The coexistence of seven sympatric fulvettas in Ailao Mountains, Ejia Town, Yunnan Province

Ji XIA[1,2,#], Fei WU[1,#], Wan-Zhao HU[1,2], Jian-Ling FANG[3], Xiao-Jun YANG[1,*]

[1] *State Key Laboratory of Genetic Resources and Evolution*, *Kunming Institute of Zoology*, *Chinese Academy of Sciences*, *Kunming, Yunnan* 650223, *China*

[2] *University of Chinese Academy of Sciences*, *Beijing* 100049, *China*

[3] *Shuangbai Ailaoshan Nature Reserve Management Bureau*, *Shuangbai*, *Yunnan* 675107, *China*

ABSTRACT

The coexistence of ecologically similar species sharing sympatric areas is a central issue of community ecology. Niche differentiation is required at least in one dimension to avoid competitive exclusion. From 2012-2014, by adopting the methods of mist-nets and point counts to evaluate spatial niche partitioning and morphological differentiations, we explored the coexistence mechanisms of seven sympatric fulvettas in Ailao Mountains, Ejia town, Yunnan Province, China. The microhabitats of these seven fulvettas were significantly different in elevation, roost site height and vegetation coverage, indicating a spatial niche segregation in different levels. Approximately, 90.30% of the samples were correctly classified by linear discriminant analysis (LDA) with correct rates at 91.20%-100%, except the White-browed fulvetta (*Alcippe vinipectus*) (65.4%) and the Streak-throated fulvetta (*A. cinereiceps*) (74.6%). The seven fulvettas were classified into four guilds based on their specific morphological characters, suggesting that the species in each guild use their unique feeding ways to realize resource partitioning in the overlapped areas. These finding indicate that through multi-dimensional spatial niche segregation and divergence in resource utilizing, the inter-specific competition among these seven fulvettas is minimized, whereas, coexistence is promoted.

Keywords:Fulvettas;Coexistence;Niche segregation; Ailao Mountains

INTRODUCTION

The competition and coexistence of ecologically similar species sharing sympatric areas is one of the hot topics in community ecology (Macarthur, 1958). According to the competitive exclusion principle, to reduce inter-specific competition, niche segregation is required at least in one dimension among sympatric congeners (Bagchi et al, 2003; Denoël et al, 2004; Munday et al, 2001; Schoener, 1974; Tschapka, 2004). The differentiation in resource use can be taken as a standard to judge niche partitioning (Fox, 2004; Svenning, 1999). Lots of studies have shown that niche partitioning was principally along three dimensions: time, space and diet (Chesson, 2000; Davies et al, 2007; Martínez-Freiría et al, 2010; Schoener, 1974). Temporal partitioning includes daily (Di Bitetti et al, 2009; Lara et al, 2011; Lucherini et al, 2009) or seasonal differences (Martínez-Freiría et al, 2010; Schuett et al, 2005) in animals' activity patterns. Spatial partitioning includes differences in habitat selection (Chiang et al, 2012; Quillfeldt et al, 2013) or in microhabitat utilization (Langkilde & Shine, 2004; Vidus-Rosin et al, 2012). Trophic partitioning includes differences in prey size (Kaifu et al, 2013) or prey type (Ward-Campbell et al, 2005). Niche segregation may occur along either some combination of these dimensions or just upon one of them (Loveridge & Macdonald, 2003). Furthermore, niche segregation could be related to species' morphology (Gustafsson, 1988) because different morphological characteristics may result in different behaviors (Miles et al, 1987) and different behaviors allow animals to partition the limited resources in different ways, hence reduce the inter-specific competitive interactions (Guillemain et al, 2002). Therefore, it is necessary to evaluate the influences of various factors in different ways as well as at different scales when exploring the mechanisms of animals'

coexistence (Li et al, 2013).

Closely related species usually have similar ecological characteristics and occupy similar ecological niches. When they contact, the inter-specific competition may arouse (Wiens & Graham, 2005). Studies on the sympatric congeners of birds in China were focused on species such as pheasants (Cui et al, 2008; Li et al, 2006), herons (Wen et al, 1998; Ye et al, 2006; Zhu et al, 1998), tits (Gao & Yang, 1991; Liu et al, 1989; Yang et al, 2012), woodpeckers (Gao et al, 1997), larks (Zhao & Zhang, 2004) and prinias (Zhou & Fang, 2000), but never on fulvettas. Alcippe is a group of Timaliidae includes 18 species worldwide (Zheng, 2002) with 15 of them distributing in China (Zheng, 2011) and 12 of them in Yunnan Province, in specific (Yang & Yang, 2004). The range of body length in fulvettas is 11-15 cm. Different species of fulvettas have similar morphology, plumage color and stripes and sexual differences are difficult to distinguish morphologically. They inhabit the undergrowth in broadleaf forests, mixed coniferous broad-leaved forests, bamboo groves, scrubs and brambles and feed on animal-based food, such as insects, caterpillars and mollusks, but sometimes on plant food (Yang & Yang, 2004). The Golden-breasted Fulvetta (*Alcippe chrysotis*), Rufous-winged Fulvetta (*A. castaneceps*), White-browed Fulvetta (*A. vinipectus*), Spectacled Fulvetta (*A. ruficapilla*), Streak-throated Fulvetta (*A. cinereiceps*), Rusty-capped Fulvetta (*A. dubia*) and Grey-cheeked Fulvetta (*A. morrisonia*) are the seven species of fulvettas coexisting in Ailao Mountains, Ejia town, Yunnan Province, China, which are excellent subjects in the study on coexistence mechanisms of sympatric congeners. In this study, we aim to: (1) understand the coexistence mechanisms of these fulvettas through exploring their spatial niche partitioning and morphological differentiation; (2) test the niche theory on animal communities in the subtropical mountain forest; and (3) discuss the necessity to evaluate the influences of various factors in different ways as well as at different scales when exploring the coexistence mechanisms of sympatric congeners.

