Reproductive Ecology of Tibetan Partridge
Perdix hodgsoniae in Lhasa Mountains, Tibet

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Abstract. Data on the breeding ecology of Tibetan Partridges (Perdix hodgsoniae) were collected in shrub environments near Lhasa, Tibet, during 1999-2001. Partridge flocks broke up in mid-March and individuals typically formed socially monogamous pair bonds. During daily activities the both members of the pair were close to each other, with 73.5% of observed individual distances less than 2 m. The egg-laying period extended from late May to late June. Average egg size was 16.1 (±SE=0.2) g in mass and 39.2 (±0.1)×28.1 (±0.1) mm in dimension. Average clutch size was 8.3 (±0.8, range 5–12). The partridge produced larger eggs and smaller clutches than its two congener species, Grey Partridge (P. perdix) and Daurian Partridge (P. dauuricae). Incubation lasted about 23 days, and 44.4% of clutches successfully hatched. Vegetation characteristics were the most important determinants of partridge nest-site choice, with patches of low, sparse, and secondary cover being preferred. Nest-sites were also significantly closer to paths than random sites.

Key words: Nest-site selection, Reproductive biology, Tibetan Partridge Perdix hodgsoniae.

Introduction

Endemic to Qinghai-Tibet plateau, Tibetan Partridges (Perdix hodgsoniae) are widespread throughout the highland, with alpine scrub and meadow as their favorable habitats (Cheng et al. 1978). Historically, the alpine vegetation was a result of forest degradation due to dried climate with the rise of Himalayas, which block off warm air of Indian Ocean from reaching the plateau (Li 1988). Now, the vulnerable ecosystem suffers an increasing pressure of human activities, mainly scrub-cutting and grazing. Tibetan Partridges are one of the crucial species in the alpine ecosystem. To evaluate possible change of the ecosystem caused by both nature and human agencies, it is necessary to know adaptation aspects of the partridges.

In recent decades, intensive agricultural practices (increasing use of pesticides, herbicides, toxicants and other farm operations) have led a rapid population decline of two other species of partridge, Grey Partridge (P. perdix) (Panek 1992, Tucker & Heath 1994, Potts & Aebischer 1995) and Daurian Partridge (P. dauuricae) (Zhang & Wu 1992, X. Lu unpublished data). Meanwhile, those partridges have been under heavy hunting.
pressure. Although there is no evidence that the number of Tibetan Partridges have obviously decreased in recent years, ones should keep close watch on the population status. The data about the species' ecology may provide a foundation on which conservation and management can effectively be conducted. We are also in a need to get the partridge's biological information comparative to its two relative species. In a previous study (Lu & Ciren 2002), we had offered the data on habitat selection and flocking behavior of this species during the non-breeding seasons in Lhasa mountains, Tibet. However, so far reproductive information on the partridges is little known (Johnsgard 1988). In the present studies, we investigated its reproductive ecology in the same area.

Methods

Field data were gathered in Xiong Se valley (29°27'N, 91°40'E, total area about 400 ha) near Lhasa, Tibet, during the breeding seasons of 1999–2002. With an annual average temperature of 4.5°C and annual precipitation of 565.6 mm (over 90% of which takes place during June to September period, Fig. 1), the study area is characterized by alpine shrub and meadow, with altitude ranging from 4,000 to 5,600 m. A detailed habitat description was given in Lu & Ciren (2002). The study mainly occurred in Rose (Rosa sericea) and Barberry (Berberis hemleyana) community on the south-facing slopes where

Fig. 1. Monthly change of mean air temperature (a) and total precipitation (b) in the study area.
there was a high partridge abundance.

The habitats occupied by Tibetan Partridges had been uncultivated and there had been no hunting activity in the study area. We counted partridges throughout the habitats. In the relatively poor cover partridges were highly sensitive to approaching investigators and thus allowed a good detectability for them. By scan-sampling method (Altmann 1974), we noted the behaviors of each mate in a pair every two minutes when it was on relatively open field for 20–60 minutes. Five exclusive categories of behaviors were identified: feeding, scanning, moving, calling and social aggression. During this study, totally focal observations of 958 minutes were made for 9 different pairs. Distance between two pair members was directly estimated once every six minutes. Other special behaviors were also recorded on any possible occasion.

