

Distribution patterns of snow finches (genus *Montifringilla*) in the Tibetan Plateau of China

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Abstract - We used data from specimen collection records and field expeditions in the Tibetan Plateau and Xinjiang to assess distribution patterns of six *Montifringilla* species. By plotting specimen localities with latitude, longitude and elevation, we found that six species overlap greatly on the Tibetan plateau, with a limited distributed area at elevations from about 2500m to 5500m, latitudes from about N26° to N38° and longitude from E 75° to E115°. At 28 of 71 localities, more than one species has been collected. However, in Xinjiang, only four species occur and they have parapatric complementary distributions. The species whose distribution ranges overlap occur in different habitats and develop different ecological and behavioral characteristics. While some breed and roost in rock crevices, others nest in Pikas (*Ochotona curzoni*, *Ochotona ladacensis*, *Ochotona alpina*, *Ochotona daurica*) burrows. Those species sharing similar habitats show significant variations in body traits. It seems that the species with similar body traits are less likely to share similar habitats than are species with rather different body traits.

Keywords: Snow Finches, *Montifringilla*, Distribution Pattern, Tibetan Plateau, China

Interpreting why some birds are limited to a particular geographic area is one of the most difficult questions in ornithological studies. The reason is that bird distribution is often influenced by many inter-related factors. When these factors shape ecological and behavioral characteristics of species, it needs the complex knowledge of the influence of history on bird ecology for determining which factors are, which are not, modified in response to distribution limitation (Vuilleumier and Simberlogg, 1980). It will be a more difficult case when most species in the genus or other higher taxa are restricted in similar limited areas. If the overlap in distributions occurs, suggesting that more competition pressure occurs and makes these congeners likely competitors. Their similarity in role and habitat use patterns makes it more difficult to determine which ecological and morphological characteristics modified in response to change demands, and how far the changes go in the way of convergence and divergence evolution. Nevertheless, still a lot of work has been done to determine the relationship between restricted distribution areas and their influence on the adaptation of species (Remsen & Graves, 1995a; 1995b, Keast *et al*, 1995). The comparative

analyses of distribution patterns maybe help us to understand the determinants of the limited distribution and their influence to the adaptation of congeners (Remsen & Cardiff, 1990; Remsen & Graves, 1995). *Montifringilla* is an interesting group for such a study due to its distribution, in fact, is characterized, by relatively uniform elevational range. Of currently seven species, only *M. nivalis* is distributed throughout the range of genus, which is along the chain of mountains from Asia to Europe. Other six species are limited on the Tibetan plateau and adjacent areas and have similar distribution areas. On their studies the birds on Tibetan plateau, Kozlova (1959) and Cheng (1981) proposed that most species of *Montifringilla* shared remarkably similar longitudinal, latitudinal and elevational ranges. Although Cheng (1976) and Fu (1998) previously mapped latitudinal and longitudinal distributions of these birds, they did not map elevational distributions of them. Without the added dimension of elevation, "the true" overlap distribution was difficult to assess. Here, we try to determine the distribution patterns of *Montifringilla* species through using data from specimen collection records, when considering on the longitudinal, latitudinal and elevational distribution for

assessing the extent of overlap distribution. We also with the aim determine the influence of these distribution patterns for ecological and morphological adaptation of congeners and possible divergence evolution.

Methods

We collected specimen data from museums in Institute of Zoology, Northwest-Highland Institute of Biology, Chinese Academy of Science for all *Montifringilla* species. Some information on geographic distributions and ecological characteristics was obtained from published papers (Demen'ev & Cladron 1970, Cheng 1981, Fu 1998, and Zhang 1999) and our field expeditions from 1999 to 2001.

Longitude-elevation-latitude plots

Following the methodology of Remsen and Graves (1995), latitude and longitude were inferred primarily from the gazetteers of China and elevation was taken from specimen labels. If a specimen label did not include elevation, the gazetteers were used to determine whether the elevation could be ascertained with reasonable precision. Many specimen localities could not be used because their elevations were uncertain. A simple plot of longitude-elevation-latitude was used to show the distribution patterns of *Montifringilla* species on the Tibetan Plateau and in the Xinjiang.

