Comparisons of the alpine bird communities across habitats and between autumn and winter in the mid-Yalong Zangbo River valley, Tibet

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(Accepted 16 July 2007)

Abstract
The extreme alpine environment around the mid-Yalong Zangbo River on the Tibetan plateau supports a unique avifauna. To understand the structure and habitat selection of this poorly known bird assemblage, we quantified abundance of the birds in four representative types of vegetation and a human settlement inside a shrub-covered alpine valley (29°27′N, 91°40′E, 4000–5200 m a.s.l.) in the Lhasa mountains, Tibet, from September 2004 to January 2005. A total of 40 species of birds was recorded, six of which were summer breeders, one vagrant autumn migrant, 29 permanent residents, and four local wintering migrants. Latitudinally migrating taxa were absent. Of the 33 wintering species, 70% were alpine specialists. Patterns of distribution of species and individuals differed across habitats. The highest bird species richness was found in Rose–Barberry shrub where vegetation was most complex, and fruiting and seeding plants abundant. From autumn to winter, birds tended to aggregate in the human settlement for foods supplemented by local Buddhists; as a consequence this habitat contained the highest individual density. In terms of trophic guilds, plant-eating birds were predominant in composition (65.8–75.8%) and numerically abundant (89.8–96.7%) in all the habitats. We concluded that vegetation diversity and food supply significantly influence species composition and individual abundance of the alpine bird community. For long-term survival of the unique bird assemblage, we argue for protection of the shrub vegetation as it is difficult to regenerate in the harsh high-altitude conditions.

Keywords: Alpine habitat, bird assemblage, conservation, non-breeding period, Tibet plateau, vegetation degradation

Introduction
Knowledge of a bird community, its composition, structure, temporal dynamics, association with habitat and response to disturbance, is useful in terms of ecological theory (Dunning 1986; DeSante 1990) and conservation practice (Kremen 1992; Chettri et al. 2001; Vickery et al. 2001). In comparison to numerous studies made in a variety of regions and biomes of the world, we know little about the bird communities inhabiting mountains around the mid-Yalong Zangbo River on the Tibetan plateau, despite its
uniqueness in zoogeography (Zhang 1999), endemcity in avifauna (Stattersfield et al. 1998), and importance for conservation (BirdLife International 2004). Almost all the ornithological data of the region have been collected during short summer visits and focused on the species’ occurrence and distribution (Walton 1906; Ludlow 1950; Vaurie 1972; Zheng et al. 1983).

Historically, with the rise of the Himalayas, the warm air of the Indian Ocean has been blocked off from reaching the Tibetan plateau, resulting in increasingly drying climates and forest degradation, and leaving behind a vast wasteland over the northern plateau, and alpine shrub around the mid-Yalong Zangbo River (Li 1988; Miehe 1996). Therefore the existing alpine environment, in terms of species composition and community structure, typically resembles the above-tree line ecosystem in primitive forests of the eastern plateau (Li 1988). Strong seasonal fluctuation in environmental conditions, harsh weather and relatively simple habitat structure in the alpine zone either render it inhospitable for occupancy to all but a few organisms, or support species at their physiological and thus distributional limits. Typically, in the alpine environment, dry conditions as a result of low rainfall and strong solar radiation are adverse for plant growth. The shrub vegetation therefore provides limited shelter and food resources for birds, especially during the winter period. Occurring in a region with a rapidly developing economy and the densest human population in Tibet, the alpine vegetation is subject to increasing human disturbances (Li 1988). A major disturbance is the extraction of firewood and housing materials, which has caused the loss of over 30% of shrubby vegetation in Lhasa during the last six decades (Winkler 2000). This clearly points to a need for baseline data about the bird community for protection of this vulnerable alpine ecosystem. In addition, it is useful to know, at a community scale, how birds are distributed among different habitats in order to coexist in the harsh high-altitude environments. Since birds can respond subtly to environmental changes (Shankar Raman et al. 1998; Canterbury et al. 2000; O’Connell et al. 2000), information about the alpine bird community is helpful for understanding ecological consequences of the large-scale succession of natural vegetation over the plateau.

With these questions in mind, we investigated autumn–winter birds within representative vegetation types in an alpine valley, near Lhasa, Tibet. Based on the data obtained, we quantitatively documented the composition, structure, and seasonal dynamics of the alpine bird community.

Methods

Study area

Field data were collected from September 2004 through January 2005 in the Xiongse valley (29°27′N, 91°40′E), 30 km from Lhasa city, Tibet (Figure 1). Climate in the alpine site is markedly seasonal with an annual average temperature of 5.5°C and annual total precipitation of 566 mm, over 80% of which falls between June and September. Poor winter precipitation along with strong solar radiation (annually 3022 h) results in no or transient snow accumulations.

