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## Abundance and breeding ecology of Brown Accentors *Prunella fulvescens* in Lhasa, Tibet

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**Abstract.** Data are presented for the first time on the abundance and breeding ecology of the Brown Accentor in Lhasa, Tibet. During the non-breeding periods, the accentors occurred across a wide altitudinal gradient in a variety of habitats and remained numerically abundant. When breeding, they were restricted to alpine zones (> 4300 m) with scattered shrubs, and the population density declined to a low level (0.02 nests per ha). Nests were built partially in lone-standing short, thorny bushes and at a low height (< 0.8 m) above the ground. Dates of clutch initiation ranged from early May to mid-July, a period of 80 days. Clutch size varied between 2 and 3 eggs, averaging 2.9 ( $\pm$  0.1). Eggs hatched after 13–14 days of incubation, and young birds fledged at 13–17 days, when they reached 97% of the adult weight. In terms of the proportion of clutches from which at least one chick fledged, breeding success was 56.3%. No evidence of multiple mating was found in this species.

**Key words:** Brown Accentor, *Prunella fulvescens*, habitat selection, abundance, nest-site selection, breeding biology, social system, nestling diet

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### INTRODUCTION

Accentors are small oscine passerines typical of the Old World. All the 13 species currently identified belong to a single family, Prunellidae, and a single genus, *Prunella*. These birds all are inhabitants of Eurasian high montane biome, with the Himalayas, Tibetan plateau and central Asia as the centre of species diversity (Zheng 2002). Regarding their abundance, breeding ecology and social biology, extensive published data are available only for two species: Dunnock *Prunella modularis* and Alpine Accentor *P. collaris* (Cramp 1988, Nakamura 1995a, b). In particular, the studies of these two species revealed an interesting, unusual mating system: cooperative polygynandry (e.g. Davies 1992, Davies et al. 1995, Nakamura 1998a, 1998b). In contrast, ecological information about those taxa occurring in the evolutionary centre of the species group is very limited (Ali & Ripley 1987, Chen & Luo 1998).

The Brown Accentor is one of the high-mountain accentors. They are distributed in the Himalayas, Tibetan plateau through central Asia,

occupying altitudes above 2000 m (Zheng et al. 1983, Ali & Ripley 1987, Grimmentt et al. 1998). Despite the wide occurrence, little was known of their ecology and social system. In this paper, I provide such information, which was collected from the Lhasa region, Tibet.

### MATERIAL AND METHODS

#### Study area

I studied Brown Accentors mainly in the Xiongse valley (29°27'N, 91°40'E), Lhasa, Tibet. The annual average air temperature of the study area is 4.5°C and precipitation is summer-biased, with 80% of the annual total precipitation of 566 mm falling between June and September. Vegetation is characterized by alpine shrub and meadow. Between 3980 and 4550 m a.s.l. on the south-facing slopes vegetation is dominated by Rose *Rosa sericea* and Lhasa Barberry *Berberis hemleyana* shrubs, and Wilson Juniper *Sabina pingii* shrubs extend from 4550 to 4980 m. North-facing slopes between 4200 and 5100 m are covered by

evergreen Rhododendron *Rhododendron nivale* shrubs with Alpine Willow *Salix sclerophylla* mixed in at lower altitudes. Near and at the top of the mountains are meadows consisting mainly of Kobresia *Kobresia pygmaea*. There are two Tibetan monasteries (human habitation) situated at 4400 and 4700 m on the south-facing slopes, respectively. Being inside the valley, the study area is free of agricultural practice and suffers less yak-grazing. However, the vegetation, especially in the valley bottom, has been subject to cutting by local people for firewood.