MATERIALS AND METHODS

Study area

The study site consisted of two adjacent areas, the Ailaoshan National Nature Reserve and Konglong River Nature Reserve, was located in the steep (30°- 40°, or even 60°) eastern slope (800-2 800 m a.s.l.) of north central of Ailao Mountains, Ejia Town, Yunnan Province (Chen & Ye, 1988; Liu et al, 1988; Wu & Yang, 2008). Because of the west monsoon climate, annual temperature differences are small, whereas, daily temperature differences are large. The large elevation gradients also lead to the vertical climatic spectrum. The radiation, rainfall, tempe-rature and forest types are all featured with obvious vertical variations (Wang et al, 1988). Four major forest types from low to high elevation are observed: (1) savanna shrub and grass; (2) dry evergreen broadleaved forest; (3) semi-moist evergreen broadleaved forest and Burma pine (*Pinus yunnanensis*) forest; and (4) moist evergreen broadleaved forest. However, most of the original vegetation in lower

elevations have been destroyed or replaced by cultivated land and villages due to long-term human disturbance (Liu et al, 1988).

Birds sampling

Fieldwork was conducted during breeding seasons and winters of 2012-2014. Mist-nets work best in field survey because fulvettas inhabit the undergrowth (Bibby et al, 1998). Point counts are effective in species survey and in montane forest bird community survey (Wu et al, 2010). Mist-nets combined with point counts will offset the weakness of each other, and provide a more accurate survey result (Pagen et al, 2002; Rappole et al, 1998). Birds inhibit in lower elevations start to reproduce earlier due to the higher temperature there. So, in breeding seasons, the fieldwork was carried out from valley to montane crest, whereas, in winters, the order was inversed.

We divided the study area into 10 units along elevation gradients with each unit containing a 200 m elevation differences. Ten mist-nets of the same specification (12 m×2.5 m, 36 mm mesh) were set up symmetrically in each unit. Due to the rugged terrain and limited access, it was difficult to set up each mist-net with 20 m elevation differences exactly. When different habitat types occurred in one unit, mist-nets were set up in each different habitat proportionally. The location, elevation and working time were recorded by GPS (NAVA 100) and the habitat type as well as environment information were also recorded meanwhile. We chose a rectangular patch (with the diagonal of 20 m×20 m) around the mist-net to estimate vegetation coverage. Observers walked along the diagonal of the rectangular patch to record the vegetation (tree, shrub and herb) of every 1 m. At each point of 1 m, if vegetations were found, then it was recorded as 1, while, if not, it was 0. Then the vegetation coverage of each type (tree, shrub and herb) was estimated according to the percentages of the vegetations recorded at all points. Mist-nets were kept open for 3 days and were remained closed during raining. We checked each mist-net hourly during the day and marked each captured individual with metal ring. Time, species and numbers of birds were recorded. Body weight (BW) was measured by an electronic balance (DIAMOND, precision=0.1 g) and other morphological characteristics such as body length (BL), wing length (WL), tail length (TL), tarsus-metatarsus length (TML), claw length (CLL), finger length (FL) and culmen length (CUL) were recorded by a vernier caliper (precision=0.05 mm) according to Zheng (1995). All the juveniles or certain species with too small sampling size were excluded from measuring.

Unlimited radius point counts were conducted in our study and the points were established on either pre-existing trails or low traffic volume roads along the elevation gradient in each unit. The points were systematically 200 m apart in a three-dimensional space. Surveys were conducted during the peak period of birds' activities from sunrise to 4 h after sunrise. We used GPS receiver (NAVA 100) to record the location of each point. There were 160 points in total in our study area and each count lasted for 10 min. During this period, we used

binoculars (Eagle 8×40) to observe birds and the indentified ones were recorded (Table 1).