Our study site is situated inside the valley and covers an area of about 400 ha where neither hunting activity nor agricultural practice has been carried out and vegetation is well-developed compared with outside the valley. The vegetation, characterized by alpine shrub and meadow, differs in species composition and structure according to slope direction and altitude (Wu 1985). Between 3980 and 4550 m on the south-facing slopes, Rose (Rosa
sericea)—Barberry (*Berberis hemleyana*) shrub (R-B) is common. The habitat is replaced at higher elevations by evergreen Wilson juniper (*Sabina pingii*) shrub (WJ) which spreads up to 4970 m. The north-facing slopes, between 4200 and 5100 m, are covered by evergreen Rhododendron (*Rhododendron nivale*) with Alpine willow (*Salix sclerophylla*) mixed at lower altitudes (R-W). Alpine meadow (AM) occupies between 4970 and 5200 m. Above AM, rocks dominate the alpine landscape. A stream system, consisting of a major stream and its branches, is distributed on both sides of the slopes. Two monasteries are located in R-B at 4400 and 4700 m, respectively. There are a total of 220 nuns and monks who have homes around the monasteries, forming a small human settlement (HS) of 1.5 ha (Figure 1).

**Vegetation survey**

Vegetation surveys were performed only in winter months and always by the same observer (X.L.). Within each type of the representative habitats, we chose 15–30 quadrats of $4 \times 4$ m and subdivided each into five $1 \times 1$ m subplots (four at the corners and one at the centre) by marking bushes with flagging tape. Vertical layers of vegetation were classified as tall (>1.5 m), short (<1.5 m) shrub, and grass. Within each subplot, we estimated the following variables: the proportion of vertical projection of canopy of each vegetation layer (by drawing a chart on graph paper), canopy height (the mean of five randomly chosen bushes), and frequencies of common shrub species. We averaged the measurements over
five subplots as the value of a quadrat and then averaged over all quadrats for the mean of the habitat investigated. For this study the data on vegetation parameters were collected from 126 quadrats.

Bird survey

The fixed-width transect method was used to produce comparable data of bird species and abundance among habitats (Bibby et al. 1992). Within each type of habitat, we set up two or three randomly located transects of 2–4 km (but only 1 km for one of the two transects within habitat HS). The transects were placed at least 200 m apart (to minimize pseudoreplication) across the altitudinal range of the vegetation investigated. We walked at a speed of 2 km h\(^{-1}\) along a transect in the morning (not later than 4 h after sunrise) and counted birds within 25 m to either side of the transect (a range within which there is a low likelihood of missing any individual birds). For species of raptors that often soared in the sky, we noted any individuals in the visual field. The procedure was conducted once per month for each transect and alternated among habitats by the same investigator (L.Y.Z.). Although there were great differences in the level of cover among habitats, overall low vegetation (<2 m) had little influence on detectability of the birds. Since the transects differed in length among habitats, to produce comparable data sets for bird abundance we firstly calculated the mean of individuals of a species encountered per h within a habitat for each month and then averaged the values over autumn (September to November) and winter months (December to January), respectively. A total of 70.5 h (55 field days) was spent walking 11 transects of about 145 km.

Each bird species was recorded as a summer breeder, year-round resident, local migrant (nesting in adjacent areas but wintering in the valley, or nesting in the valley but wintering in adjacent areas), or latitudinal migrant (breeding far north of the region). The distribution data of wintering birds around the mid-Yalong Zangbo River, which were obtained from our long-term field observations, allowed us to identify whether a species wintered only in alpine habitat or not. Based on published data (Zheng 1993) and our long-term field study at this site, we also grouped each bird species as frugivore–granivore, frugivore–omnivore, granivore–insectivore, granivore, omnivore, omnivore, insectivore, or carnivore.

Data analysis

Kruskal–Wallis ANOVA was used to test differences between the various vegetation parameters measured. This test was also run to assess differences in bird abundance among habitats for both bird assemblage and species level, where the measures during each transect survey were assumed independent, as the survey on each transect was made once per month and there were temporal variations in bird species and their abundance. Because these tests were performed for many species, it is to be expected that some of them will be significant by chance alone even if the null hypothesis is true. To reduce the probability of committing a Type I error, we used a false-discovery-rate approach (Benjamini and Hochberg 1995) because of its suggested advantage compared to the conservative sequential Bonferroni correction (Garcia 2004; Nakagawa 2004). We ranked \( P \)-values in ascending order and proceeded from highest to lowest \( P \) to find the first that satisfies \( P_j \leq \frac{\alpha j}{m} \), where \( P_j=P \) required for rejection of \( H_0 \), \( \alpha=\) unadjusted alpha level of 0.05, \( j=\) rank, \( m=\) number of multiple tests. Comparisons of seasonal (from autumn to winter) changes in
abundance for all habitats or for a single habitat were performed using Mann–Whitney \(U\) tests. We used row \(\times\) column tests of independence with a \(G\)-statistic to test for significant heterogeneity in the frequency of species within a specific trophic guild among habitats.

Bird community structure in each habitat was expressed using the Shannon–Wiener species diversity index \((H' = -\sum p_i \times \ln p_i)\), where \(p_i = N_i/N\), \(N_i\) = number of individuals recorded for species \(i\), \(N\) = total number of individuals recorded on a transect; Magurran 1988). We also calculated an evenness index \(D = 1 - \sum (p_i)^2\) based on the probability that two randomly sampled individuals from an assemblage represent two different species (Simpson 1949). We assessed the similarity between bird assemblages using the Jaccard index \[q = c/(a + b - c),\] where \(a=\) the total number of species in community \(A\), \(b=\) the total number of species in community \(B\), \(c\) = the number of common species both in \(A\) and \(B\) (Krebs 1999). A Wilcoxon test was used to examine whether similarity indices statistically differ between autumn and winter bird assemblages. To illustrate relative importance of different species among a bird assemblage, a dominance diversity curve was constructed for each habitat by ranking the log of the species density values from highest to lowest (May 1975). Exponential functions (Lamont et al. 1977) are fitted to these curves.