### Data collection

**Abundance estimation.** Accentor abundance was quantified in the non-breeding period from August 2004 to January 2005. I randomly set up 2–5 transects (usually 2 to 3 km in length, but only 1 km for one transect within the human habitation) across the altitudinal range of each of the five habitats. The transects were placed at least 200 m apart to minimize pseudoreplication. Based on the fixed-width transect method (Bibby et al. 1992), each month I counted the birds seen within 25 m of a transect that was walked in the morning at a speed of 1.5 km/h. A total of 79 h were spent on 17 transects. The overall sparse vegetation and the species' preference for more dispersed cover led to little variation in bird detectability among habitats. In other seasons, accentor abundance was assessed relying only on descriptive records (abundant or rare). I also used nest density to estimate the species' abundance. This was made by systematic nest searches over a 183 ha plot on the south-facing slopes throughout the 2004 breeding season. In addition, field ornithological surveys were conducted in a variety of habitats in the Lhasa region to obtain data on the occurrence and general abundance of the accentors.

**Breeding biology.** Brown Accentors are the only *Prunella* species nesting in the Xiongse valley. During the breeding seasons of 1999–2004, I searched for their nests over the valley, by systematically checking bushes or by following birds performing nesting behaviour. I have done ornithological research at this alpine site for more than ten years and during my field work I collected data of nest sites of a variety of species covering the full altitudinal range of the valley. Therefore my efforts for sampling accentor nest sites had no bias with respect to altitude.

For each located nest, I made a description and measurement of it (altitude, slope direction, plant

species and height, vegetation cover within a 10 × 10 m, nest height, distance to nearest stream) and its contents (eggs or nestlings). Vegetation features around accentor nest sites were compared with data obtained from my general vegetation survey over the valley. To obtain further nesting parameters and know their fate, I inspected the nests at an interval of 1 to 5 days to determine egg-laying date, egg size, clutch size, hatching date, fledging date, chick development, and reproductive success. A few nests were not visited frequently enough because of remoteness and they only provided data on nest-site, egg or clutch parameters. For nests discovered after hatching, I determined their earliest possible date of the first eggs by back-dating from the parameters (obtained from the complete clutches) of subsequent breeding events.

**Nestling diet.** I used the neck-collar method to collect the prey transported to the nestlings at ages of 8–12 days in three different nests. The food items were stored in alcohol and brought to the laboratory for classification and measurement.

**Behavioural data.** In the course of long-term studies on avian ecology in the Xiongse valley, I opportunistically noted social interactions of the accentors. Because the accentors are sexually monomorphic in plumage and size, I considered two individuals as a mating pair if they were in close association, performing courtship behaviour (such as chasing and pre-copulation displaying), mate following or parental activities (such as caring for chicks). I assumed that the individual that was chased or followed was the female. When observing at a nest, I closely watched a parental bird to keep visual contact with it. The individuals that typically exhibited incubating or brooding behaviours were considered to be female. In addition, a nesting female was trapped and marked, which aided my behavioural observations and sex identification.

**Gregariousness.** During the study, I also opportunistically noted social units of the accentors as singles, pairs or small flocks (defined as an association of more than two individuals that behaved together). Because no censuses were made for all months of any single year, the data from different years were pooled to obtain a sample set that covers an annual cycle.

### Statistics

I used non-parametric procedures with two-tailed significances for all statistical analysis. Values were given as mean ± SD.

## RESULTS

### Habitat use

Field observations on occurrence of the accentors in the Lhasa region showed that during the non-breeding season (October–April), the birds were present over a wide altitude and in a variety of habitats, from lowland (3600 m) river banks, village, farmland, garden marsh up to the alpine zone (5000 m). In my alpine valley, the accentors were one of the most dominant species among the local bird assemblages (Author's data). They used all the five types of habitat, but abundances differed among the habitats (Kruskal-Wallis test, autumn,  $H = 90.6$ ,  $df = 4$ ,  $p = 0.06$ ; winter,  $H = 13.92$ ,  $p = 0.01$ , Fig. 1), with more individuals aggregating around the human habitation area. Among the natural vegetation, Rose-Lhasa Barberry shrub supported more accentors (Fig. 1). In terms of microhabitat, the birds were more likely associated with open habitats where shrub cover was lower and scattered. During the breeding period (May to September), however, the accentors were seen only in the alpine zone above 4200 m.

