumped snowfinch in an alpine meadow, northeastern Tibetan plateau. The time of clutch initiatation is arranged in 5-day periods. [Distribución temporal de la fecha de puesta del primer huevo del gorrión alpino de Mandelli en una pradera alpina de la altiplanicie tibetana. La fecha de inicio de puesta está ordenada en periodos de 5 días.]
**Egg-laying, egg and clutch size**

One egg was deposited daily (observation for 30 eggs in 9 nests), usually before 08:00 h (observations for 5 eggs in 5 nests). During the laying period both sexes did not roost in the nest burrow during night based on inspection in early morning for 6 nests. The egg-laying period lasted 4 - 7 days (4.7 ± 0.8, N = 23). The eggs were elliptical in shape and pure white in coloration. Fresh mass of six eggs averaged 3.6 g (± 0.2, 3.4 - 3.8), length 25.7 mm (± 0.8, 24.8 - 26.2) and width 16.9 mm (± 0.8, 16.5 - 17.8). Clutch size ranged from 2 to 6 eggs (4.7 ± 1.5, N = 7).

**Incubation**

Only females undertook incubation. During 1,026 minutes of observations on 14 pairs, a female spent 48 % of her daytime in the nest, with on-nest bout averaging 26.3 min (± 13.1, 10 - 65, N = 14 pairs of 24 observations) and off-nest 7.4 min (± 6.0, 2 - 29, N = 14 pairs of 22 observations). Over the observational period, we recorded no male with food entering the nest in which the female was sitting. The incubation period ranged from 9 to 15 days (12.7 ± 1.6, N = 34 pairs, not including the four where incubation was delayed by pika excavation activities that blocked the nests). Clutches started later tended to have a longer incubation duration (r = 0.39, N = 34, P = 0.02).

**Nestling development and parental care**

Newly-hatched young were naked, with a cluster of gray down on the forehead and occiput. Eyes opened at about day 7 after hatching (N = 11 nestlings from 3 nests). Nestlings fledged at age of 18 to 24 days (21.3 ± 2.0, N = 16 nests) when they had plumage similar to the adult’s and reached 79 % (± 8, 59 - 99, N = 241) of the adult female weight. Growth of nestling weight followed a logistic model (w = 32.6 / (1+e^(-1.499–0.212t)), r^2 = 0.90, N = 14 nestlings from three broods, fig. 2).

Direct watches on young caring activity were made of 21 pairs for 2,598 minutes in total (mean watch length 1009 ± 33 minutes,
Females spent 27% (± 23, N = 21, 0 - 71) of their daytime brooding in the early nestling period (< day 10), with the brooding bouts lasting 29.7 minutes (± 28.2, 5 - 91). Both parents fed their young and a parent carried one or more prey items each feeding trip. Of 730 trips recorded across the nestling period, 405 were made by females and 325 by males. Average feeding rate per hour in females was 6.5 (± 5.1, 0 - 16.8, N = 21 pairs) and 6.1 (± 7.6, 0 - 34.7) in males, not differing between sexes (paired-samples t-test, t_{20} = 0.32, P = 0.76).

Most double-brooded pairs (18 of 24) started their second clutches during the nestling period of the first clutch and the remaining did so after completion of the first one. In the former cases the females alternatively carried food to the nestlings and nest materials to the new nest. The distances between the first and second nests were less than 50 m.

Shortly after fledging (less than 3 days), juveniles received food at the nest burrow entrance from their parents. Observations based on 16 trapping attempts in the early morning for 8 nests showed that at this stage parental birds did not roost in the burrow at night. The juveniles moved away the nest burrows as they grew up and during the night they roosted in randomly selected pika burrows. Parents fed the juveniles continuously for 2 to 3 weeks until they were able to feed themselves (observations for 5 broods).

**Breeding success**

Brood size at fledging was 3.3 ± 0.8 (2 - 5, N = 36) in 2006 and 3.6 ± 0.8 (1 - 6, N = 31) in 2007, without statistical difference between the two years (t = 0.55, df = 69, P = 0.59). On average, successful single-brooded pairs produced 3.4 fledglings (± 0.9, 1 - 5, N = 38); double-brooded pairs fledged 3.7 young (± 1.1, 2 - 6, N = 12) in their first broods, statistically similar to 3.3 (± 1.0 young, 1 - 5) of the second broods (t_{11} = 0.94, P = 0.36). There was no significant difference in brood size between single- and double-brooded pairs (t_{67} = 0.31, P = 0.76). Brood size was independent of laying date (partial correlation coefficient controlling for year, r = 0.002, N = 66, P = 0.99).