Results

Vegetation characteristics

Species composition and structure of vegetation differed among habitats (Table I). Habitat R-B contained the most abundant shrub species among the four habitats. Besides the two diagnostic species, Cotoneaster (\textit{Cotoneaster hebephyllus}) and Caraganas (\textit{Caragana} spp.) were commonly found in it. Associated with the high species richness, this habitat had the largest variation in the vertical layer (the coefficient of variation (CV) values obtained from the height data of all bushes measured within a habitat). Habitat WJ was structurally simplest because it was almost completely dominated by short Wilson junipers. Habitat R-W had the most dense shrub cover, which was formed mainly by evergreen rhododendron, but its low species richness was associated with a relatively less variable vertical layer.

Table I. Vegetation characteristics of five major alpine habitats in a valley near Lhasa, Tibet.

| Habitat type | R-B | HS | WJ | R-W | AM |
|-------------|-----|----|----|-----|----|
| Sample size | 26  | 15 | 30 | 30  | 25 |
| Slope degree| 37.9±0.5 | 20–30 | 39.6±0.4 | 39.1±0.4 | 30.2±0.7 |
| Shrub species per quadrat | 3.6±0.27 | 3.5±0.26 | 1.2±0.07 | 1.9±0.12 | 30.2±0.7 |
| No. of shrub species recorded | 7 | 5 | 2 | 3 | 0 |
| Tall shrub height (cm) | 174.3±6.1 | 181.8±4.9 | 0 | 181.9±2.5 | 0 |
| Short shrub height (cm) | 77.0±5.6 | 87.9±5.0 | 74.4±4.6 | 93.7±2.8 | 0 |
| CV of shrub height (%) | 45.7 | 35.8 | 33.7 | 33.9 | 0 |
| Grass height (cm) | 10.5±0.8 | 8.6±1.0 | 7.6±0.5 | 8.4±0.4 | 6.9±0.4 |
| Tall shrub cover (%) | 31.2±2.3 | 11.9±2.7 | 0 | 32.9±4.5 | 0 |
| Short shrub cover (%) | 38.8±1.6 | 5.7±1.7 | 47.8±1.9 | 86.6±2.6 | 0 |
| Grass cover (%) | 6.8±0.4 | 3.5±1.0 | 5.6±0.6 | 6.0±0.6 | 41.2±3.0 |

\(a\) R-B, Rose–Barberry; HS, human settlement; WJ, Wilson juniper; RW, Rhododendron–Willow; AM, alpine meadow. \(b\) Comparisons were made among the habitats in which the tested components were present. \(c\) Those species recorded at least three times among all quadrant samples.
Vegetation cover in habitat HS was lowest. In all the shrub habitats, grasses were short and displayed low coverage. Within each of the two south-facing habitats, shrubs were patchily distributed (with individual clumps of shrub 3–5 m apart) and bare plots occurred, with herbaceous plants mainly present around the base of shrubs. Because of sparse rainfall and cold climates at the extremely high altitude, grasses in habitat AM displayed low cover.

Avifaunal patterns

A total of 40 species of birds was recorded among 2105 individuals detected in the valley during autumn and winter surveys across all five habitat types (Table II). Besides six summer breeders that left the valley by November, and one vagrant migrant (Yellow-bellied tit) during autumn, 33 species regularly wintered there. Of these wintering species, 29 (88%) were permanent residents (including Tibetan-eared pheasant and Giant babax, two endemics to this region) and the remaining four (12%) were local migrants. No latitudinally migrating species were present either in autumn as passage migrants or in winter as overwintering migrants.

Bird species richness among habitats

The pattern of species distribution varied across habitats (Table III). Habitat R-B supported 87% of all the 38 species recorded in autumn and 79% of the 33 species in winter; the corresponding values were only 45 and 49% in habitat AM. The number of species in habitats HS (61% in autumn and 52% in winter), WJ (61 and 49%) and R-W (50 and 58%) were intermediate between R-B and AM. Patterns in species diversity index among habitats was slightly inconsistent to that in species compositions: HS had the highest value (2.01 in autumn and 2.21 in winter), followed by R-B (1.95 and 1.99), then by the three other habitats (1.39–1.65, 1.48–1.70). Out of the 33 wintering species, six were specifically found in a single habitat (Horned lark and Ground tit in AM, Tree sparrow in HS, White-browed tit, Coal tit, and White-browed rosefinch in R-B), and three species (Tibetan partridge, Eurasian magpie, and Pink-rumped rosefinch) were common to all the five habitats. Beyond those identified as habitat specialists or generalists, 23 species occurred in two to four habitats.