We systematically searched for partridge nests over the habitats. Once a clutch was located, the progress of its reproduction was monitored to get the parameters of egg-laying, incubation and hatching. We also measured egg length and maximum breadth (to 0.1 mm) and weighted them (to 0.1 g) during regular nest-site visits. Incubation length was determined from those successful clutches located during egg-laying period. For some clutches found when incubation had begun or broods less than five-day old, we determined their first egg-laying dates by back-dating from the species' average reproductive parameters such as egg-laying interval, incubation length, mean daily egg mass loss during incubation (obtained from the successful clutches) or age of chicks. In this study, 9 active nests and 10 broods less than five-day old were recorded. The old partridge nests were easy to be identified by their location, shape, and especially fragments of eggshells left after hatching. Data from 7 old nest-sites were used to analysis of nest-site choice.

For each of both active and old nest-sites, we measured its geographical location (altitude in m, slope degree, distance to water in m and distance to path in m) and vegetation traits associated with nest patches. Centered on a nest-site, we set a 10×10 m quadrate and subdivided it into four 5×5 m quadrates. Vertical layers of vegetation were classified as the high (≥1.5 m) and the low (<1.5 m) shrub. Within each subplot, we estimated proportion of vertical projection by canopy of each vegetation layer by drawing a chart on a grid paper. The mean of four subplots was treated as percent cover value of the sampling plot. We determined canopy height (in cm) by taking to the top of each of five randomly chosen bushes in a sampling plot and then averaged those measurements to produce a single value for each quadrate. In the study area, bushes in some plot were cut by local Buddhists for firing so that vegetation in the plots differed in cover and height from those of the unexploited. We scored the cut-plot as 0 and uncut-plot as 1. Considering possible importance of physical characteristics at a nest-site, we recorded whether a nest-site was situated (scored as 1) or not (scored as 0) in rocky areas which were often topographically complex. To evaluate available nesting habitats, we randomly chose samples equal to number of located nest-sites over the habitats and took the same measurements as those at a nest-site.

Nonparametric procedures, Kruskal-Wallis and Mann-Whitney U tests, were used to examine significance of difference between variables. Principle component analysis (PCA), based on a covariance matrix with varimax rotation, was run to identify major
tends of nest-site selection. Prior to analysis, the data of percent vegetation cover were arcsine-transformed. All p-values presented are two-tailed. All expressions in the text are given as mean ± SE.

Results

Social organization dynamics

Since mid-March partridge flocks broke up and more monogamous pairs formed as the season progressed, and by late April, most individuals in the population had already mated (Table 1). Once paired, cocks and hens kept together until hens started to incubate. According to the data on individual reproductive timing (see below), it appeared that a pair union must have kept together for at least two months prior to incubation. A few solitary individuals encountered during late April to early May were more likely the surplus that failed to obtain a mate. As more hens entered incubating from early June onset, single birds (mostly cocks) were increasingly counted. The first young were seen in late June and since then encounter rate of family flocks increased.

| Time of season | Social unit | ≥3 birds | 2 birds | 1 bird | Family flock |
|---------------|-------------|----------|---------|--------|-------------|
| Early March   | 100.0(11)b  |          |         |        |             |
| Late March    | 27.8( 5)    | 50.0( 9) | 22.2( 4)|        |             |
| Early April   | 7.9( 3)     | 68.4(26) | 23.7( 9)|        |             |
| Late April    | 90.5(19)    | 9.5( 2)  |         |        |             |
| Early May     | 95.1(39)    | 4.9( 2)  |         |        |             |
| Late May      | 88.2(30)    | 11.8( 4) |         |        |             |
| Early June    | 60.9(14)    | 39.1( 9) |         |        |             |
| Late June     | 47.6(10)    | 47.6(10) | 4.8( 1) |        |             |
| Early July    | 35.7( 5)    | 28.6( 4) | 35.7( 5)|        |             |
| Late July     | 12.5( 2)    | 12.5( 2) | 75.0(12)|        |             |
| After August  | 7.1( 1)     | 7.1( 1)  | 85.8(12)|        |             |

a Not include chicks.
b Percentage of the total number of observation (the number of observation)