Table 1 Information recorded by point counts

| Items	Details
Distance	Horizontal distance from the observer to the detected bird or the average horizontal distance to a group of birds
Roost site	Position of a bird was initially sighted (A: trunk of a tree; B: branches of a tree; C: substratum of crown canopy; D: superstratum of crown canopy; E: inner part of a shrub; F: outer part of a shrub; G: ground)
Roost site height	Vertical distance from ground to the position of a bird was initially sighted or to the central position of a group of birds
Time	Time when the bird was detected
Animal subject	Bird species and numbers of each species

Data analysis
Statistical analysis was conducted using R software (R Core Team, 2013). Shapiro and Levene statistics were used to test for normality and homogeneity. Function "pair-wise-*t*-test" was used to conduct multiple comparisons for unbalanced design when variance analysis was afforded (Crawley, 2012). Kruskal-Wallis rank sum test was used when data was not in normality or homogeneity (Crawley, 2012) and function "gao_cs" in the "nparcomp" package (Gao et al, 2008) was applied to conduct unbalanced multiple comparisons. The tested variables were morphological characteristics and habitat variables. All the data was displayed in mean±*SD*. Statistical tests were two-tailed-tests and the confidence level was 95%. We used model selection based on generalized linear models (GLM) with Poisson error to find major factors affecting birds' habitat selection. Morphological characteristics were applied in linear discriminant analysis (LDA) to estimate the similarity among different species and to predict resource partition. Morphological data was standardized by dividing the cubic root of body weight to avoid the influence of body size (Amadon, 1943). Culmen length was excluded from standardization because it was primarily related to the size of food (Hespenheide, 1973). Logarithmic transformation was conducted before the relative length data (L'=L/BW1/ 3, L: the relative length of morphological characteristics) was applied to LDA (Z'=$\log_{10}$Z, Z: the relative length data) (Atchley et al, 1976). Data collected by mist-nets and point counts were analyzed independently to avoid influences of different methods (Barlow et al, 2007).

RESULTS

Habitat variables
Elevational distribution All of the seven fulvettas in Ailao Mountains, Ejia Town, Yunnan Province, were documented in

this study and their elevation distributions were demonstrated in Figure 1. The Grey-cheeked Fulvetta occupied the lowest elevation, while the Golden-breasted Fulvetta preferred relatively higher elevation. Numbers documented by mist-nets and point counts was 413 and 417, respectively (Table 2). Significant differences in elevation were detected both by mist-nets (x^2=253.6158, *P*<0.01) and point counts (x^2= 269.1986, *P*<0.01). Further analysis of data from mist-nets showed that there were no significant differences among White-browed Fulvettas, Streak-throated Fulvettas and Golden-breasted Fulvettas and similar results were also occurred between Rusty-capped Fulvettas and Spectacled Fulvettas. Significant differences were detected among the other pairs. Rufous-winged Fulvettas were excluded from analyses because of the small sample size (only two records). However, non-significant differences were only found between Streak-throated Fulvettas and Rufous-winged Fulvettas in all of the 21 combinations of point counts (Table 3).
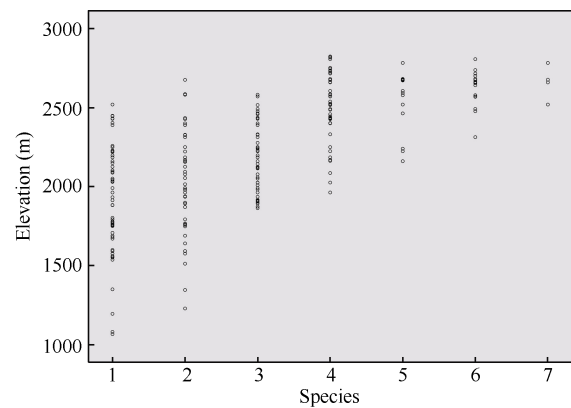
Figure 1 Scatter diagram of fulvetta species' distribution along elevation gradients
1: Grey-cheeked Fulvetta (*A.morrisonia*); 2: Rusty-capped Fulvetta (*A.dubia*); 3: Spectacled Fulvetta (*A.ruficapilla*); 4: Streak-throated Fulvetta (*A.cinereiceps*); 5: Golden-breasted Fulvetta (*A.chrysotis*); 6: White-browed Fulvetta (*A.vinipectus*); 7: Rufous-winged Fulvetta (*A.castaneceps*).

Roost site choice and roost site height Significant differences (x^2=248.811, *P*<0.01) were found in the roost site height of the 417 fulvettas documented by point counts. Only three combinations consisted of White-browed Fulvettas, Spectacled Fulvettas and Streak-throated Fulvettas did not show significant differences in all of 21 combinations of the seven fulvettas in nonparametric multiple tests (Table 4). Rufous-winged Fulvettas occupied the highest roost site while Rusty-capped Fulvettas held the lowest one (Table 4). Although five species mainly chose the inner part of a shrub to roost, subtle differences were still detected (Figure 2). Golden-breasted Fulvettas preferred the substratum of crown canopy and Rufous-winged Fulvettas preferred branches of trees. White-browed Fulvettas and Streak-throated Fulvettas, which did not show significant differences in distribution elevations or roost site height, made similar choices over roost sites located in the inner part of shrubs, and the percentage was more than 80%.