The bird assemblages were more uniform in species composition between habitats R-B and HS (similarity 65% in autumn and 59% in winter) than between any two others (24–60% in autumn and 27–57% in winter; Table IV). Habitat AM had a bird assemblage highly distinct from either shrub habitats or HS. Further, we compared the mean autumn

Table II. Sample size and characteristics of bird community in five major alpine habitats in a valley near Lhasa, Tibet.
Table III. Residency type, distribution status, trophic category and average number of bird individuals encountered per h along a 50 m-wide line transect during autumn and winter in five different alpine habitats in a valley near Lhasa, Tibet.

| Bird species                  | RC | DSR | DSH | TG | Autumn          | Winter         |
|-------------------------------|----|-----|-----|----|-----------------|----------------|
|                               |    |     |     |    | R-B  | HS  | WJ  | R-W | AM  | R-B  | HS  | WJ  | R-W | AM  |
| White-winged grosbeak Mycerobas carnipes | R  | AS  | G   | FG | 0.78 | 0.17 | 1.00 | 1.83 | 0.83 | 2.75 | 0.75 | 0.75 |      |
| White-throated redstart Phoenicurus schisticeps | R  | AS  | G   | I  | 1.30 | 0.17 | 0.17 | 0.50 | 1.83 | 0.50 | 0.25 | 0.75 |      |
| White-browed tit Parus superciliosus | R  | AS  | G   | GI | 0.44 |     |     |     |     | 0.17 |     |     |     |      |
| White-browed rosefinch Carpodacus thura | R  | AS  | G   | G  | 0.22 |     |     |     |     |     | 0.17 |     |     |      |
| Tibetan-eared pheasant Crossoptilon harmani | R  | AS  | G   | O  | 4.00 | 3.33 | 1.00 | 3.17 | 6.33 | 11.75 | 2.75 | 4.50 |      |
| Tibetan snowcock Tetraogallus tibetanus | R  | AS  | S   | O  | 0.33 | 4.00 |     |     | 2.00 | 6.50 | 1.50 |     | 7.00 |      |
| Giant babax Babax waddelli      | R  | AS  | G   | FO | 1.00 | 0.50 |     | 1.67 | 0.67 | 1.25 |     | 1.50 |     |      |
| Great tit Parus major           | R  | RG  | G   | GI | 0.67 | 3.17 |     | 0.50 | 0.67 | 5.00 |     | 0.75 |     |      |
| Common hoopoe Upupa epops       | SB | RG  | G   | I  | 0.11 | 1.00 | 0.50 |     | 0.17 |     |     |     |      |      |
| Eagle owl Bubo bubo             | R  | AS  | G   | C  | 0.17 |     |     |     |     | 0.25 |     |     |     |      |
| Himalayan griffon Gypis himalayensis | R  | RG  | G   | C  | 0.50 | 0.33 | 1.50 | 0.83 | 0.25 | 0.25 | 0.25 |     |      |      |
| Tibetan partridge Perdix hodgsoni | R  | AS  | G   | O  | 5.33 | 2.67 | 0.83 | 2.33 | 3.50 | 4.50 | 5.25 | 2.25 | 1.75 | 1.25 |
| Godlewski's bunting Emberiza godlewskii | R  | RG  | G   | G  | 0.72 | 1.67 | 0.33 |     | 0.50 | 0.50 | 0.25 | 0.50 |     |      |
| Ground tit Pseudopodoces humilis | R  | RG  | S   | GI | 0.67 |     |     |     | 2.83 | 24.75 | 1.50 | 1.75 |     |      |
| Brown accentor Prunella fulvescens | R  | AS  | G   | GI | 1.50 | 8.33 | 0.83 | 0.67 | 2.83 | 24.75 | 1.50 | 1.75 |     |      |
| Hodgson's redstart Phoenicurus hodgsoni | SB | AS  | G   | I  | 0.33 |     |     | 0.17 |     |     |     |     |      |      |
| Common stonechat Saxicola torquata | SB | AS  | G   | I  | 0.22 |     |     | 0.50 |     |     |     |     |      |      |
| Wallcreeper Tichodroma muraria | R  | RG  | G   | I  | 0.11 | 0.17 |     |     | 0.17 |     |     |     |      |      |
| White-winged redstart Phoenicurus erythrogaster | LM | RG  | G   | I  | 0.11 |     |     | 0.17 | 0.17 | 0.25 |     | 1.00 |     |      |
| Common kestrel Falco tinnunculus  | R  | AS  | G   | C  | 0.33 | 0.17 | 0.17 |     | 0.17 |     |     | 0.25 |     |      |
| Red-billed chough Pyrrhocorax pyrrhocorax | R  | AS  | G   | O  | 3.00 | 1.50 | 2.00 |     | 2.83 | 1.25 | 1.25 |     | 0.50 |      |
| White-browed tit warbler Leptopoei sophiae | R  | AS  | G   | GI | 0.50 | 0.17 | 0.50 | 0.67 | 1.67 | 2.75 | 0.50 | 0.75 |     |      |
| Tickell's leaf-warbler Phylloscopus affinis | SB | AS  | G   | I  | 1.72 | 0.33 | 0.67 | 1.50 |     |     |     |      |      |      |
| Yellow-bellied tit Parus venustus | P  | AS  | G   | GI | 0.33 |     |     |     |     |     |     |     |      |      |
| Twite Carduelis flavirostris | LM | RG  | G   | G  | 0.56 | 0.50 | 0.50 | 3.67 | 0.17 | 0.50 |     |     |      |      |
| Grey-backed shrike Lanius tephronotus | SB | RG  | G   | C  | 0.17 | 0.33 | 0.33 |     |     |     |     |     |      |      |
| Brown-checked laughingthrush Garrulax henrici | R  | AS  | G   | FO | 1.22 | 4.00 | 0.50 | 0.83 | 4.50 | 21.75 | 1.25 | 1.00 |     |      |
| Winter wren Troglodytes troglodytes | R  | AS  | G   | I  | 0.17 |     |     |     | 0.17 | 0.25 | 0.50 | 0.25 |     |      |
| Golden eagle Aquila chrysaetos | R  | RG  | G   | C  | 0.28 | 0.17 | 0.17 | 0.17 | 0.25 | 0.50 | 0.25 |     |      |      |
| Tree sparrow Passer montanus | R  | RG  | S   | O  | 11.33 |     |     |     |     |     |     | 17.75 |     |      |
Table III. Continued.