Field surveys

Our field surveys were conducted in different field sites of Tibetan plateau (Haibei: N 37°34' E 101°22' A 3268 m., Tianjun: N 37°18' E 99°45' A 3413 m., Heimahe: N 36°45' E 99°37' A 3366 m., Huashixia: N 35°06' E 98°52' A 4257 m., Maduo: N 35°06' E 98°51' A 3886 m., Tuotuo river: N 34°13' E 92°26' A 4598 m., Naqu: N 31°24' E 92°00' A 4480 m., Changdu: N 31°06' E 71°06' A 3339 m., Bangda: N 30°12' E 97°12' A 4358 m., Langkazi: N 29°11' E 90°33' A 4498 m., Dingri: N 28°35' E 86°37' A 4798 m.) from May to October from 1999 to 2001. Data on the ecological and behavior characteristics of these birds were collected. The field surveys were also conducted to find the sites where two or more species were observed to occur.

Ecological and morphological adaptations of congeners

If overlap distribution occurs, interspecific competition could be expected. For species whose distribution ranges overlapped, their body traits were analyzed and the differences were tested.

The original data were consisted of skin measure-

ments of 337 congeners individuals (*M. nivalis*: n = 15, *M. adamsi*: n = 95, *M. taczanowskii*: n = 89, *M. ruficollis*: n = 109, *M. blanfordi*: n = 28, *M. davidiana*: n = 9). On skin we measured, body length, body mass, wing length, tail length, bill length and tarsus length, provided the input for determining the differences among congeners. Body traits of male and female represented no significant difference (All species, ANOVAS, P > 0.05). Therefore in the analysis male and female were pooled.

For help to understand which traits express in a better way the body dimension, the principal component analysis was used to find the most important indicative characteristics and the relationship among body traits. PCA analysis was based on the correlation matrices of the log-transformed variables. Results presented for analyses were correlation (loading) of body traits with orthogonally rotated multivariate factors (varimax rotations of the principal components).

Positions (factors scores) of individuals were ranked and the ranks of each individuals were clustered. This was to test whether the body traits loading strongly in components could separate the six species.

The indicative body traits of congeners were analyzed for the difference in means with one-way ANOVAS. The significance was determined at 0.05 level.

Results

Distribution patterns

In Xinjiang (35°-N44°) (Fig. 1), four species were found with a little complementary elevational distribution and minor segregation. In this area, *M. nivalis* was found in 10 localities with elevations below 3500m, and *M. blanfordi* in 4 localities with elevations above 4500m. *M. taczanowskii* and *M. ruficollis* occurred at an elevation ranging from 3500m to 4500m. However, they overlapped slightly in longitudinal and latitudinal ranges. In Xinjiang, 2 localities out of 18 had more than one species.

Six species occurred on the Tibetan Plateau (Fig. 2), where they seemed to overlap greatly in elevational, longitudinal and latitudinal ranges. These species occupied a limited distribution range (latitude from about N26° to N38°, longitude from E 75° to E105° and elevation from about 2500 m to 5500m). *M. davidiana* inhabited in the lower elevations from about 2500 to 3500 m and with a narrow altitude range between N 34° and N 40°. Its range scarcely overlapped with those of the other five species. Ranges overlap on Tibetan Plateau appeared to be higher than in Xinjiang. Four species were collected in 13 localities out of 71, three species were collected in 18, and two species were collected in 28.