Table 2 Numbers of each fulvetta species recorded by mist-nets or point counts

Species	Numbers of each species recorded by mist-nets (n)	Numbers of each species recorded by point counts (n)
White-browed Fulvetta (*A.vinipectus*)	31	22
Rufous-winged Fulvetta (*A.castaneceps*)	2	23
Golden-breasted Fulvetta (*A.chrysotis*)	32	46
Streak-throated Fulvetta (*A.cinereiceps*)	74	92
Spectacled Fulvetta (*A.ruficapilla*)	85	50
Rusty-capped Fulvetta (*A.dubia*)	41	78
Grey-cheeked Fulvetta (*A.morrisonia*)	148	106
Total	413	417

Table 3 Comparisons of the distribution elevations of the fulvetta species recorded by mist-nets or point counts (m)

Species	Elevations of the species recorded by mist-nets	Elevations of the species recorded by point counts
Rufous-winged Fulvetta (*A.castaneceps*)		2 552.130±66.213[b]
White-browed Fulvetta (*A.vinipectus*)	2 633.742±108.005[a]	2 516.455±65.236[c]
Golden-breasted Fulvetta (*A.chrysotis*)	2 600.438±163.993[a]	2 576.478±31.804[a]
Streak-throated Fulvetta (*A.cinereiceps*)	2 554.919±223.930[a]	2 559.185±140.016[b]
Spectacled Fulvetta (*A.ruficapilla*)	2 190.459±211.938[b]	2 159.380±234.746[d]
Rusty-capped Fulvetta (*A.dubia*)	2 090.634±332.147[b]	2 023.295±361.512[e]
Grey-cheeked Fulvetta (*A.morrisonia*)	1 838.588±334.220[c]	1 728.330±260.232[f]

Same superscripts indicate non-significant differences.

Table 4 Sampling size and roost site height of the seven fulvetta species

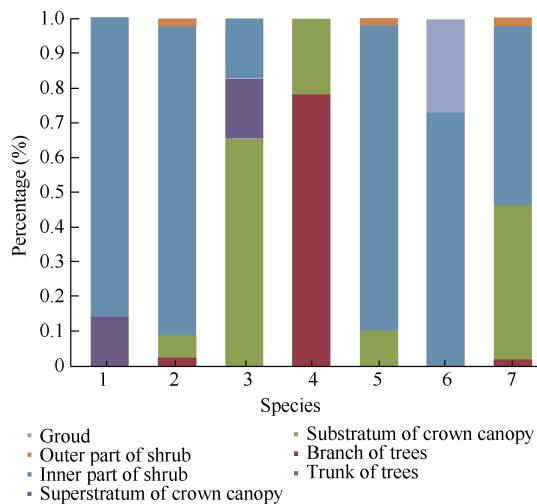| Species	Numbers (n)	Roost site height (m)
Rufous-winged Fulvetta (*A.castaneceps*)	23	11.087±2.109[a]
White-browed Fulvetta (*A.vinipectus*)	22	3.386±6.353[d]
Golden-breasted Fulvetta (*A.chrysotis*)	46	5.978±3.480[b]
Streak-throated Fulvetta (*A.cinereiceps*)	92	1.328±1.345[d]
Spectacled Fulvetta (*A.ruficapilla*)	50	1.300±0.909[d]
Rusty-capped Fulvetta (*A.dubia*)	78	0.559±0.408[e]
Grey-cheeked Fulvetta (*A.morrisonia*)	106	3.774±2.737[c]

Same superscripts indicate non-significant differences.

Vegetation coverage and mountain slope inclination
Significant differences were found in tree coverage (x^2=34.9663, P<0.01), shrub coverage (x^2=49.2832, P<0.01), herb coverage (x^2=50.828, P<0.01) as well as in the shrub and herb coverage between White-browed Fulvettas and Streak-throated Fulvettas (Table 5). Because no niche segregation was found between these two Fulvetta species in earlier analysis, these differences in vegetation coverage indicate the specific choices of these two species over microhabitat utilization and their relaxed inter-specific competition. No significant differences were found in the mountain slope inclination (x^2= 10.1526, P=0.1184). Rufous-winged Fulvetta was excluded from analyses due to the small sampling size.

Key factors affect habitat selection
According to earlier analyses of habitat variables, we chose the elevation, tree coverage, shrub coverage and herb coverage as habitat selection factors and used function "aictab" in the "AICcmodavg" package (Mazerolle, 2013) to determine the key factors affecting habitat selection. The results showed that the first 4 models' cumulative weight of QAICc (Cum.Wt) reached 100%. The first two models' delta QAICc were<2 and their cumulative weight reached 81%. The first one had the smallest QAICc and its weight reached 57% (Table 6). Because the weight of the first model was more than twice of the second one and it was succinct, the first model was considered as the optimal model. Because the

Figure legend:
- Groud
- Outer part of shrub
- Inner part of shrub
- Superstratum of crown canopy
- Substratum of crown canopy
- Branch of trees
- Trunk of trees

Figure 2 Comparison of roost site choices of species

1: White-browed Fulvetta (*A.vinipectus*); 2: Streak-throated Fulvetta (*A.cinereiceps*); 3: Golden-breasted Fulvetta (*A.chrysotis*); 4: Rufous-winged Fulvetta (*A.castaneceps*); 5: Spectacled Fulvetta (*A.ruficapilla*); 6: Rusty-capped Fulvetta (*A.dubia*); 7: Grey-cheeked Fulvetta (*A.morrisonia*).

first model was composed of elevation, herb coverage and shrub coverage, these factors were taken as the key factors affecting fulvettas' habitat selection.