| Bird species                              | RC<sup>a</sup> | DSR<sup>b</sup> | DSH<sup>c</sup> | TG<sup>d</sup> | Autumn | Winter |
|-------------------------------------------|----------------|----------------|----------------|-------------|--------|--------|
|                                           | R  | AS  | G  | GI | R-B | HS  | WJ  | R-W | AM  | R-B | HS  | WJ  | R-W | AM  |
| Coal tit *Parus ater*                     | LM | AS  | G  | GI | 2.11| 1.83| 0.50| 0.50| 0.33| 0.83| 3.00| 0.50| 1.00| 1.00|
| Streaked rosefinch *Carpodacus rubicilloides* | R  | AS  | G  | G  |     |     |     |     |     |     |     |     |     |     |
| Robin accentor *Prunella rubeculoides*     | LM | AS  | G  | GI | 0.11| 9.67| 0.33| 1.00| 2.67| 26.25| 1.00| 0.50| 1.00| 1.00|
| Oriental turtle-dove *Streptopelia orientalis* | SB | RG  | G  | O  | 0.22| 0.17| 0.17|     |     |     |     |     |     |     |     |
| Pink-rumped rosefinch *Carpodacus eos*     | R  | AS  | G  | G  | 10.28| 1.50| 1.67| 1.50| 2.33| 3.17| 7.50| 1.25| 0.75| 4.25|
| Eurasian blackbird *Turdus merula*         | R  | AS  | G  | FG | 3.22| 0.50| 3.33| 0.17| 2.75|     |     |     |     |     |
| Eurasian magpie *Pica pica*                | R  | RG  | G  | O  | 0.54| 1.83| 0.50| 1.33| 0.67| 2.33| 1.00| 1.25| 0.50| 1.25|
| Rufous-breasted accentor *Prunella strophiata* | LM | AS  | G  | GI | 0.67| 1.33|     |     | 0.25|     |     |     |     |     |
| Horned lark *Eremophila alpestris*         | R  | RG  | S  | G  | 0.33|     |     |     | 1.00|     |     |     |     |     |
| Common buzzard *Buteo buteo*               | R  | RG  | G  | C  | 0.11| 0.17| 0.17| 0.17|     |     |     |     |     |     |

<sup>a</sup>RC, residency category: R, permanent resident; SB, summer breeder, LM, local migrant.  
<sup>b</sup>DSR, distribution status at region scale: AS, alpine specialist; RG, region generalist.  
<sup>c</sup>DSH, distribution status at habitat scale: S, habitat specialist; G, habitat generalist.  
<sup>d</sup>TG, trophic guild: C, carnivore; FG, frugivore–granivore; FO, frugivore–omnivore; G, granivore; GI, granivore–insectivore; I, insectivore; O, omnivore.
(0.46 ± 0.04) and winter similarity indices (0.43 ± 0.03) between any two habitats and found the difference was insignificant (Wilcoxon test, \( z = -0.66, N = 10, P = 0.51 \)). Excluding the six summer breeders, however, we detected a significantly reduced similarity index from autumn (0.50 ± 0.04) to winter (\( z = -2.09, P = 0.04 \)).

**Bird abundances among habitats**

Significant among-habitat variation in total relative abundance was not detected in autumn (Kruskal–Wallis ANOVA, \( \chi^2 = 6.99, P = 0.14 \)), but was in winter (\( \chi^2 = 16.22, P = 0.003 \)). Although containing comparatively fewer species, habitat HS supported the highest density of birds in both autumn (37.0% of all bird individuals detected per unit time over all the five habitats) and winter (58.4%), followed by R-B (27.1 and 16.9%). The relative numbers of birds in habitat WJ were invariably lowest in both seasons (8.1 and 6.4%).

Regardless of habitat types, the first five species with the highest mean detection rate were Pink-rumped rosefinch (3.5), Tibetan partridge (2.9), Brown accentor (2.4), Tibetan-eared pheasant (2.3), and Tree sparrow (2.3) in autumn, and Robin accentor (6.3), Brown accentor (6.2), Brown-cheeked laughingthrush (5.7), Tibetan-eared pheasant (5.1), and Tree sparrow (3.6) in winter. Although the contributions to overall abundance within each habitat differed, a few dominant species were found commonly across more than one habitat: Tibetan partridge in autumn, Tibetan partridge, Tibetan-eared pheasant, and Brown accentor in winter, over four habitats; Tibetan-eared pheasant, Red-billed chough, and Pink-rumped rosefinch in autumn, Brown-cheeked laughingthrush in winter, over three habitats (Table III). At the species level, no species (except for those habitat specialists) in autumn was significantly different in abundance between habitats (Kruskal–Wallis ANOVA, \( \chi^2 < 14.27, P > 0.007 \) in all cases, adjusted alpha level = 0.002). In winter, however, Robin accentor, Brown accentor, Brown-cheeked laughingthrush, and Great tit were significantly abundant in a few specific habitats (\( \chi^2 > 14.56, P < 0.006 < 0.007 \) of adjusted alpha level).