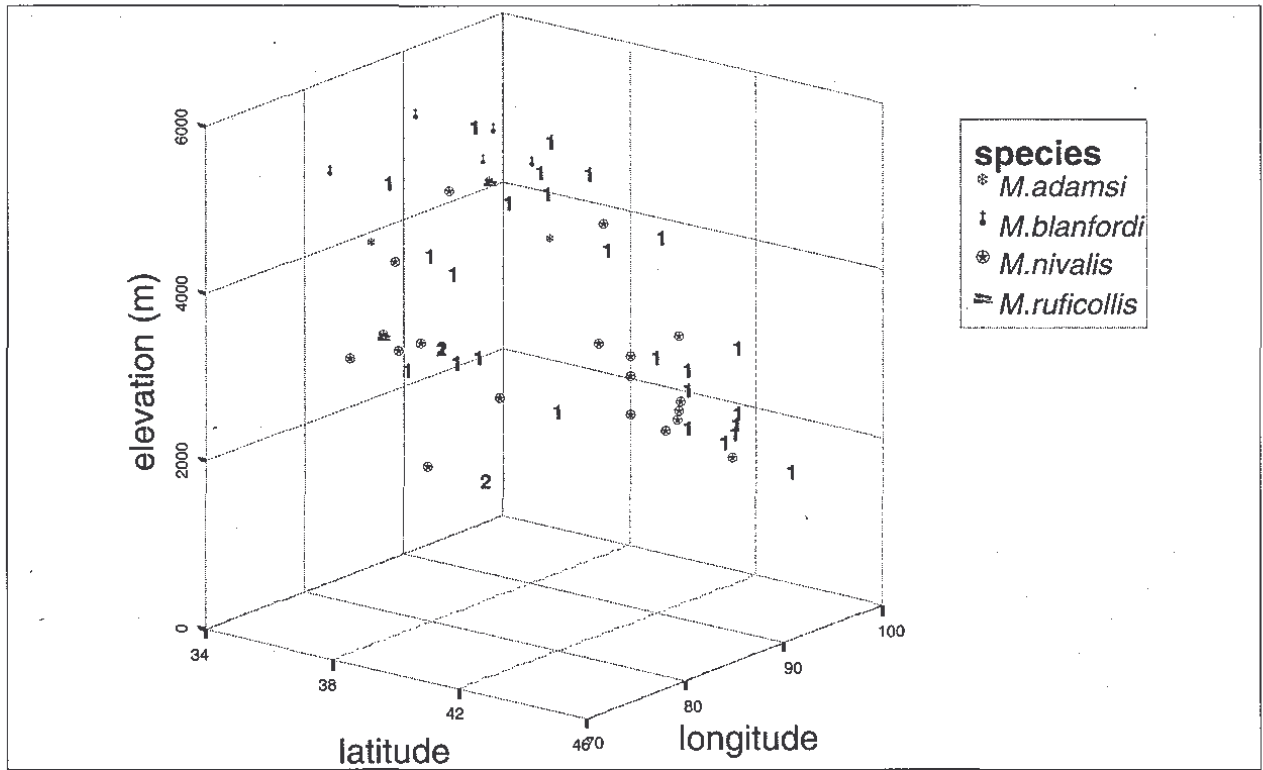


Fig. 1 Distribution of four *Montifringilla* species in Xinjiang. Each point represents the specimen collection site from which one or more species were collected (indicated by labels). In this and other figure (represented in Fig.1-2), lower limit of distribution is about 2500m, and upper limit usually is about 5500m.