Overall reproductive success, measured as the percentage of broods from which at least one young survived to fledge, was 54% (N = 82) in 2006 and 75% (N = 108) in 2007. Double-brooded pairs reached a reproductive success in their first attempts (100%, N = 12) similar to that in the second attempts (93%, N = 15; χ² = 0.83, P = 0.36). Overall, the proportions of successful single-brood pairs (60%, N = 132) were significantly lower than those of double-brooded pairs (96%, N = 27; χ² = 13.28, P < 0.001). Snowfinch nests placed in active pika burrows were more likely to be successful (67%) than those in inactive burrows (17%). Nest fates were related to laying date, late broods having a higher likelihood of success (Logistic regression: Beta = 0.078, Wald = 11.6, P = 0.001).

Of 65 failed attempts, 18 (28%) occurred before laying, 12 (19%) during incubation, 28 (43%) during the nestling period and 7 (11%) shortly after fledging. For 51 nests where the reasons of failure were identified, 37% failed due to nest collapse caused by excavating activities of underground-dwelling mammals and other 37% due to desertion; killing of nestlings, fledglings or parents by carnivorous mammals and birds accounted for 18% and 8%, respectively (table 2). Brood mor-

**Nestling diet**

Nestling diet consisted entirely of arthropods. Of 63 food items collected from 17 nestlings in 6 broods before mid-May, 95% belonged to larvae of Lepidoptera and Coleoptera. In contrast, among 72 items from 13 young in 7 broods after mid May, 85% was adult insects (Hymenoptera 35%, Coleoptera 29%, Diptera 21%), and only 15% Lepidoptera larvae.
The causes of nesting failure of the white-rumped snowfinch in an alpine meadow, northeastern Tibetan plateau.
[Causas del fallo en la reproducción del gorrión alpino de Mandelli en una pradera alpina del noroeste de la planicie tibetana.]

<table>
<thead>
<tr>
<th>Reasons of breeding failure</th>
<th>2006 (N = 38)</th>
<th>2007 (N = 27)</th>
<th>Both years (N = 65)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Preyed by raptor birds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>black-eared kite Milvus lineatus</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>upland buzzard Buteo hemilasius</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>sake falcon Falco cherrug</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Preyed by carnivorous mammals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stone marten Martes foina</td>
<td>1</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>domestic cat</td>
<td>0</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Destroyed by ground-dwelling mammals</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>black-lipped pika Ochotona curzoniae</td>
<td>7</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>striped hamster Cricetulus barabensis</td>
<td>2</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>common zokor Myospalax frontanieri</td>
<td>3</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Desertion</td>
<td>13</td>
<td>6</td>
<td>19</td>
</tr>
<tr>
<td>Unknown</td>
<td>10</td>
<td>4</td>
<td>14</td>
</tr>
</tbody>
</table>

Social behaviour

Mating of the snowfinches shows them to be socially monogamous. Pair bonds were first seen in late March, when they began to establish territory by fighting with conspecifics or other small animals (including pikas and several passerines) at some specific points (hourly aggressive frequency, 36.7 ± 53.9, 1 - 300, N = 43 pairs of 47.7-h observation). At the same time, followed by her mate, the female frequently visited and checked pika burrows to locate nest-sites. This process lasted a few days until they found a suitable one. Males continued guarding their mates during nest-building and egg-laying period (pair distances, 2.1 ± 1.6 m, 0.2 - 6.0, N = 39; movement initiated by female, 84% of 82 records). When females were incubating, males were not seen near the nest. However, near the off-nest time, they always came to the burrow entrance to call their mates or entered the burrows if there was no response from the females (11 records for 7 nests). If the females stayed outside the nest for more than 10 minutes (59 records of 300 off-nest events for 21 pairs), the males routinely (97% of the 59 records) flew in a semicircular trajectory over the females (less than 20 cm) and gave a short, loud call. In response to the males’ display, the females returned to the nest to incubate.

A total of 16 copulation attempts, all being initiated by males, were noted for 13 pairs during 521 minutes of observation within three days after completion of nest construction, but none was successful. During observations of 1,239 minutes for 14 pairs during the incubation period and of 3,638 minutes for 25 pairs of 2009, 173-187
during the nestling period, copulation attempts were never observed.