**Distributional patterns of bird assemblages among habitats**

Overall, the bird assemblages showed similar distributional patterns in different habitats (Figure 2), as suggested by very high \( r^2 \) values in all the dominance–diversity curves when regressed using exponential functions (Table V). Species–abundance relationships approached a lognormal model that characterizes communities formed by a few species with high or low abundances, and a large number of species with intermediate abundances. In autumn, the five most abundant species (see below) comprised 60% of the individuals
recorded per ha in R-B, 64% in HS, 46% in WJ, 57% in R-W, and 68% in AM; the corresponding values in winter were 53, 74, 59, 59, and 68%, respectively. However, the curves for habitat HS (slope 0.21 in autumn and 0.27 in winter) and AM (0.22 and 0.21) were steeper than those for the three shrub habitats (0.10–0.17 and 0.13–0.17). Winter
bird assemblages had steeper dominance–diversity curves (mean slope of the regression functions, \(-0.1909 \pm 0.0229\) ) than autumn ones (\(-0.1633 \pm 0.0236\); Figure 2), though the difference was statistically insignificant (Wilcoxon test, \(z = -1.21, P = 0.23\)). The higher slope, characteristic of a geometric model, suggests that bird assemblages in winter tend to possess both more numerically dominant and rare species.

**Seasonal changes of bird species and abundance**

Except for the six summer breeders, birds were encountered more frequently in winter for all habitats combined (47.5 individuals \(\pm 23.2\) ) than in autumn (31.5 individuals \(\pm 8.3\) ) (Mann–Whitney \(U\) test \(z = -2.15, n_1=115, n_2=94, P = 0.03\)). For individual habitats, however, a significant seasonal difference in total relative abundance was found only in HS (\(z = -2.46, n_1=23, n_2=17, P = 0.01\)). At the species level, significant seasonal increases in encounter rate were detected in four out of the 33 winter species (Brown accentor 12.16 to 30.83, Robin accentor 11.11 to 31.42, White-browed tit 1.84 to 5.67, and Brown-cheeked laughingthrush 6.55 to 28.50). In addition, relative abundances of Tibetan-eared pheasants (11.50 to 25.33) and Tibetan snowcocks (7.83 to 17.00) exhibited obvious, but statistically insignificant, increases. These changes contributed to the overall winter increase in individual detection rate because most of these species were dominant members of the alpine avifauna. The cause leading to this seasonal pattern differed according to species. For two accentors, it was a result of the arrival of local migrants, and for several other species it may be associated with recruitment of young to the populations and winter aggregation. A few species, including Himalayan griffon (3.16 to 0.75), Twite (5.23 to 0.67), and Eurasian blackbird (7.05 to 2.92), exhibited obvious, but statistically insignificant, abundance declines from autumn to winter. Local migration is likely responsible for the autumn increase of the former two, and a low likelihood of detection during transect surveys due to winter grouping and increased mobility for the blackbird.

**Distribution pattern of species and individuals among different trophic guilds**

All seven trophic groups were found to coexist in all five habitats both in autumn and winter, except for AM where frugivore–granivores and frugivore–omnivores were absent (Table VI). Differences in species assemblages were insignificant across habitats (autumn \(G_{24}=9.92, P = 0.97\); winter \(G_{24}=13.97, P = 0.93\)). Within each habitat, the numbers of species with different diet categories were relatively even (autumn 5.3–21.1%, winter 5.9–23.5%). In order to conclude general patterns of food resource use, the data of five plant-based trophic categories were pooled as the plant-eating guild (including the granivore–
insectivore group because of greater proportions of plant food in their diet during the wintering period). With all habitats combined there was a strong dominance by this guild (65.8% in autumn and 75.8% in winter), and a rarity of insectivorous species (18.4 and 12.1%). The same trend was true for each individual habitat (Table VI).

Abundances among trophic groups varied substantially (Kruskal–Wallis ANOVA, \(\chi^2 = 8.57, P = 0.01\); winter \(\chi^2 = 7.35, P = 0.03\)). Plant-eating species were proportionally the most dominant individuals in both autumn (89.8%) and winter (96.7%), with the most dominant members of bird assemblages being in this group both in autumn and winter. Both carnivores (3.9 and 1.4%) and insectivores (6.3 and 2.3%) had the lowest abundances. Within individual habitats, the abundance distribution of different trophic groups showed similar patterns (Table III).

**Discussion**

Our alpine site is located at mid-latitude and has relatively mild winter climates. However, we recorded no latitudinal migrants using the alpine habitats as stopovers during autumn migration or wintering there, a case quite different from lowland China (Zhang and Yang 1997) or North America (Cox 1985) where mass autumn movement of birds from higher latitudes is remarkable. There is a biogeographical explanation for this observation. The landscape beyond Lhasa up to northeastern China and west Mongolia is dominated by vast meadow and desert (Figure 1), which are characterized by the species residing year-round or migrating locally (such as skylarks, mountain finches, and snow finches; Zheng et al. 1983; McKinnon et al. 2000). Those migratory species breeding in northern China, Mongolia, or Siberia are less likely to fly up the Tibetan plateau; rather, they prefer migration routes in central and eastern China (Zhang and Yang 1997).