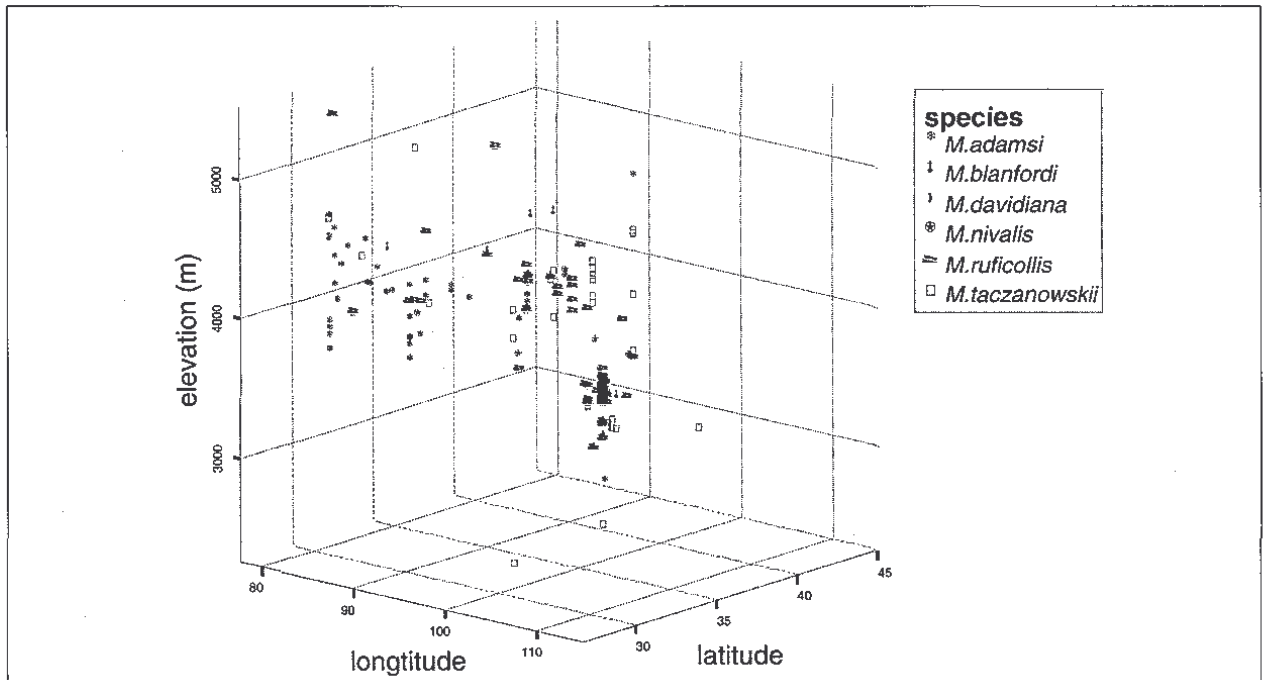


Fig. 2. Distribution of six species of *Montifringilla* in the Tibetan Plateau. Each point represents the specimen collection site from which one or more species were obtained.

Ecological and behavioral characteristics

In field observations, we found these species were year-around residents across the mountain steppe zones at the high elevation (above 3000m). *M. taczanowskii*, *M. ruficollis*, *M. blanfordi*, *M. davidiana* occurred in solitary pairs on flatter and more arid grassy areas and bred inside the Pikas (*Ochotona curzoniae*, *O. ladacensis*, *O. alpina*, *O. daurica*) burrows. These species showed strong long-term territoriality during breeding and brooding season. *M. nivalis* and *M. adamsi* preferred more heterogeneous and humid environments, and bred in rock crevices and fed mainly on alpine grassland rich in vegetation. They bred in loose colonies or solitary pairs and shared communal feeding at any stage of nesting. Their territoriality ceased after pair formation.

In June, 2000, we found that *M. davidiana*, *M. ruficollis*, *M. taczanowskii* and *M. davidiana* made nests in *O. ladacensis* burrows in Heimahe, Cuona and Wenquan sites. We also found *M. nivalis* and *M. adamsi* juveniles in crevice rock in Maduo and Huashixia sites. In July, 2001, we found two nests of *M. davidiana* juveniles (five and six respectively), three nests of *M. ruficollis* juveniles (two, four and five respectively), two nests of *M. taczanowskii* juveniles (three and five respectively) and three nests of *M.*

davidiana juveniles (four, five and six respectively) in *O. curzoniae* burrows in Huashixia, Maduo and Heimahe. Two nests of *M. nivalis* juveniles (four and five respectively) and *M. adamsi* juveniles (three and four respectively) in crevices rock.