**Discussion**

Cavity-nesters may gain direct or indirect fitness benefits from thermal protection provided by the cavities (Stoleson and Beissinger, 1995; Beissenger et al., 2005; Godard et al., 2007). The benefits should be more obvious for the snowfinches nesting in the harsh alpine habitats where the daily temperature during the breeding period changes sharply (-4.7 to 23.4°C). Indeed, the birds initiated breeding 2-5 weeks earlier than several open-nesting passerines in the alpine meadow habitats (table 3). The early onset of reproduction resulted in a wide breeding window (about 70 days) and allowed some snowfinches to have second clutches. This could also contribute to the improved survival probability of snowfinch nestlings reared in the later broods. The double-brooded pairs did not start their first clutches earlier than those producing a single clutch, a result of reduced time constraint on the cavity-nesting birds. Nevertheless, like some subalpine birds that breed twice per season (cited from Badyaev, 1997), overlaps between the two attempts where only the male snowfinches continued to provision the first brood while the female snowfinches incubated a second clutch should be an adaptive strategy to deal with the limitation of breeding time available.

Being protected from inclement climates and nest predators, birds nesting in cavity enjoy a high breeding success compared with open-nesting species (Martin and Li, 1992; Clark and Shuttle, 1999). The same situation may be seen in the passerines breeding in the alpine meadow (table 3). The white-rumped snowfinches, along with three other local cavity-nesters, produce larger clutches than do the four open-nesters. Martin (1993) argued that the larger clutches of secondary-cavity nesters are a response of increased reproductive efforts to the limited availability of nest sites or breeding opportunities. This hypothesis could not apply to the white-rumped snowfinches in our study area where pika burrow densities are very high and competition among the birds for nest burrows was expected to be less severe (Zeng and Lu, 2009). It is also the case for two other secondary-cavity nesters, the rufous-necked snowfinch (nesting in pika burrows) and the black redstart *Phoenicurus ochruros* (nesting in natural holes or burrows created by the Tibetan ground tit *Pseudopodoces humilis*). Adaptation to the low nest predation rates which characterize cavity-nesting birds should be an acceptable explanation for the difference in clutch size between the two types of nester (Slagsvold, 1982; Lima, 1987). Similarly, the reduced nest predation risk also permits a prolonged young development period of these cavity-nesting species (Lack, 1948, 1968).

Species with females as the sole incubator must balance the thermal demands of embryos by staying on the nest with their own nutritional needs by leaving the nest to forage (Conway and Martin, 2000). Snowfinch females take long on- and off-nest periods compared to several open-nesting alpine passerines (table 3). Warmer microclimates in nest burrows, allowing the eggs to remain unattended for longer (Slagsvold, 1982; Lima, 1987), should be responsible for the differences. In many bird species, males often feed incubating females and the behaviour can reduce energy constraints on the females, and in turn increase nest attentiveness and improve hatching success (e.g. Lifjeld and Slagsvold, 1986; Halupka, 1994; Martin and Ghalambor, 1999). Nest attentiveness shown by the snowfinches was relatively short compared to that shown by the open-nesting species, although they received no food from their mates. This may be associated with the advantage of microclimates in nest burrows (White and Kinney, 1974; Lifjeld et al., 1987; Nilson and Smith, 1988). Interestingly, the absence of male feeding of females in the snowfinches is different from the general pattern in that the
A comparison of life history traits with respect to nest type for several passerine species breeding in the alpine meadow habitats, northwestern Tibetan plateau.