We conducted model average of these four factors (elevation, tree coverage, shrub coverage and herb coverage) to learn effect trends. The results (Table 7) also showed that tree coverage did not significantly affect fulvettas' habitat selection because 0 occurred within its 95% confidence interval. The estimators of elevation and shrub were > 0, indicating their positive effects on fulvettas' habitat selection. Herb coverage had negative effects on fulvettas' habitat selection because its estimator < 0. Therefore, we concluded that fulvettas prefer the habitats with relatively high elevation and thick shrubs.

Morphological characteristics

Significant differences were detected in body weight (x^2=292.4995, P<0.01), body length (x^2=273.2875, P<0.01), wing length (x^2=270.8071, P<0.01), tail length (x^2=252.251, p<0.01), tarsus-metatarsus length (x^2=183.7224, P<0.01), claw length (x^2=81.1642, P<0.01), finger length (x^2=169.0881, P<0.01) and culmen length (x^2=264.6239, P<0.01). The Rufous-winged Fulvetta had the smallest tail length and tarsus-metatarsus length, while, the Golden-breasted Fulvetta was the smallest in the other morphological characteristics. Data of the Rusty-capped Fulvetta and the Grey-cheeked Fulvetta were relatively large (Table 8).

Table 5 Comparisons of vegetation coverage of the habitats of seven fulvetta species

Species	Percentage of tree coverage (%)	Percentage of shrub coverage (%)	Percentage of herb coverage (%)
White-browed Fulvetta (*A.vinipectus*)	60.461±30.204[abc]	40.268±37.980[b]	78.148±39.234[b]
Golden-breasted Fulvetta (*A.chrysotis*)	64.853±14.120[bc]	61.050±17.664[b]	84.141±17.565[a]
Streak-throated Fulvetta (*A.cinereiceps*)	67.850±24.946[ab]	72.761±32.170[a]	52.393±41.027[c]
Spectacled Fulvetta (*A.ruficapilla*)	53.357±26.087[c]	80.808±26.292[a]	38.211±43.193[c]
Rusty-capped Fulvetta (*A.dubia*)	63.019±25.633[abc]	72.461±30.159[a]	40.637±43.533[c]
Grey-cheeked Fulvetta (*A.morrisonia*)	71.719±24.159[a]	77.666±24.346[a]	34.364±42.520[c]

Same superscripts indicate non-significant differences.

Table 6 Results of model selection according to quasi-likelihood of the second-order Akaike's information criterion

Candidate models	QAICc	Delta_QAICc	QAICcWt	Cum.Wt	Quasi.LL
1/3/4	295.87	0.00	0.57	0.57	−142.83
1/2/3/4	297.62	1.75	0.24	0.81	−142.67
1/3	299.14	3.27	0.11	0.92	−145.5
1/4	299.77	3.9	0.08	1	−145.82
1	312.52	16.65	0	1	−153.22
3/4	322.2	26.33	0	1	−157.03
3	325.07	29.2	0	1	−159.49
4	339.48	43.61	0	1	−166.7

1: Elevation; 2: Percentage of tree coverage; 3: Percentage of shrub coverage; 4: Percentage of herb coverage.

Table 7 Model-averaged parameter estimations of habitat factors

Factors	Estimator	*SE*	Lower 95% CI	Upper 95% CI
Elevation	0.0012	2e-04	7e-04	0.0016
Percentage of tree coverage	−0.0021	0.0037	−0.0094	0.0051
Percentage of shrub coverage	0.0094	0.0041	0.0013	0.0175
Percentage of herb coverage	−0.0064	0.0028	−0.0118	−0.001