Those results were based on observations carried out at field sites and here we also observed two or more species to occur in the same habitats: in Heimahe (*M. ruficollis*, *M. taczanowskii* and *M. davidiana*), in Huashixia and Maduo (*M. ruficollis*, *M. taczanowskii*, *M. blanfordi*, *M. nivalis*), in Tuotuo river (*M. ruficollis*, *M. taczanowskii*, *M. blanfordi*), Dingri (*M. ruficollis*, *M. taczanowskii*, *M. adamsi*), in Haibei, Naqu, Bangda, Changdu (*M. taczanowskii* and *M. ruficollis*) and Langkazi (*M. ruficollis* and *M. adamsi*).

Variations in body traits of species with the same habitats

PCA result showed component 1 accounted for 49.70% of the total variances and loaded strongly for all length traits, including body length, wing length, tail length, bill length and tarsus length. The component 2 accounted for 30.25% of the total variances and loaded strongly for the mass characteristic (Tab. 1). Along the two components, all individuals separated into six clusters, which much followed the six species assemblages (Fig. 3). Along component 1 axis, all six

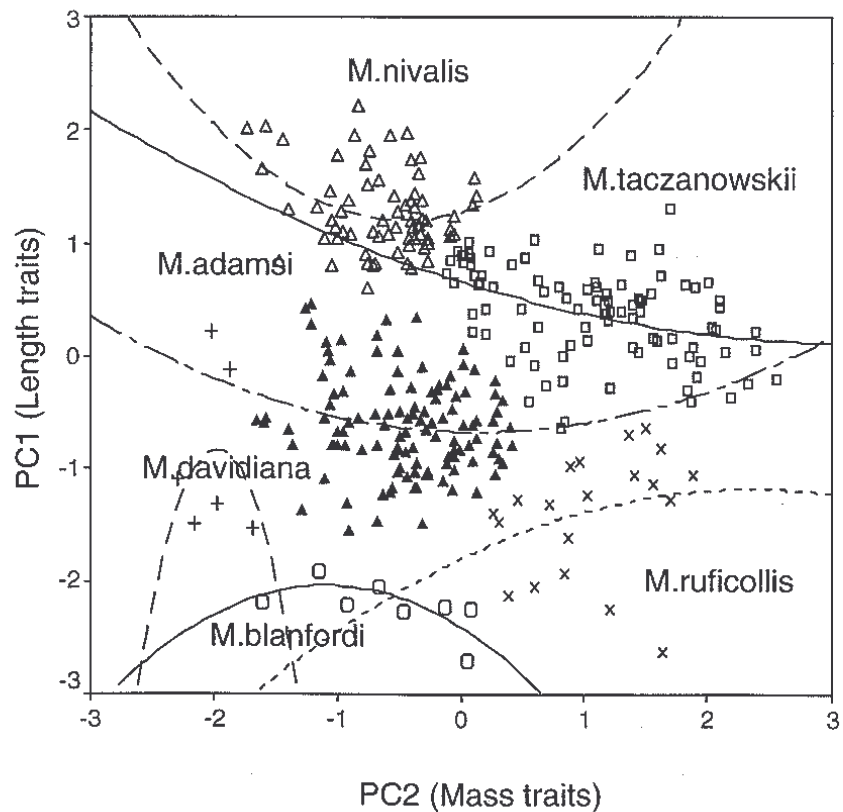


Fig. 3. Plot of factors (PCs) resulting from principal components analyses comparing six *Montifringilla* species for six body traits.

species were separated into two mainly assemblages, while *M. nivalis*, *M. adamsi* and *M. taczanowskii* tightly clustered by longer length traits, other three species fell into one group by shorter length traits. Along component 2, each group was separated by difference in body mass. *M. taczanowskii* was a special cluster by its higher body mass and longer length traits.

As suggested by PCA result, all six traits contributed strongly to the variances in body traits of six species (Tab. 1). Therefore, all six traits were used to test for the differences among co-existing species.

As suggested by literature and our field observations, these *Montifringilla* species occurred in different habitats. We hypothesized it was a kind of ecological divergence for decreasing competition pressure. During ANOVAS analyses, we treated those co-existing species as a group of compared units.