<table>
<thead>
<tr>
<th>Species</th>
<th>Breeding start date</th>
<th>Clutch size</th>
<th>Incubation period (d)</th>
<th>On-nest length (min)</th>
<th>% nest attentiveness</th>
<th>Male behavior during incubation</th>
<th>Nestling period</th>
<th>*Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>horned lark <em>Eremophila alpestris</em></td>
<td>late April</td>
<td>2.4</td>
<td>11</td>
<td>8.7</td>
<td>62</td>
<td>nest defense</td>
<td>11.3</td>
<td>1</td>
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<tr>
<td>oriental skylark <em>Alauda gulgula</em></td>
<td>mid-May</td>
<td>2.8</td>
<td>12</td>
<td>25.2</td>
<td>75</td>
<td>nest defense</td>
<td>8.8</td>
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<td>robin accentor <em>Prunella rubeculoides</em></td>
<td>mid-May</td>
<td>3.2</td>
<td>11.5</td>
<td>–</td>
<td>–</td>
<td>feeding female</td>
<td>11.9</td>
<td>3</td>
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<tr>
<td>twite <em>Carduelis flavirostris</em></td>
<td>late June</td>
<td>4.5</td>
<td>15</td>
<td>24.8</td>
<td>88</td>
<td>feeding female</td>
<td>14.0</td>
<td>4</td>
</tr>
<tr>
<td>black redstart <em>Phoenicurus ochruros</em></td>
<td>early May</td>
<td>4.8</td>
<td>13.5</td>
<td>–</td>
<td>71</td>
<td>nest defense</td>
<td>17.9</td>
<td>5</td>
</tr>
<tr>
<td>Tibetan ground tit <em>Pseudopodoces humilis</em></td>
<td>early May</td>
<td>6.8</td>
<td>15</td>
<td>22.9</td>
<td>63</td>
<td>feeding female</td>
<td>17.9</td>
<td>6</td>
</tr>
<tr>
<td>white-rumped snowfinch <em>Montifringilla taczanowskii</em></td>
<td>mid-April</td>
<td>4.7</td>
<td>13.1</td>
<td>27.0</td>
<td>48</td>
<td>nest defense</td>
<td>21.3</td>
<td>7</td>
</tr>
<tr>
<td>rufous-necked snowfinch <em>M. ruficollis</em></td>
<td>early April</td>
<td>4.0</td>
<td>12.5</td>
<td>39.0</td>
<td>68</td>
<td>nest defense</td>
<td>21.9</td>
<td>8</td>
</tr>
</tbody>
</table>

behaviour is more common or extensive in cavity-nesting than open-nesting birds (Lyon and Montgomerie, 1987; Martin and Ghalambor, 1999).

All the eight passerine species inhabiting the alpine meadow are socially monogamous and both parents feed the young. However, male parental behaviour during the incubation period differs and two distinct strategies may be identified: (i) defending the nest without incubation feeding, and (ii) feeding the females without nest guarding (table 3). The white-rumped snowfinch adopts the former. The difference may reflect a species-specific trade-off between paternity protection and female energy supplement (Wright, 1998).

Seasonal decline in clutch size of single-brooded temperate passerines is thought to be an adaptive response to reduced food availability, along with shortened day length (Perrins, 1970; Klomp, 1970). Brood size at fledging in the white-rumped snowfinches, which is mainly a single-brooded nester, does not change with laying date after accounting for the number of breeding attempts. This suggests that the birds suffer no food shortage in the late breeding season, as indicated by increased nesting success with laying date.

Altitude creates environmental gradients along which breeding performances and life histories of birds varies. Because of ecological severity at high altitudes, birds nesting there start to lay later than those nesting at low altitudes (Bears et al., 2009). It is the case for the white-rumped snowfinch breeding at three different altitude sites in the Tibetan plateau (table 4). It has been shown that high-altitude birds produce fewer broods, smaller clutches, larger offspring, and make greater parental efforts than their lowland conspecifics (Krementz and Handford, 1984; Badyaev, 1997; Badyaev and Ghalambor, 2001; Lu, 2005; Bears et al., 2009). This shows that birds shift their life history strategy from r- to k-selection as altitudes increase (Pianka, 1970). The comparisons among the three populations showed that the higher altitude snowfinches have smaller clutch and brood sizes, longer incubation and nestling periods, and more frequent feeding trips, supporting the predication.

However, unlike what was expected, the average number of broods produced per year by a snowfinch pair is the same at the 3,600-m and 4,300-m sites. Also, the birds at the two altitudes enjoy a similar high reproductive success. It is likely that the nature of cavity-nesting reduces the constraint of seasonal time on reproduction and the nest predation. Large eggs may lead to well-surviving offspring because they contain more yolk and lose heat less rapidly in cold climates due to a lower surface area-to-volume ratio (Rhymer, 1988; Williams, 1994; Smith and Bruun, 1998; Martin, 2008). An important method used by birds to cope with stress conditions is to trade off between offspring number and quality (Partridge and Harvey, 1988; Blackburn, 1991). However, inconsistent with the predication, we find snowfinch eggs to be smaller in the north of Tibet. This may be attributed to the small female body size of the highland population. Additionally, the harsher ecological conditions at higher altitudes could constrain the production of eggs, not only on their numbers but also on their sizes. Johnson et al. (2006) observed smaller eggs at a passerine inhabiting the higher altitude and argued that selection might favour sacrificing egg size before sacrificing egg number (clutch size).