Table 2. Percent time allocation (mean±SE, ranges are given in parentheses) of members in Tibetan Partridge pairs (n = 9) among several typical behaviors when they were in relatively open field.

| Behavior          | Hen          | Cock         | Mann–Whitney U test |
|-------------------|--------------|--------------|---------------------|
| Feeding           | 67.1±5.1 (36.8–83.3) | 50.8±3.9 (31.3–74.1) | z = −0.75, p = 0.45 |
| Moving            | 9.4±2.3 (0.0–18.8) | 10.7±2.2 (0.0–18.2) | z = −0.40, p = 0.69 |
| Preening          | 12.0±5.5 (0.0–42.1) | 10.3±3.2 (0.0–25.0) | z = −0.27, p = 0.78 |
| Scanning          | 7.6±2.4 (0.0–22.4) | 23.3±2.3 (11.1–31.0) | z = −2.13, p = 0.03 |
| Calling and aggression | 3.9±2.7 (0.0–22.2) | 4.9±2.6 (0.0–22.2) | z = −0.95, p = 0.34 |
Two members of a pair usually were close to each other (individual distance: ≤1.0 m 59.2%, 1.1–2.0 m 23.1%, 2.1–5.0 m 23.1%, >5.1 m 3.4%, n=145 observations). There seemed to be a dominance hierarchy among cocks. When two pairs met, one cock usually attacked vigorously another and sometimes chased after the latter for over 100 m. As a result they left the mates alone temporarily. Then two members in the same pair came to contact by loud calls until united again. Occasionally, when met, four birds of two pairs chased each other. During the mating period, feeding was the most predominated behavior for both sexes (Table 2, Kruskal-Wallis test, female, $H=22.81$, $df=4$, $p<0.01$; male, $H=23.64$, $p<0.01$). Cocks were more vigilant than hens: when hens were foraging they frequently scanned surroundings, and if a danger appeared they often called nervously and ran away with the hens followed. In total, cocks devoted 28.2% of their time to protect hens (scanning, calling and aggression). For other activities, no significant sexual differences were detected.

Nest, egg, clutch, incubation and hatching

The partridge nests consisted of a simple hollow on the ground, averaging 18.1±2.2 cm (range 15.0–23.6, n=15) in diameter and 7.7±1.0 cm (range 5.4–9.0) in depth. The nest materials included sticks of bushes and grasses gathered nearby, as well as some feathers from hen’s plumage.

Out of 19 clutches (including 10 broods), 4 (21.1%) had their first eggs in late May, 12 (63.2%) in early June, and 3 (15.8%) in late June. The egg color was dark white without spot. The average size of 48 eggs was 39.2±0.1 mm (range 37.1–41.2)×28.1±0.1 mm (range 27.0–29.1) and fresh mass measured from 36 eggs was 16.1±0.2 g (range 14.2–18.3). Average clutch size was 8.3±0.8 (n=9), ranging from 5 to 12 eggs.

Only hens incubated eggs for about 23 days. Average daily mass loss per egg was 0.15±0.01 g (range 0.09–0.20, n=21). The hatching span extended about 24 h. Forty-four (93.6%) out of 47 eggs from four surviving clutches successfully hatched. The weight of hatchlings before leaving nest averaged 12.6±0.2 g (n=3). In nine active clutches, four (44.4%) hatched successfully, and other five, of which one was abandoned shortly after incubating and four were destroyed by predators during incubation.

After the last egg hatched, hens still stayed in nests for about 15–16 h (n=2). Having spent the first night after hatching, the hen and chicks left the nest and fed nearby in accompany with the cock, who often was more vigilant. For one observed brood, its roost-site of the first night was about 80 m from the nest and the second night about 150 m. When chicks were very young, the hens frequently brooded them.