Table 8 Comparison of morphological characteristics of species

Species	*n*	Body weight (g)	Claw length (mm)	Culmen length (mm)	Wing length (mm)	Body length (mm)	Tail length (mm)	Tarsus-metatarsus length (mm)	Finger length (mm)
White-browed Fulvetta (*A.vinipectus*)	26	10.150± 0.858[c]	5.571±1.299[c]	5.598± 0.287[c]	57.837± 3.049[b]	111.038± 5.495[b]	55.577± 3.177[b]	24.946±0.827[a]	11.848± 0.730[b]
Streak-throated Fulvetta (*A.cinereiceps*)	63	9.756± 0.680[c]	6.551±1.386[ab]	5.629± 0.321[c]	54.817± 2.489[c]	107.873± 6.831[c]	52.397± 3.314[c]	24.495±0.931[a]	11.618± 1.029[b]
Rusty-capped Fulvetta (*A.dubia*)	31	15.803± 1.086[a]	6.861±0.884[a]	6.842± 0.354[a]	59.452± 1.748[b]	132.032± 4.199[a]	61.677± 3.250[a]	25.079±0.961[a]	13.848± 1.403[a]
Grey-cheeked Fulvetta (*A.morrisonia*)	120	14.496± 1.187[b]	5.828±0.733[c]	6.751± 0.362[a]	64.208± 1.878[a]	133.000± 3.043[a]	62.192± 3.537[a]	23.634±0.830[b]	11.927± 0.876[b]
Golden-breasted Fulvetta (*A.chrysotis*)	31	7.126± 0.390[e]	4.716±0.613[d]	4.771± 0.236[d]	52.742± 1.751[d]	99.645± 4.079[d]	48.903± 3.944[d]	22.792±0.944[c]	10.132± 0.661[d]
Rufous-winged Fulvetta (*A.castaneceps*)	10	9.610± 0.985[c]	6.575±0.834[ab]	5.875± 0.196[b]	56.100± 2.132[bc]	104.100± 6.999[cd]	42.600± 2.836[e]	20.210±0.778[d]	12.300± 0.707[b]
Spectacled Fulvetta (*A.ruficapilla*)	58	8.479± 0.876[d]	5.911±1.235[bc]	5.650± 0.237[c]	53.517± 2.011[d]	105.483± 3.267[c]	50.741± 3.081[d]	22.516±1.076[c]	10.635± 0.630[c]

Same superscripts indicate non-significant differences.

Linear discriminant analysis

We conducted LDA to the eight morphological characteristics in Table 8, and got six linear discriminant functions. The cumulative proportion of LD1 and LD2 reached 0.9284 (Table 9), indicating that they could account for 92.84% variability in the linear discriminant model. The proportions of the last four linear discriminant functions were small, indicating the weak influences they exert on the results. The absolute values of coefficients of body length (BL) and tarsus-metatarsus length (TML) in LD1 were high, indicating that LD1 primarily reflected the discriminant effects of body length and tarsus-metatarsus length. The absolute value of coefficient of wing length (WL) in LD2 was the largest coefficient, indicating that LD2 primarily reflected the discriminant effect of wing length (Table 10).

Approximately, 90.3% of the samples were correctly classified into different species via LDA. Samples were divided into four groupings and two of them were consisted of a single species, Golden-breasted Fulvettas and Rufous-winged Fulvettas, respectively. One group was consisted of Grey-cheeked Fulvettas and Rusty-capped Fulvettas, and the fourth group was consisted of White-browed Fulvettas, Streak-throated Fulvettas and spectacled Fulvettas (Table 11). The accuracy rates of LDA for each species were relatively high (91.20%-100%) except for White-browed Fulvettas (65.40%) and Streak-throated Fulvettas (74.60%). Misclassifications were found among White-browed Fulvettas, Streak-throated Fulvettas and spectacled Fulvettas, as well as between Grey-cheeked Fulvettas and Rusty-capped Fulvettas. Misclassification rate was relatively high between White-browed Fulvettas and Streak-throated Fulvettas (Table 11).

Table 9 Proportion of trace of linear discriminant analysis

Functions	LD1	LD2	LD3	LD4	LD5	LD6
Proportion of trace	0.8523	0.0761	0.0516	0.0139	0.0051	0.001

Table 10 Coefficients of linear discriminant analysis

Morphological characteristics	LD1	LD2	LD3	LD4	LD5	LD6
BW	−0.8811885	0.3735774	−0.4774164	0.624646	0.1744586	0.2523426
CUL	−1.340453	0.1253922	1.2647371	−1.54594	1.4543998	−1.077508
CLL	0.7308699	4.5448938	3.6643598	−4.682241	6.6273355	5.5899434
WL	−14.8874514	−48.0531867	−12.1749091	30.530741	42.8527554	−2.7700184
BL	−22.2927648	−2.5958555	−15.5078565	4.240833	−26.0764156	15.6511549
TL	−3.5438221	9.4093755	−14.3753771	−29.584098	−7.0460453	−16.0740137
TML	20.7689209	37.1068074	−33.2364027	16.419393	25.9016113	7.8645413
FL	3.1495686	8.2214066	17.5987326	12.287153	−6.1706657	−17.0493372

Table 11 Classification rates of linear discriminant analysis of morphological characteristics