One-way ANOVAS used to test for differences in body traits among co-existing species showed significant variations in most body traits between *M. adamsi* and *M. nivalis* (Tab. 2), which occurring in the same habitat. They differentiated significantly in body mass ($F_{1,93} = 17.11$, $P < 0.001$), wing length ($F_{1,93} = 4.89$, $P < 0.05$), bill length ($F_{1,93} = 4.08$, $P < 0.05$) and tarsus length ($F_{1,93} = 11.1$, $P < 0.01$), but no significant differences in body length and tail length ($P > 0.05$, ns).

Other four species (*M. taczanowskii*, *M. ruficollis*, *M. blanfordi* and *M. davidiana*) showed significant variations in body traits (Tab. 3, ANOVA, all, $P < 0.001$). *M. taczanowskii* differentiated significantly with other three species in all of body traits ($P < 0.001$). *M. ruficollis* and *M. blanfordi* accounted for a significant amount of variations in body length ($F_{1,131} = 6.8$, $P < 0.001$), tail length ($F_{1,131} = 4.9$, $P < 0.05$), bill length ($F_{1,131} = 32.08$, $P < 0.001$) and tarsus length ($F_{1,131} = 151.3$, $P < 0.001$). However, body mass and wing length did not show statistically meaning ($P > 0.05$). The body traits of *M. david-*

Table 1 The correlations of body traits with Varimax rotated multivariate for six *Montifringilla* species

Body traits	Correlation with	
	Component 1	Component 2
Body length	0.864	0.016
Body mass	0.620	0.646
Wing length	0.870	0.366
Tail length	0.874	0.346
Bill length	0.837	0.142
Tarsus length	0.708	0.500
Percent explained	49.705%	30.242%

Table 2. Comparison of body size of *M. nivalis* and *M. adamsi* (mean \pm SD) by ANOVA

Body size	<i>M. nivalis</i> (n = 15)	<i>M. adamsi</i> (n = 95)	anova result (F) Df = 1 and 93
Body length	160 \pm 9.97	161 \pm 10.93	0.94ns
Body mass	32 \pm 2.11	28 \pm 3.06	17.1***
Wing length	111 \pm 3.66	107 \pm 5.12	4.89*
Tail length	70 \pm 3.32	71 \pm 5	0.76ns
Bill length	13 \pm 0.61	13 \pm 0.91	4.08*
Tarsus length	21 \pm 1.79	22 \pm 1.12	11.1**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns $P > 0.05$

iana differentiated significantly from *M. ruficollis* in body length ($F_{1,110} = 4.3$, $P < 0.05$), body mass ($F_{1,110} = 4.21$, $P < 0.05$), tail length ($F_{1,110} = 7.89$, $P < 0.01$), bill length ($F_{1,110} = 11.2$, $P < 0.01$) and tarsus length ($F_{1,110} = 190.8$, $P < 0.001$) and from *M. blanfordi* in body length ($F_{1,29} = 11.33$, $P < 0.01$), body mass ($F_{1,29} = 14.72$, $P < 0.001$), tail length ($F_{1,29} = 10.28$, $P < 0.003$) and tarsus length ($F_{1,29} = 11.5$, $P < 0.01$). It showed no significant differences in wing length with *M. blanfordi* ($P > 0.05$ ns) and *M. ruficollis* ($P > 0.05$, ns), and also no significant differences in bill length with the latter ($P > 0.05$, ns) (Tab. 4).

Table 3. Comparison of body size of *M. taczanowskii*, *M. ruficollis*, *M. blanfordi* and *M. davidiana* (mean \pm SD)