### Abundance

Although accentors occurred in the alpine zone throughout the year, there was a seasonal change in abundance. During the non-breeding season, an increase from autumn to winter was observed (Fig. 2). Relative to those in natural habitats, the birds in the human habitation were major contributors to the change. From spring through the breeding period, although no quantitative investigations were regularly made, I was aware that the population density was at a high level

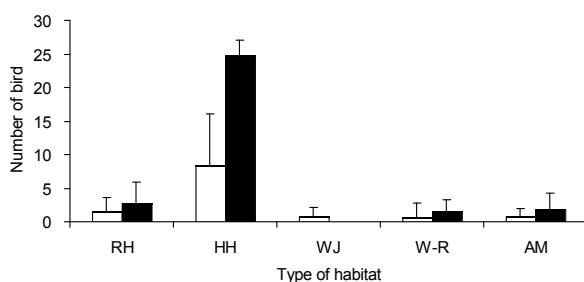


Fig. 1. Brown Accentor abundances (individuals encountered along 50m-wide transects/h, mean + SD) during autumn and winter periods (2003–2004), among different habitats in an alpine valley. RH — rose-barberry shrub (5 transects), HH — human habitation (2 transects), WJ — Wilson juniper shrub (3 transects), W-R — willow-rhododendron shrub (4 transects), AM — alpine meadow (3 transects), open bar — autumn, closed bar — winter.

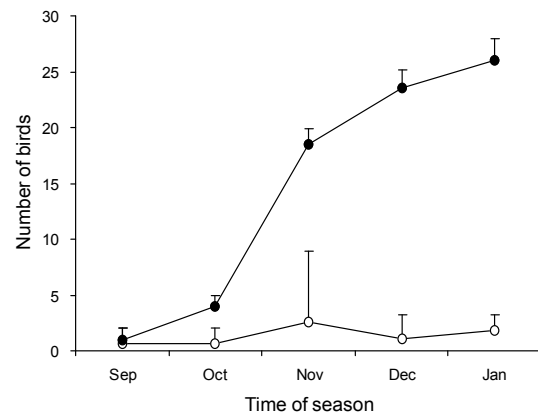


Fig. 2. Seasonal change of Brown Accentor abundances (individuals encountered along 50m-wide transects per hr, mean + SD) in natural habitat (open circle, pooled data of the four vegetation types, 15 transects) and human habitation (closed circle, 2 transects) during autumn and winter periods (2003–2004).

until mid-May shortly after the first clutches were initiated. After this the birds started to decline rapidly (field records from three breeding seasons) and a low density, approximately 3–5% of the non-breeding density (I usually encountered  $\leq 2$  accentors during 5 to 8 h of observation each day), remained throughout the breeding season. During the 2004 breeding season, within the 183 ha plot on the south-facing slopes, only 4 accentor nest-sites were located. This produced a breeding abundance of 0.4 pairs/10 ha.

### Gregariousness

Flock size varied seasonally (Kruskal-Wallis test,  $H = 63.26$ ,  $df = 11$ ,  $p < 0.001$ , Fig. 3). During the non-breeding period of high abundance, the birds formed loose temporary associations of up to 20 individuals on their foraging ground (on average 27.8% of social units consisted of more than two birds). During the breeding season,

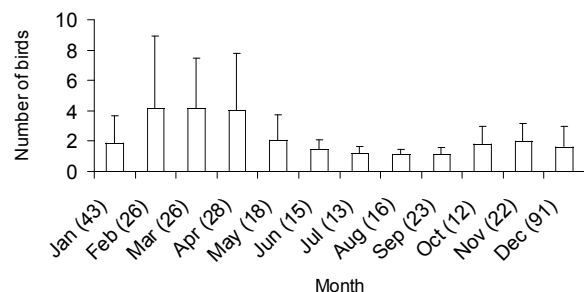


Fig. 3. Annual change of Brown Accentor flock size (mean + SD). Data of different years and habitats were pooled (sample size in parentheses). Newly-fledged young were not included because of poor detectability of them.

single birds and pairs were the predominant social units (average 92.9%). However, the difference in the proportions of these social units did not reach significance ( $\chi^2$  test = 1.88, df = 1,  $p = 0.17$ ), indicating a weak gregariousness.