Species	White-browed Fulvetta (*A.vinipectus*)	Streak-throated Fulvetta (*A.cinereiceps*)	spectacled Fulvetta (*A.ruficapilla*)	Rusty-capped Fulvetta (*A.dubia*)	Grey-cheeked Fulvetta (*A.morrisonia*)	Golden-breasted Fulvetta (*A.chrysotis*)	Rufous-winged Fulvetta (*A.castaneceps*)
White-browed Fulvetta (*A.vinipectus*)	65.40%	30.80%	3.80%				
Streak-throated Fulvetta (*A.cinereiceps*)	15.90%	74.60%	9.50%				
Spectacled Fulvetta (*A.ruficapilla*)		8.80%	91.20%				
Rusty-capped Fulvetta (*A.dubia*)				93.50%	6.50%		
Grey-cheeked Fulvetta (*A.morrisonia*)					100%		
Golden-breasted Fulvetta (*A.chrysotis*)						100%	
Rufous-winged Fulvetta (*A.castaneceps*)							100%

DISCUSSION

Spatial niche segregation in different scales

According to the competitive exclusion principle, niche segregation was required among sympatric congeners to avoid competitive exclusion (Hardin, 1960; Levin, 1970; Schoener, 1974). Niche theory could well explain species coexistence in temperate forest (Nakashizuka, 2001). According to this study, the niche theory could also be used in subtropical montane forest to explain the coexistence of the seven fulvettas in Ailao Mountains, Ejia Twon, Yunnan Province. Through spatial niche segregation in different scales, fulvettas reduced inter-specific competition and promoted species coexistence.

Habitat partitioning was relatively more important than other dimensions (Schoener, 1974). Habitat heterogeneity was vital for habitat segregation (Vidus-Rosin et al, 2012). In this study, results of model selection based on GLM with Poisson error indicated that the elevation, shrub coverage and herb coverage were the key factors affecting fulvettas' habitats selection (Table 6). Elevation analysis showed that niche segregation was detected through both mist-nets and point counts. No significant differences were found either among the three fulvettas occupying relatively high elevations or between Spectacled Fulvettas and Rusty-capped Fulvettas through mist-nets, whereas, through point counts, only one pair was found with non-significant differences. Chiang et al (2012) reported that elevation gradients might be the main factor in explaining the coexistence of species in spatial dimension. In the study area of this study, elevations were ranged from 800 m to 2 800 m and both the climate and forest types were showed with obvious vertical variations, therefore, the habitat heterogeneity along elevation gradients offered

opportunities of these fulvettas to choose different habitats.

Niche overlaps were also existence for some fulvettas even though segregation in elevation had been detected. Schoener (1983) found that when species were similar in one dimension, resource differentiation would occur in other dimensions to reduce inter-specific competition. Vertical height was an important component of spatial niche. Studies on tits had shown that segregation in vertical height could facilitate species' coexistence (Song, 1983; Yang et al, 2012). Through analysis of roost site height, we found niche overlaps among White-browed Fulvettas, Spectacled Fulvettas and Streak-throated Fulvettas. However, Spectacled Fulvettas had significant differences with the other two in elevation. Golden-breasted Fulvettas was widely overlapped with White-browed Fulvettas and Streak-throated Fulvettas in elevation documented by mist-nets. They had significant differences in roost site height with the other two species. Similar results were also found between Rufous-winged Fulvettas and Streak-throated Fulvettas documented by point counts. Vertical height reflects the activity space chosen by birds. Because of their unique physiological and activity pattern, birds have high demand for energy supply. Foraging behavior accordingly occupies a large proportion in birds' activities. Therefore, differentiation in roost site height mainly reflects segregation in foraging height. Studies on tits (Liu et al, 1989), prinias (Zhou & Fang, 2000), hummingbirds (Lara et al, 2011) and other bird communities (Gao & Yang, 1991) found that foraging height segregation reduced inter-specific competition and facilitated coexistence. Hence, we assumed that foraging height segregation permitted fulvettas that widely overlapped in elevation to relax the intensity of inter-specific competitive interactions.

Through analysis of elevation and vertical height, we did not found significant differences between White-browed Fulvettas and Streak-throated Fulvettas documented by mist-nets. However, significant differences were then detected in the key factors of shrub coverage and herb coverage (Table 5). Vegetation coverage was an important component of microhabitat chosen by animals. Segregation in microhabitat could facilitate species' coexistence (Dammhahn et al, 2013; Traba et al, 2013). Study on Blue Eared Pheasant (*Crossoptilon auritum*) found that concealment condition provided by vegetation coverage had a significant influence on birds' habitat selection (Liu et al, 2005). Study of breeding ecology showed that fulvettas' nests were primarily located in undergrowth consisted of shrubs and herbs (Lee et al, 2010; Gong, 1994; Huang et al, 1988; Zhou, 1989). Therefore, segregation in this scale allowed fulvettas to use different concealment conditions in their home range and avoided complete niche overlap accordingly.