Body size	<i>M. ruficollis</i> (n = 109)	<i>M. blanfordi</i> (n = 28)	<i>M. taczanowskii</i> (n = 89)	<i>M. davidiana</i> (n = 6)	ANOVA result (F) Df = 3, 231
Body length	139 \pm 9.73	134 \pm 8.65	160 \pm 11.15	124 \pm 4.55	42.09***
Body mass	26 \pm 2.82	26 \pm 2.12	32 \pm 3.52	22 \pm 1.64	45.64***
Wing length	90 \pm 4.57	90 \pm 4.58	100 \pm 3.51	89 \pm 0.54	38.17***
Tail length	56 \pm 5.83	54 \pm 5.57	65 \pm 5.86	46 \pm 5.57	21.55***
Bill length	11 \pm 0.78	10 \pm 0.62	13 \pm 0.98	11 \pm 0.47	30***
Tarsus length	21 \pm 0.85	17 \pm 1.17	24 \pm 1.68	19 \pm 1.4	47.60***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns $P > 0.05$

Table 4. Variation of body traits in *M. taczanowskii*, *M. ruficollis*, *M. blanfordi*, and *M. davidiana* by A NOVA analysis

Taxon	Body traits (ANOVA, F)						
	Df	Bodylength	Bodymass	Winglength	Taillength	Billlength	Tarsullength
<i>M.t & M.r</i>	1,192	180.5***	177.6***	458.3***	162***	212***	502***
<i>M.t & M.b</i>	1,123	84.7***	8.14***	33.32***	29.94***	140.2***	264.7***
<i>M.t & M.d</i>	1,100	31.5***	36.97***	10.16**	14.5***	32.53***	95.75***
<i>M.r & M.b</i>	1,131	6.8*	0.6ns	0.05ns	4.9*	32.08***	151.3***
<i>M.r & M.d</i>	1,110	4.3*	4.12*	1.48ns	7.08**	11.2**	190.8***
<i>M.b & M.d</i>	1,29	11.33**	14.72***	1.49ns	10.28**	1.29ns	11.5**

- $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns $P > 0.05$
- *M. t* (*M. taczanowskii*), *M. r* (*M. ruficollis*), *M. b* (*M. blanfordi*), *M. d* (*M. davidiana*)

Discussion

On the Tibetan Plateau, six *Montifringilla* species are distributed in the similar longitudinal, latitudinal and elevational regions. Whilst in Xinjiang, where is a part of adjacent areas of Tibetan plateau, the distribution of these species shows some longitudinal, latitudinal overlap and a slight elevational segregation. For example, in 28 collection sites of Tibetan plateau, two or more species are found to occur in the same habitat. Six species occur in the same ranges that span from 3000 m. to 5000 m in the elevation, E 70° to E105° in longitude and N 30° to N 38° in latitude. In contrast, in Xinjiang, only two collection sites were found to have more than one species to share same habitat. Four species overlap in their distribution with a longitudinal range between E 75° and E 100° and a latitudinal range between N 36° and N 44°. Nevertheless, these species are found to occur on the different elevational gradients. The *M. nivalis* occupies on the elevation below 3500 m., and *M. blanfordi* occupies on the elevation above 4500 m. The elevation gaps between the distribution of *M. nivalis* and *M. blanfordi* are for the most part filled by *M. adamsi* and *M. ruficollis*.

Compared to the highly overlap distribution on Tibetan plateau, the complementary elevational segregation of these species in Xinjiang seems to provide evidence for their dispersal from inner plateau outward adjacent areas. *M. davidiana* is distributed to northeast Ningxia of China and to Mongolia, while *M. nivalis* has the widest distribution, from eastern part of the plateau to the north part of Europe.

The Tibetan Plateau is the region inhabited by six out of the seven *Montifringilla* species. The relative uniformity in longitude, latitude and elevation limits supports the hypothesis that congeners share similar distribution ranges. When most species of *Montifringilla* are distributed in similar restricted areas, this distribution pattern might have enhanced habitat segregation and differences in eco-ethology.

As our field observations suggested, *M. nivalis* and *M. adamsi* are active in rocky habits during both the breeding and wintering seasons. Both species use rock crevices as roosting and nesting places. These birds don't select burrows of pikas or small rodents as nest site. On the other hand, *M. taczanowskii*, *M. ruficollis*, *M. blanfordi* and *M. davidiana* prefer short grass, flatter, steppe-like habitats. Their nest sites mostly select burrows of Pikas or other small rodents, where they also use for roosting and refuge.