### Nest-site selection

Over six breeding seasons, only 18 accentor nest-sites were located. All of them occurred on south-facing slopes, 17 in Rose-Lhasa Barberry shrubs and 1 in a Wilson Juniper shrub. These nests were distributed from 4280 up to 4713 m ( $4458 \pm 124$ ), showing a nesting preference for higher altitudes when contrasted to the 3980–4900 m altitudinal range of shrub vegetation in the valley. Being at high altitude, most nest-sites (88.9%) were far away from active streams. Vegetation cover around the nest-sites was 29.5% ( $\pm 17.3$ , 10–60), relatively poor compared with the average of 37% of Rose-Lhasa Barberry shrub.

Most accentor nests were built in two thorny shrub species (Table 1). Almost all the chosen nesting bushes were shorter than average as a result of cutting by local people. The canopy of the nesting bushes had an average projection area of 2.0 m<sup>2</sup> ( $\pm 1.6$ , 0.8–6.3,  $n = 16$ ) and most nests (62.5%) were placed at the edge of the bush canopy. Sixteen (88.9%) of the 18 nests were located from 0.1 to 0.8 m above the ground and the remaining two (11.1%) at ground level.

### Breeding season

Egg-laying dates of the accentors spread from the first week of May (earliest record 1 May) to the middle of July (latest record 17 July), a span of nearly 80 days (Fig. 4). The distribution of the date of clutch initiation is based on a small sample, but seemed to show two periods of intensive laying activity in late May and mid-July. However, the influence of year to year differences in egg laying dates on the observed pattern should not be ruled out where the data from different years were analyzed together. There was no relationship between clutch initiation date and the altitude at which the nests were sited ( $r_s = 0.3$ ,  $n = 18$ ,  $p = 0.22$ ).

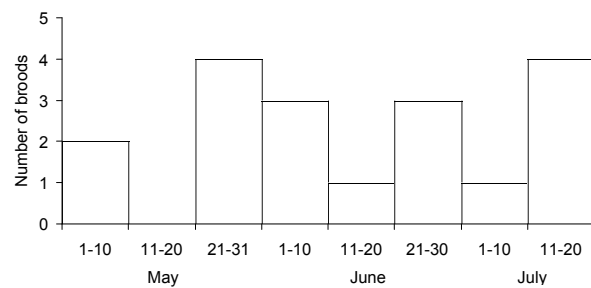


Fig. 4. Temporal distribution of laying dates of the first egg by Brown Accentors. The clutches started are arranged in a 10-day period with pooled data from different breeding seasons ( $n = 18$ ).

### Nesting parameters

The accentors built a cup-shaped nest. On the outside of the nest cap were finer grasses or bush stems, on the inside was moss, yak hair and on some occasions (3 of 9 described nests) bird feathers. Measurements (in mm) taken from 8 nests were as follows: exterior diameter  $105.2 \pm 9.1$  (94–120), interior diameter  $58.4 \pm 5.0$  (51–65), depth  $48.4 \pm 7.0$  (41–64) and height  $102.8 \pm 19.1$  (75–127).

Egg-laying did not occur immediately after nest completion. The delay was at least 5 days in one nest and more than 11 days in another. In one case a bird was observed sitting on the already-completed nest a few days before the first egg. One egg was laid per day ( $n = 5$  eggs from two nests). Eggs were bright blue-green with or without scattered dark-brown spots. Some eggs were ellipsoid without an obviously larger end. Fresh egg mass was  $2.2 \pm 0.07$  g (2.1–2.3,  $n = 5$ ). Egg dimensions (in mm) measured for 23 eggs were  $19.8 \pm 0.5$  (18.5–20.6) in length and  $14.6 \pm 1.1$  (13.8–19.5) in width. Clutch size ranged from 2 (10%) to 3 (90%) eggs, averaging  $2.90 (\pm 0.32, n = 10)$  clutches). Incubation period was 13–14 days ( $n = 2$  nests). Hatching took place over one ( $n = 2$  clutches) or two days ( $n = 1$  clutch). Brood size at hatching was  $2.63 \pm 0.52$  (2–3,  $n = 8$ ).