In contrast, several species in our alpine valley were engaged in seasonal movement between altitudes. Local migration affected the avian assemblages in several ways. Twites, for example, were found to nest in Lhasa city (3650 m) and further north in open environments (4400 m), but never in our alpine valley. Their peak arrival time to our valley was in the middle of the autumn (Figure 3). Among the two numerically dominant accentor species, only Brown accentors regularly breed in higher altitudes of the valley, but at a low density; Robin accentors were found to nest in a valley 30 km away (Xin Lu, personal observation). From late autumn they arrived in the valley in high numbers and wintered there until late spring. Two rosefinch species tended to move to lower altitudes with cold temperatures.

### Table VI. Number of species of different trophic guilds in bird assemblages during autumn and winter among alpine habitats in valley near Lhasa, Tibet (the percentage of total species in a habitat is given in parentheses).

| Trophic type\( ^a \) | Autumn | Winter |
|------------------------|---------|---------|
|                        | R-B | HS | WJ | R-W | AM | R-B | HS | WJ | R-W | AM |
| FG                     | 2 (6.1) | 2 (8.7) | 1 (4.2) | 2 (10.5) | 0 | 2 (7.7) | 1 (5.9) | 1 (6.3) | 2 (10.5) | 0 |
| FO                     | 2 (6.1) | 2 (8.7) | 2 (8.3) | 2 (10.5) | 0 | 2 (7.7) | 2 (11.8) | 1 (6.3) | 2 (10.5) | 0 |
| G                      | 5 (15.2) | 4 (17.4) | 4 (16.7) | 2 (10.5) | 3 (17.6) | 5 (19.2) | 4 (23.5) | 3 (18.8) | 3 (15.8) | 2 (13.3) |
| GI                     | 6 (18.2) | 5 (21.7) | 4 (16.7) | 3 (15.8) | 3 (17.6) | 6 (23.1) | 4 (23.5) | 2 (12.5) | 4 (21.1) | 4 (26.7) |
| O                      | 6 (18.2) | 6 (26.1) | 4 (16.7) | 4 (21.1) | 4 (23.5) | 5 (19.2) | 5 (29.4) | 5 (31.3) | 3 (15.8) | 4 (26.7) |
| I                      | 7 (21.2) | 3 (13.0) | 4 (16.7) | 2 (10.5) | 4 (23.5) | 4 (15.4) | 1 (5.9) | 2 (12.5) | 1 (5.3) | 2 (13.3) |
| C                      | 5 (15.2) | 1 (4.3) | 5 (20.8) | 4 (21.1) | 3 (17.6) | 2 (7.7) | 0 | 2 (12.5) | 4 (21.1) | 3 (20.0) |

\( ^a \)FG, frugivore–granivore; FO, frugivore–omnivore; G, granivore; GI, granivore–insectivore; O, omnivore; I, insectivore; C, carnivore.
temperatures so that their overall population densities were lower than expected based on breeding population size (Figure 3).

Food resources have been demonstrated as one of the factors causing movement of birds along altitudinal gradients (Loiselle and Blake 1991). In particular, the associations of local distribution of frugivorous bird abundance with fruit availability have been observed in many passerines (Johnson and Sherry 2001; Kwit et al. 2004). At our alpine site, from late August through late October, rose hips are an important food resource for several alpine species such as Brown-cheeked laughingthrush, Blackbird, and White-winged grosbeak (Zhang 2005). However, we found no apparent fluctuations in abundance of the locally breeding frugivores or arrival of novel species. Reduced seed availability towards winter could explain the rosefinch decrease at the higher altitudes and increase at the bottom of the valley. Any causal links of the transient aggregation of Twites at the high-latitude site and persistent winter existence of accentors with food availability or other factors remains to be resolved.

Our transect surveys showed that among the five alpine habitats, R-B had highest species richness and also relatively high individual density. The among-habitat variation may depend on different food availability and vegetation structure. In this habitat, roses are the most dominant fruiting plant and their berries are a highly preferred autumn–winter food of several bird species referred to above. The beans of Caraganas (*Caragana bicolor* and *C. tibetica*) remain important to the diets of rosefinches as well as Tibetan partridges. The
grasses including Smartweeds Polygonum spp. and Millets Setaria spp., despite being less developed as a whole, grow better around the base of shrubs in habitat R-B in particular than those in other habitats, providing more seed foods for granivorous Godlewski’s buntings, Twites, accentors, and rosefinches. Meanwhile, more complex vertical layers of vegetation associated with high species diversity probably allows coexistence of more bird species with different ecological niches in the habitat. Although a number of seeds are produced annually by the junipers in habitat WJ, they are consumed only by Tibetan-eared pheasants and occasionally by White-winged grosbeaks. Higher altitudes and shorter, simpler vegetation in this habitat are also probably responsible for poor bird species richness and population density. For habitat R-W, despite its extremely dense vegetation cover, the two most common diagnostic plants provided no food for birds during the autumn–winter period. Additionally, the colder climate on the northern-slope habitat could represent a limit to birds. Some species appeared there probably because of the relatively heterogeneous microhabitats around streams. As natural foods became diminished towards winter, several species, especially numerically dominant omnivores, altered their habitats to HS to take advantage of supplemented foods that are consistently available due to frequent religious activities. Also, voluntary protection of wildlife by the local Buddhists contributed to the high bird abundances. In habitat AM, poorly developed grasses made it unsuitable for many birds, except for several habitat specialists. These observations support the idea that food availability (Hutto 1985; Leisler 1990; Newton 1998; Johnson and Sherry 2001) and vegetation heterogeneity (Karr and Roth 1971; Söderström et al. 2001) are explanations underlying non-random distributions of birds among habitats.