Besides that, these birds also develop other ecological characteristic divergence. *M. nivalis* and *M. adamsi* are not well adapted to ground living as other four *Montifringilla* species. They often are found flying more and better than the latter. Moreover, they are social birds defending relatively small territories with few specialized social display movements. They sing relatively seldom, but have a rich call repertoire that shows differences in function and structure with other four *Montifringilla* species.

Other four species are well adapted to ground living. They are able to burrow with their legs and bill, and fly less than *M. nivalis* and *M. adamsi* do. They are often found spending much more time in hopping, walking and climbing than latter. They are less social and some species are very aggressive in intraspecifically and interspecifically. All four species have marked territorial and pair display behavior with different visual movements. They sing with a specific repertoire of calls and perform song types different from *M. nivalis* and *M. adamsi* do (Gebauer, 1994).

Our field surveys results further corroborate the findings of previous studies of Ivanitskii (1992) and Gebauer (1994) that *Montifringilla* species share different habitats and develop different ecological and behavioral adaptations. Occurring in the same restricted areas, the overlap in niches makes these *Montifringilla* species shape different ecological, behavior characteristics and habitat choice. This maybe suggests that interspecific competition govern

characteristic shape and divergence for decreasing potential competition pressure.

For the species with the same distribution ranges, the similarities in shape, plumage, and foraging behavior might promote interspecific competition and make them potential competitors. The ecological differences might have decreased some competition pressure. However, for species sharing the same habitat, interspecific competition might be an important factor in influencing food and territory acquisition. In our study, species sharing similar habitat (vegetated alpine meadow), *M. adamsi* and *M. nivalis*, showed divergence in some body traits (body mass, wing length, bill length and tarsus length). The other four co-occurring species (*M. taczanowkii*, *M. ruficollis*, *M. blanfordi* and *M. davidiana*) were also differentiated in some body traits.

The bill size or body size is frequently used by ecologists as indicator of prey size. Large bodied or large billed individuals would select larger food items than do smaller bodied or smaller billed ones (Pulliam & Enders 1971, Brown & Lieberman 1973). There is the positive correlation between bill or body size and prey size (Lederer, 1975; Smith & Zack, 1979). Generally, a larger bill or larger bodied individual favors taking prey of a larger size of items than a smaller bill or smaller bodied individual does (Grant, 1968; Herrera, 1978). For co-existing species of *Montifringilla*, the difference of bill length and body length maybe indicates the differences in preying size.

Long tails and long pointed wing promote long-distance fly. The two characteristics are closely related fly ability. These characteristics can be applied to *M. nivalis*, *M. adamsi*. The slightly longer tails and wings would predict that they are more adaptive to fly living.

Some researches have proposed that the difference in body traits of co-existing species is a strategy for decreasing potential competition among interspecific or intraspecific (Hutchinson, 1959; Schoener, 1984; Letcher, 1994). Generally, species with more similar body traits seem to be more likely to compete for resources and therefore would have more ecological overlap than species with differences in body traits. Some same examples can be found in studies on other co-existing birds. Three species of *Grallaria* differ in body traits when they overlap widely in elevational distribution and are syntopic species elsewhere in their ranges. *Xiphorhynchus ocellatus* and *X. guttatus* with difference in body traits are syntopic species (Terborgh *et al*, 1984). Graves (1985) also pointed to that, in addition to the *Cacicus* and *Grallaria* examples, two other sets of congeners (*Coeligena* and *Thripadectes*) noted by Terborgh as having overlap-

ping distributions in the Vilcabamba also differ in their body traits.

For these co-existing species, the basic question posed is that we hypothesize there is ecologically and morphological divergence for decreasing competition pressure from sharing similar restricted areas. As suggested by studied results, there would seem to be scope for the hypothesis. Nevertheless, we still need more studies to develop a comprehensive data set on just which characteristics are modified in response to the ecological and morphological divergence and precise functions and significance of these characteristics.

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