Newly-hatched young were naked with pink skin, with a cluster of dark grey down of about 10 mm on the forehead, orbits, occiput, shoulder, forearm, midline of the back and flank. The mouth corners were white. Nestlings opened eyes

Table 1. Nest-site selection, nest height above ground and nesting bush height in Brown Accentors.

Location of nest site	No. of nest (%)	Nest height (cm)	Nesting bush height (cm)
<i>Caragana bicolor</i>	8 (44.4)	$25.6 \pm 3.2$ (10–40)	$113.1 \pm 13.0$ (50–150)
<i>Berberis hemleyana</i>	7 (38.9)	$48.6 \pm 10.3$ (10–80)	$131.4 \pm 16.3$ (50–180)
<i>Cotoneaster divaricatus</i>	1 (5.6)	66.0	170.0
Rock wall	1 (5.6)	0	–
Ground	1 (5.6)	0	–

at 5–6 days after hatching. For 10 nestlings measured more than three times from 4 different broods, their growth rate was consistent with the logistic model of body mass averaged  $0.55 \pm 0.07$  (0.47–0.69). The fledgling period lasted 13 days in one clutch and 17 days in another. The nestlings ready to fledge had an average body mass of 17.7 g ( $\pm 0.5$ , 17.0–18.1,  $n = 4$ ), being 96.7% of the adult mass. Brood size at fledging was  $2.33 \pm 0.50$  (2–3,  $n = 9$ ).

Of 26 eggs, 15 (57.7%) hatched successfully. Hatching failure was due to infertility (1), egg loss (2) or clutch loss (9). Among 21 hatchlings observed, 13 (61.9%) survived to fledging. Of 16 known-fate nesting attempts, 9 (56.3%) successfully produced at least one young.

### Nestling diet

All the food items delivered to young consisted of arthropods (Table 2). Among the nine prey taxa, the adults of Homoptera were highly preferred ( $\chi^2 = 83.28$ ,  $df = 9$ ,  $p < 0.001$ ). Of 78 prey items I collected, 74.4% had body lengths smaller than 5 mm.

### Courtship display

The courtship display of the accentors was characterized by a ground chase. A male followed a female that ran round on the ground. The female frequently raised, sometime quivered, her tail to expose her cloaca to the male. In the course of display, no individuals other than pair members were involved. Over my long-term ornithological study at this site, I only observed 5 cases of the courtship display, all of which took place between 26 May and 26 June. None of these displays led to successful copulation. This suggested a low copulation rate of this species. Being at a low density, solitary pairs were widely dispersed

over the preferred nesting habitats. Territoriality didn't seem obvious because most courtship displays I observed occurred around the monastery areas where no nest-sites were located. I did not observe physical competition between males for mating.

### Parental behaviour

Only the female undertook incubation during which she frequently left the nest to forage. Over 429 min of observation on two nests, on-nest time averaged 15.2 min ( $\pm 6.2$ , 8–30,  $n = 17$ ) and off-nest 9.5 min ( $\pm 3.4$ , 3–15,  $n = 18$ ). During 481 min of observation on five different nests, I saw once that the incubating bird was fed by another (assumed to be the mate).

Females brooded the nestlings. In one clutch I observed that the nestlings at an age of 12–13 days were still brooded. For one clutch with two 6-day old nestlings, the female brooded for 10–13 min ( $n = 4$  bouts). Both parents fed the young. Usually several food items were carried in the bill to the nest at each visit. The provisioning rate, based on 258 min of observation for three nests each contained 3 nestlings at an age of 9–10 days, was 4.9 trips per h with an average interval of 12.3 min ( $\pm 8.3$ , 1–29,  $n = 21$  bouts).