Nest-site selection

PCA (Table 3) revealed that 94.5% of accumulated variance among sites was attributed to the first three PCs. PC 1, which explained 59.6% of overall variation and reflected differences between nest-sites and random-sites, had heavy loads for four vegetation parameters, suggesting that the partridges preferred to nest in patches with lower poorer bushes (Table 4). PC 2 (explaining 20.7% of variation) represented a gradient of altitude. But this may be misunderstood because our nest-searching efforts
Table 3. Principal component analysis (PCA) of covariance matrix (Varimax rotation with Kaiser Normalization) of the habitat traits measured in Tibetan Partridge nest-site and random-site.

| Variable              | PC 1  | PC 2  | PC 3  |
|-----------------------|-------|-------|-------|
| Altitude              | -0.06 | 0.98  | 0.15  |
| Slope degree          | -0.01 | 0.33  | 0.02  |
| Vegetation use        | -0.53 | 0.03  | -0.01 |
| High-scrub cover      | 0.70  | -0.11 | -0.21 |
| Low-scrub cover       | -0.32 | 0.27  | -0.16 |
| High-scrub height     | 0.95  | -0.04 | -0.12 |
| Low-scrub height      | 0.44  | 0.28  | -0.16 |
| Distance to water     | -0.15 | 0.15  | 0.14  |
| Distance to path      | 0.17  | 0.31  | 0.98  |
| Rock                  | 0.15  | 0.03  | -0.19 |
| Variation explained   | 59.57 | 21.49 | 13.29 |
| Cumulative variation  | 59.57 | 81.06 | 94.35 |

* Boldfaces indicate values with a higher factor loading on each PC.

Table 4. Measurements (mean±SE, ranges are given in parentheses) of several main habitat parameters at Tibetan Partridge nest-sites (n=15) and at random-sites (n=15).

| Variable          | Nest-site        | Random-site      | Mann-Whitney U test |
|-------------------|------------------|------------------|---------------------|
| Altitude          | 4,160.0±31.9 (3,950.0–4,360.0) | 4,256.7±46.1 (4,000.0–4,500.0) | z = -1.16, p = 0.24 |
| Slope degree      | 30.0±2.2 (12.0–45.0) | 40.7±1.1 (15.0–55.0) | z = -3.55, p < 0.01 |
| High-scrub cover  | 9.0±4.0 (0.0–50.3) | 32.5±4.5 (0.0–60.1) | z = -3.01, p < 0.01 |
| Low-scrub cover   | 27.3±2.1 (15.0–44.7) | 25.3±2.6 (15.0–55.0) | z = -1.08, p = 0.28 |
| High-scrub height | 82.7±23.7 (0.0–195.0) | 153.7±16.3 (0.0–195.0) | z = -2.02, p = 0.04 |
| Low-scrub height  | 48.3±4.1 (25.0–80.0) | 71.3±1.3 (60.0–80.0) | z = -3.69, p < 0.01 |
| Distance to water | 121.5±27.9 (12.0–400.0) | 85.0±17.9 (15.0–210.0) | z = -1.00, p = 0.32 |
| Distance to path  | 28.1±9.0 (1.0–120.0) | 83.0±22.5 (5.0–300.0) | z = -2.35, p = 0.02 |

* See text for unit of the variables.

were mainly made around 4,000 m. Whereas we frequently encountered the partridge pairs and family flocks from the foot (3,900 m) to near the top (4,650 m) of the mountain, suggesting that they might nest in a more extended range of altitudes. The third PC (18.7%) was about distance of nest-sites from a path, to which most nests were much close.

Discussion

Jenkins (1961) reported that mate system of Grey Partridge is socially monogamous and mated cocks strongly guard their mates and often initiate attacks on other potential rivals. Dahlgren (1990) also observed that cocks of this species devoted most of their time to surveillance during pairing period while their mates forage. Similar to Grey Partridges, cocks of Tibetan Partridges maintained close proximity to their mates and spent a
considerable proportion of daytime to mate guarding. Such male behaviors were more likely to prevent his mate from extra-pair attempts by other males (Birkhead & Möller 1992).