The pattern of relative abundance distribution of bird species in most habitats closely fits the lognormal model (Preston 1948; Hughes 1986). The distribution model characterizes communities that consist either of fewer species with a large difference in abundance, or of more species with intermediate abundance (Tacey and Glossop 1980; Magurran 1988), indicating that a series of ecological factors may affect division of resources among community members. Supporting the prediction of the model, our alpine bird assemblages were represented by the coexistence of abundant plant-eating dominant species and rare insectivorous species. Moreover, the dominance–diversity curves of either habitat HS or habitat AM assemblage tended to depart from the lognormal model, and rather to approach the geometric one. A similar pattern held during the wintering period of the birds. The geometric distributional pattern may be displayed by some communities composed of fewer species competing for resources in a stressed environment (Whittaker 1975). As predicted by the model, the two non-shrub habitats (HS and AM), where the types of food the birds consumed were simple, contained comparatively fewer, but numerically dominant, avian taxa. The change of bird community organization from autumn to winter followed the same pattern.

Based on our field observations on the wintering birds in the Lhasa area (Xin Lu, unpublished data), it may be concluded that as much as 70% of the 33 wintering species recorded in the valley are alpine specialists that here occur at the upper limits of their geographical distribution, highlighting the importance of maintaining the bird assemblages occurring in a zoogeography unique in the world (Stattersfield et al. 1998; Zhang 1999). Such conservation becomes urgent because these alpine habitats have been subject to intensive degradation as a result of long-lasting collection of fuelwood and building materials by local people (Niu 1999; Winkler 2000). Around the mid-Yalong Zangbo River, the well-developed vegetation is confined within valleys, like our study site, and provides crucial refuges for alpine birds. Our measurements in habitat R-B outside the
valley showed that shrubs were shorter than 1.5 m on average and had coverage below 15%, compared to 1.7 m and 35% at our study site. The vegetation degradation is associated with a sharp decline of bird assemblages. During nine visits (each lasting 1–2 h) to the habitats outside the valley, we detected only about one-third of the species found inside the valley and most of these occurred at low densities. In particular, several species of conservation concern, for example Tibetan-eared pheasant and Giant babax, were absent. Taking the alpine environment around the mid-Yalong Zangbo River as a whole, the within-valley habitats so far account for less than 30% of the existing vegetation (Li 1988). Moreover, growth of shrubs under the severe alpine climatic conditions is slow (mean annual growth rate, Rose 15.4 cm, Barberry 10.6 cm, Wilson juniper 2.1 cm; Xin Lu, personal data) and thus the ability to regenerate is poor, as has been widely observed in extensively exploited stands outside the valley. This adds conservation value to the alpine habitats.

Among these habitats surveyed inside the valley, our results suggested that habitat R-B was most important for conservation because it supported more wintering species and individuals and also was a key nesting habitat of many alpine birds (Lu and Zheng 2003; Lu et al. 2003; Lu 2004, 2005). Unfortunately, the habitat is more vulnerable to human pressures than other habitats because of its high provision of fuelwood and relatively easy access to local people. The fact that the majority of birds used a variety of available habitats over the valley and a handful of bird species have restricted themselves to specific habitats implies a need for conservation of all other vegetation types. This is particularly true in the high-altitude environments where birds face an overall shortage of food resources. HS not only had high species diversity, but also provided refuges for a number of wintering omnivores, including the endangered Tibetan snowcocks and Tibetan-eared pheasants. This brings up an interesting question: how to promote the role of Tibetan Buddhism in natural conservation? Throughout Tibet, influences of Buddhism are overwhelming, and spontaneous conservation based on a Buddhist belief, the non-killing of life, contributes to high wildlife diversity around many monasteries (Xin Lu, personal observation). However, frequent religious activities, as seen in our alpine valley, have increasing needs for fuelwood and housing materials. Unfortunately the Buddhists are not aware that their practice of cutting shrubs contributes indirectly to the killing of wildlife. Thus, promoting modern conservation ideas among Buddhist circles and finding alternative solutions to reduce human pressures on shrub vegetation should be a key part of any long-term management plan for birds and their habitats on the plateau.

Acknowledgements

We thank the Buddhists in Xiongse monastery for accommodation, G. H. Gong and H. Q. Shi for assistance in the field, and Dr. Susan Shirley for valuable comments on the manuscript. This work was conducted at the Field Research Station for Tibetan Wildlife, which is jointly administered by Wuhan University and Tibet University. Financial support was provided by the National Sciences Foundation of China (grant no. 30425036).

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