## DISCUSSION

### Abundance and habitat selection

During the breeding season, Brown Accentors were numerically abundant, occurred over a wide altitudinal range and used various habitats. However, breeding populations were restricted to the alpine zone where they occurred at a low density. The widespread occurrence and substantial population fluctuation characterized by the large non-breeding abundance seemed not to be a result of recruitment of young because of the small breeding population and relatively low nesting success. Seasonal movements, either at a local or at a regional scale, should be responsible for these. However, the lack of data on abundance and migration from other areas within the species' range limits my ability to make further comments. In most *Prunella* species, patterns of seasonal movement are complex, including residents, local or long-distance migrants, and in specific regions migration may partially occur with wintering and breeding populations having different origins (Cramp 1988).

From winter through early spring, the accentors were mostly observed around human

Table 2. Composition and size of preys brought by the adult Brown Accentors to their nestlings.

Prey type	No. of prey item	%	Prey size (body length, mm)	
			Mean $\pm$ SD	Range
Araneae	8	10.3	4.2 $\pm$ 4.0	1.5–13.0
Orthoptera	5	6.4	7.4 $\pm$ 4.0	4.0–14.0
Coleoptera	10	12.8	7.8 $\pm$ 4.7	2.5–17.0
Diptera	5	6.4	3.0 $\pm$ 1.1	1.5–4.0
Lepidoptera	2	2.6	13.0 $\pm$ 1.4	12.0–14.0
Homoptera	30	38.5	2.4 $\pm$ 0.8	1.0–5.0
Plecoptera	3	3.8	6.2 $\pm$ 0.3	6.0–6.5
Psocoptera	11	14.1	2.6 $\pm$ 0.6	1.5–3.5
Mecoptera	1	1.3	8.0	8.0
Larvae	3	3.8	12.7 $\pm$ 8.1	8.0–22.0
Total	78	100.0	4.5 $\pm$ 4.0	1.0–22.0

habitation. The between-habitat variation may be related to differences in vegetation and food availability. Brown Accentors are an open-habitat dweller and dense cover of Rose-Lhasa Barberry and Alpine Willow-Rhododendron shrubs was unsuitable for them. Although Wilson Juniper shrub and Kobresia meadow were potentially suitable vegetation conditions, poor food supply and harsh climates (low temperature and prevailing wind) at the high-altitude habitats could be major factors limiting the birds. In contrast, the human habitation, where there was no dense vegetation and both natural and supplementary food was available, was preferred, especially during early spring when seeds in the field had diminished.

I confirmed that the accentors preferred to nest at higher altitude, which is located in the upper two-thirds of the valley where shrubs are sparse and short. The observed highest nesting site of 4713 m is higher than the breeding upper limit of 4300 m so far recorded for this species (Zheng et al. 1983). Like several other mountainous accentors such as Radde's Accentor *P. ocularis* and Alpine Accentors, Brown Accentors are alpine open-habitat nesters, contrasting to Black-throated Accentor *P. atrogularis*, Dunnock and Siberian Accentor *P. montanella* which prefer to nest in relatively dense vegetation. In the preferred habitats, Brown Accentors nested low in short thorny shrubs, assumed to be of benefit by protecting the nests against prevailing wind in the alpine zone. Following a similar pattern, Alpine Accentors breeding on the mountain tops of the French Pyrenees build their nests in rock crevices (Davies et al. 1995).

### Life history

The 80-day breeding period of Brown Accentors in the alpine valley was relatively long compared to 40–50 days of many other local passerines (author's own data). The extended

breeding season seems to be a characteristic of *Prunella* species, although they breed in montane habitats. For example, the laying period spreads from March or April until July or later for European Dunnock (Cramp 1988), and May to August for Alpine Accentor in Mt. Norikura of Japan (36°, 2600–3026 m, Nakamura 1990) and for Robin Accentor *P. rubeculoides* in the northern Tibet plateau (38°, 3300 m, Zhang 1982). This potentially allows a female to rear more than one brood during a nesting season.