Relative to clutch size of Gery Partridge (15–17 eggs, Cramp & Simmons 1980, Hupp et al. 1980) and Daurian Partridge [16–20, in the Altai region, Dementiev & Gladkov 1967; averaging 17.1 (8–20) in northern China, Zhao & Du 1996, Zhang & Liang 1997], Tibetan Partridges had a smaller clutch. However, they laid larger eggs than Grey Partridge (14.6 g, 36.0 × 27.0 mm, Cramp & Simmons 1980) and Daurian Partridge (12.0 g, 34.0 × 26.3 mm, Zhang & Liang 1997). Body mass of female Tibetan Partridge (290–360 g) was between Daurian (250–340 g) and Grey (310–450 g) Partridges. In terms of life history evolution (Pianka 1970), the high-altitude dwelling Tibetan Partridge seemed to take a k-selection strategy compared to the two other low-altitude partridge species. The similar altitude-related breeding strategy has also been observed in Grouses (Bonasa spp.) (Liu & Geng 1994) and Snowcocks (Tetraogallus spp.) (Liu 1994).

Tibetan Partridges had a slightly higher nesting success (44.4%, percentage of initiated nests hatching) than Grey Patridges (about 30%, Johnsgard 1988) but markedly lower than Daurian Partridge (61.1%, Zhang & Liang 1997). Predation is demonstrated to be the principal source of nesting mortality in several Galliform species (Tapper et al. 1996, Jimenez & Conover 2001). The nest-site complexity and concealment, depending to a greater extent on physical characteristics at a nest-site, often represent key cues of nest-site selection by ground-nesters (Ricklefs 1969, Hanson 1970). Thus a site that can provide adequate camouflage from potential predators should be selected for. Zhang et al. (1994) found that nest-sites of Daurian Partridges are associated with higher vegetation in a locality in northern China, where Thick-billed Crows (Corvus macrorhynchos) and several raptor species are major predators of the breeding partridges. However, Tibetan Partridges in the study area preferred to place their nests in relatively poor covers. In terms of local adaptation, we explained this nest-site choice as follows: In the study, two avian predators, Golden Eagles (Aquila chrysaetos) and Sparrow Hawks (Accipiter nisus), had a very low density (Lu 1997) and thus they had little threat to nesting partridges. This allowed the partridges to nest in the lower poor bushes. Siberian Weasels (Mustela sibirica) is a common carnivore and have been demonstrated to be responsible for 20% nest failure of Tibetan Eared Pheasant (Crossoptilon harmani), a ground nester in the same area (X. Lu unpublished data). Relative to dense vegetation patches, the poor cover patches where the partridge nested were randomly distributed over the nesting habitats and thus provided a less clear clue for the weasels, a non-specialist nest predator. Although the four partridge clutches were more likely destroyed by the weasels, we got no evidence of the incubating hens being killed. Probably when a nest-site was located both in the sparse understory and access to a path, it was convenient for hens to escape the prey's attack. The present results seemed to indicate that scrub-cutting had a relatively weak impact on nesting selection of the partridges. But, management of the alpine vegetation must take account into the animal community supported by the ecosystem as a whole. In addition, it has showed that both Grey Partridges (Rands 1988) and Daurian Partridges (Zhang et al. 1994) tend to nest where amounts of dead grass, leaf litter and
bramble were greater. In our study area, however, poorly developed bushes produced few of the materials.

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**チェベット、ラサ山地におけるチェベットヤマウズラ *Perdix hodgsoniae* の繁殖生態**

1999年から2001年の間に、チェベットのラサ近郊の低木林環境で、チェベットヤマウズラ *Perdix hodgsoniae* の繁殖生態についてのデータを収集した。チェベットヤマウズラは3月中旬に群れが解消し、社会的には典型的な一夫一妻のつがいを形成した。日中の活動時間帯にはつがいの両者がお互いに接近しており、観察された個体の73.5%で個体間距離が2 mより近かった。産卵期は5月下旬から6月下旬までであった。平均の卵重量は16.1 (±SE = 0.2) gで、卵径が39.2 (±0.1) × 28.1 (±0.1) mmであった。平均の一腹卵数は8.3 (±0.8, 範囲 5–12) であっ

た。チェベットヤマウズラは近縁の2種、ヨーロッパヤマウズラ (*P. perdix*) とヤマウズラ (*P. dauuricae*) より大きな卵を産み、一腹卵数が小さかった。抱卵は約23日間続いた。抱卵していた巣の44.4%が孵化に成功した。植生の特徴がチェベットヤマウズラの営巣場所選択の最も重要な決定要因であり、低くまばらな二次植生で覆われたパッチを好んでいた。営巣場所もランダムではなく、有意に近い場所で見いだされた。

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