Overall, the harsher ecological conditions experienced by high altitude breeders must limit their annual reproductive output. It is the case for the snowfinches. The lower productivity along with poorer resources also contributes to lower population densities of the higher-altitude snowfinches. Nevertheless, the reduced investment in the current reproduction by the breeders will potentially increase their chance of surviving to the future breeding seasons and thus contribute to their lifetime success (Bears et al., 2009). The “slow life history” performed by high altitude birds also highlights a conser-
A comparison of nesting parameters of the white-rumped snowfinch at three different altitudes. Shown are means ± SD, followed by sample sizes in parentheses and ranges.

<table>
<thead>
<tr>
<th>Nesting parameter</th>
<th>South Guansu</th>
<th>North Qinghai</th>
<th>North Tibet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude (°N)</td>
<td>34.2</td>
<td>37.6</td>
<td>30.5</td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>3,600</td>
<td>3,300</td>
<td>43,00</td>
</tr>
<tr>
<td>Annual mean temperature (°C)</td>
<td>1.2</td>
<td>-1.4</td>
<td>1.3</td>
</tr>
<tr>
<td>Annual total precipitation (mm)</td>
<td>626</td>
<td>484</td>
<td>481</td>
</tr>
<tr>
<td>Population density (pairs per 100 ha)</td>
<td>15</td>
<td>14</td>
<td>5</td>
</tr>
<tr>
<td>Body size (body mass/tarsus)</td>
<td>1.7 ± 0.2 (69), 1.1-2.1</td>
<td>–</td>
<td>1.6 ± 0.1 (15), 1.4-1.9</td>
</tr>
<tr>
<td>Duration of egg-laying period (d)</td>
<td>early April- late June</td>
<td>late April- mid-July</td>
<td>early May- late July</td>
</tr>
<tr>
<td>% double-brooded pairs</td>
<td>9 (147)</td>
<td>–</td>
<td>14 (14)</td>
</tr>
<tr>
<td>No. of broods produced annually</td>
<td>1.1</td>
<td>–</td>
<td>1.1</td>
</tr>
<tr>
<td>Egg volume (length x width², mm³)</td>
<td>7.3 ± 0.3 (6), 7.1-7.9</td>
<td>7.0 (4)</td>
<td>7.0 ± 0.5 (4), 6.6-7.5</td>
</tr>
<tr>
<td>Clutch size</td>
<td>4.7 ± 1.5 (7), 2-6</td>
<td>4.5 ± 0.3 (8), 3-6</td>
<td>3.3 ± 0.6 (3), 3-4</td>
</tr>
<tr>
<td>Incubation period (d)</td>
<td>12.7 ± 1.6 (34), 9-15</td>
<td>10-12 (6)</td>
<td>16.5 ± 0.7 (2), 15-16</td>
</tr>
<tr>
<td>Female feeding trip per h</td>
<td>6.5 ± 5.1 (21), 0-17</td>
<td>–</td>
<td>7.7 ± 3.2 (6), 0-18</td>
</tr>
<tr>
<td>Male feeding trip per h</td>
<td>6.1 ± 7.6 (21), 0-35</td>
<td>–</td>
<td>6.7 ± 4.9 (6), 0-18</td>
</tr>
<tr>
<td>Nestling period (d)</td>
<td>21.3 ± 2.0 (16), 18-24</td>
<td>15-16 (6)</td>
<td>19 (1)</td>
</tr>
<tr>
<td>Brood size at fledging</td>
<td>3.5 ± 0.8 (67), 2-6</td>
<td>3.5 (6), 2-6</td>
<td>2.9 ± 0.3 (10), 2-3</td>
</tr>
<tr>
<td>Annual productivity (brood size x brood number)</td>
<td>3.9</td>
<td>–</td>
<td>3.2</td>
</tr>
<tr>
<td>% nests with ≥ 1 fledgling</td>
<td>66 (190)</td>
<td>–</td>
<td>67 (15)</td>
</tr>
</tbody>
</table>

Ref. This study Zhang, 1982; Lu et al., 2009
Zhang & Deng, 1986

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BIBLIOGRAPHY


flavirostris at the Haibei alpine meadow, Qinghai. Zoological Research Sinica, 24: 137-139.


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