The clutch size of 2–3 eggs in the Brown Accentor at this alpine site is smaller than that of other congeners breeding at relatively low localities (3–4, up to 7, Table 3). Clutch size in birds is usually related to the number of offspring that the parents can rear (Lack 1966). Small clutches seem to be an adaptation to harsh ecological conditions at high altitudes (Badyaev 1997, Badyaev & Ghalambor 2001). Nevertheless, this statement should be treated with caution because clutch size may increase with latitude (Lack 1968). Furthermore, I compare relative egg size by dividing egg volume (length × breadth<sup>2</sup>) by wing length among accentor species (Table 3). The result shows that Brown Accentors do not lay relatively larger eggs (0.57) compared with other species (average 0.59, 0.49–0.67), inconsistent with observations on Blackbird *Turdus merula* at the alpine site (Lu 2005).

### Nestling diet

The food of Brown Accentor young in my alpine site was invariably made up of arthropods. This was consistent with the results obtained from mountain-living Alpine Accentors (Cramp 1988, Davies et al. 1995), but differed slightly from two species adapted to dense vegetation, Dunnock and Black-throated Accentor, where plant food (mainly seeds) often appeared in their young's diet (Cramp 1988). In my study species,

Table 3. A comparison of clutch size and egg size according to latitude and altitude among *Prunella* species. Average clutch size, if any, is given in parentheses. Wing length is the average of female specimens.

Species	Location	Latitude	Altitude (m)	Clutch size	Egg dimension (mm)	Wing length (mm)	Source
<i>P. fulvescens</i>	South Tibet	29°N	4500	2–3	19.8 × 14.6	74	This study
<i>P. rubeculoides</i>	North Qinghai	38°N	3300	2–4 (3.4)	20.5 × 15.1	75	Zhang 1982
<i>P. ocularis</i>	Caucasus	39°N	2500	3–4	-	74	Cramp 1988
<i>P. collaris</i>	Alps	40°N	2800	3–4	23.3 × 16.7	97	Cramp 1988
<i>P. strophiatea</i>	North Qinghai	37°N	3200	3–4	19.2 × 14.3	66	Chen & Luo 1998
<i>P. atrogularis</i>	South-central USSR	63°N	1000	3–5 (4.0)	19.6 × 15.0	71	Cramp 1988
<i>P. immaculata</i>	South Gansu	35°N	2950	4 (4.0)	19.6 × 14.5	77	Jiang et al. 2002, 2003
<i>P. modularis</i>	West Europe	55°N	1000	3–7 (5.1)	19.6 × 14.6	69	Cramp 1988
<i>P. montanella</i>	Siberia	63°N	1000	4–6	18.7 × 13.8	72	Cramp 1988

Homoptera was the dominant taxon among the nestling diet, which differed from the observations on three other *Prunella* species (Dunnock, Black-throated and Alpine Accentors), where Diptera and in some cases Coleoptera or Araneae accounted for a large proportion of their nestling diets (Cramp 1988, Davies et al. 1995).

Prey carried by the parental Brown Accentors to nests was obviously small (mean body length  $4.5 \pm 4.0$  mm), compared with several other passerine species with similar or smaller bodies in the alpine site (White-throated Redstart *Phoenicurus schisticeps*  $13.6 \pm 6.5$ ; Stonechat *Saxicola torquata*  $14.6 \pm 7.1$ ; Chinese Shortwing *Hodgsonius phoenicuroides*  $8.8 \pm 5.9$ ; Tickell's Leaf Warbler *Phylloscopus affinis*  $8.2 \pm 2.9$ ; Stoliczka's Tit Warbler *Leptopoeile sophiae*  $11.9 \pm 3.2$ , Xin Lu unpubl. data). The same was true for several other *Prunella* species and it has been suggested that the foraging specialization for small prey for chick rearing could impose a constraint on feeding efforts of the parental birds and promote the formation of a multiple mating system (Davies & Lundberg 1984, Davies 1986, Davies et al. 1995).

### Social system

It has been suggested that ecological factors may affect the mating system of accentor species. In Dunnock, which has a variable mating system, females defend territories of different sizes as a result of the patchy distribution of favourable foraging habitats (Davies & Lundberg 1984). This allows males to monopolize females to different degrees, from one male defending one female (monogamy) or several females (polygyny) to two males sharing one female (polyandry) or several females (polygynandry) (Davies 1992). For Alpine Accentor occurring on harsh mountain tops, food distribution is dispersed and patchy, leading to larger, undefended female ranges that overlap with each other (Davies et al. 1995). This makes it difficult for a single male to monopolize females by territorial defence, but makes it possible for several males to associate with several females. Therefore only the polygynandrous mating system is formed in this species (Davies et al. 1995, Nakamura 1998a, 1998b).

Although Brown Accentors in my study area inhabited an alpine environment similar to those of Alpine Accentors in France (Davies et al. 1995) and Japan (Nakamura 1998a, 1998b), and they also performed specialized foraging for small prey, a factor related with multiple mating (Davies & Lundberg 1984, Davies 1986, Davies et al. 1995),

I still think that their mating system is social monogamy for the following reasons:

- 1) social units of the accentors encountered during the nesting period consisted of 1–2 individuals, and courtship displays involved only two pair members and occurred at a very low frequency. In contrast, in two multiple mating species, investigators (Nakamura 1990, 1998a, 1998b, Heer 1994, 1996, Davies et al. 1995) may regularly observe breeding social groups of 5–11 birds, multiple breeders that get involved in a courtship display and high rates of the display (e.g. in Alpine Accentor, average 0.5 per h, based on 2 358 records over four breeding seasons, Nakamura 1998a);
- 2) for Brown Accentors, I had no evidence of more than one male attending the young, which is unusual in species with multiple mating systems (Davies 1985, 1986, Davies et al. 1995, Hartley et al. 1995, Nakamura 1998a);
- 3) variation in clutch size is great in Dunnock (3–7 eggs) in part as a result of females adjusting their clutch size according to the mating pattern, laying larger clutches if they can expect two males to feed the young (Davies & Hatchwell 1992). A similar strategy is less likely to take place in my species that had small clutches (2–3 eggs) and limited variation in their size (90% being 3 eggs). It was possible that low breeding density in my study area limited the formation of a complex social system, as argued by Bishton (2001) who studied a low-density Dunnock population.

Based on the difference in mating systems between Dunnock and Alpine Accentor, Davies et al. (1995) suggested that there is a phylogenetic component in the evolution of social systems of the *Prunella* species, with the variable mating system in lowland Dunnock having derived from the polygynandry typical of the high mountain-living Alpine Accentors. The question about the origin of social systems of *Prunella* species would be more interesting if monogamy is the only mating pattern adopted by my accentor species, which occupy an extremely harsh alpine habitat. Further detailed research, especially through marking individuals, is necessary to provide convincing evidence for the mating system of the Brown Accentor.

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## STRESZCZENIE

### [Występowanie i ekologia lęgowa płochacza płocego w Lhasie, Tybet]

Badania prowadzono w dolinie Xiongse, w górach Tybetu. Liczenia ptaków prowadzono na transektach przebiegających przez wszystkie siedliska spotykane w dolinie, na całym badanym terenie poszukiwano gniazd. Stwierdzono, że w okresie połęgowym gatunek ten występuje w dość szerokim gradiencie wysokości i wielu środowiskach, choć jego największe liczebności notuje się w okolicach ludzkich siedzib (Fig. 1). Na badanym terenie zaobserwowano wzrost liczebności w poszczególnych miesiącach jesienno-zimowych (Fig. 2), a ptaki spotykane były w tym okresie w niewielkich grupach (Fig. 3). W okresie lęgowym gatunek ten występuje wyłącznie w piętrze alpejskim (powyżej 4.300m n.p.m.), a zagęszczenia populacji są bardzo niskie — 0.2 pary/10 ha. Gniazda budowane są w ciernistych krzakach, nisko nad ziemią (Tab. 1). Jaja składane są od początków maja do połowy lipca (Fig. 4). W składzie pokarmu młodych można było wyodrębnić dziewięć rzędów stawonogów, wśród których równoskrzydłe stanowiły najliczniejszą grupę (Tab. 2). Sukces lęgowy wyniósł 56,3%. Nie stwierdzono, aby u tego gatunku występowała poligamia. Uzyskane dane dotyczące wielkości zniesienia porównano z innymi gatunkami płochaczy (Tab. 3).