Morphological differentiations
Morphological characteristics provide an insight into the ecology of animals (Landmann & Winding, 1993; Miles et al, 1987). It reflects the adaptions to the environmental

conditions consisted of abiotic and biotic factors during animals' life history (Martin, 2001). We detected significant differences in eight morphological characteristics of the seven fulvettas (Table 8) and four qualitative groupings were resulted from LDA (Table 11). Numerous of studies on the relationships between birds' niche use and morphology found that differences in morphological characteristics led to differentiation in their competitive abilities (Kalinoski, 1975; Gao et al, 1997), their foraging behaviors (Salewski et al, 2003), their resource preferences (Hill & Lein, 1988) and the varieties, sites and vertical height of trees they chose (Alatalo, 1981; Richards et al, 2000; Salewski et al, 2003). In this study, LDA primarily reflected discriminant effects of body length, tarsus-metatarsus length and wing length. These three characteristics have great influences on bird's activities. Studies on herons (Wen et al, 1998; Ye et al, 2006; Zhu et al, 1998), hummingbirds (Lara et al, 2011) and woodpeckers (Gao et al, 1997) showed that body size played a key role in deciding birds' competitive ability. Wing length decides birds' flying ability. Tarsus-metatarsus length has a strong correlation with birds' behavior and influences habitat selection (Liu et al, 2013). Therefore, we predicted that fulvettas of different groupings present different features in resource use which helped them to realize niche partition. Misclassifications within groups indicated the similarity in resource use among group members. However, we also detected segregations among fulvettas within each group. For example, in the first group, White-browed Fulvettas was different from Streak-throated Fulvettas in microhabitat use, and they had significant differences with Spectacled Fulvettas in elevation. Significant differences were also detected in elevation and roost site height between Grey-cheeked Fulvettas and Rusty-capped Fulvettas of the second group (Table 11).

In conclusion, different morphological characteristics of each group benefited fulvettas to partition resource in the overlapped regions and spatial niche segregation relaxed the intensity of inter-specific interactions among members within each group. However, the misclassifications indicated that intense competition could still occur among members within each groups in the overlapped regions and these competitions might become new selective pressures facilitating further differentiations.

The findings of this study showed that niche theory could explain the coexistence mechanisms of the seven fulvettas in the subtropical montane, Ejia Town, Yunnan Province. Through elevation, roost site height and vegetation coverage partitioning, these seven sympatric fulvettas realized spatial niche segregation in different scales. Combined with differentiations in resource use due to different morphological characteristics, they were able to minimize the intensity of inter-specific interactions and promote the coexistence. Moreover, the mutability and unpredictability of environment, the interference effects, the migration of species and the heterogeneity provided by large environmental gradient might also play important roles and

should be considered along with the competition effects when exploring the coexistence mechanisms of sympatric congeners.

ACKNOWLEDGEMENTS

REFERENCES

Alatalo RV. 1981. Interspecific competition in tits Parus spp. and the goldcrest Regulus regulus: foraging shifts in multispecific flocks. *Oikos,* **37**(3): 335-344.

Amadon D. 1943. Bird weights as an aid in taxonomy. *The Wilson Bulletin,* **55**(3): 164-177.

Atchley WR, Gaskins CT, Anderson D. 1976. Statistical properties of ratios. I. Empirical results. *Systematic Biology,* **25**(2): 137-148.

Bagchi S, Goyal SP, Sankar K. 2003. Niche relationships of an ungulate assemblage in a dry tropical forest. *Journal of Mammalogy,* **84**(3): 981-988.

Barlow J, Mestre LAM, Gardner TA, Peres CA. 2007. The value of primary, secondary and plantation forests for Amazonian birds. *Biological Conservation,* **136**(2): 212-231.

Bibby CJ, Jones M, Marsden S. 1998. Bird Surveys: Expedition Field Techniques. London: Expedition Advisory Centre, Royal Geographical Society.

Chen YS, Ye LF. 1988. Geology and geomorphy of the Ailaoshan Mountain Natural Reserve and its vicinity. *In*: Xu YC, Jiang HJ. Comprehensive survey of Ailaoshan Nature Reserve. Kunming: Yunnan Ethnic Press, 11-23. (in Chinese)

Chesson P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics,* **31**(1): 343-366.

Chiang PJ, Pei KJC, Vaughan MR, Li CF. 2012. Niche relationships of carnivores in a subtropical primary forest in southern Taiwan. *Zoological Studies,* **51**(4): 500-511.

Crawley MJ. 2012. The R Book. 2nd ed. West Sussex: John Wiley and Sons.

Cui P, Kang MJ, Deng WH. 2008. Foraging habitat selection by sympatric Temminck's tragopan and blood pheasant during breeding season in southwestern China. *Biodiversity Science,* **16**(2): 143-149. (in Chinese)

Dammhahn M, Soarimalala V, Goodman SM. 2013. Trophic niche differentiation and microhabitat utilization in a species-rich montane forest small mammal community of eastern madagascar. *Biotropica,* **45**(1): 111-118.

Davies TJ, Meiri S, Barraclough TG, Gittleman JL. 2007. Species coexistence and character divergence across carnivores. *Ecology Letters,* **10**(2): 146-152.

Denoël M, Schabetsberger R, Joly P. 2004. Trophic specialisations in alternative heterochronic morphs. *Naturwissenschaften,* **91**(2): 81-84.

Di Bitetti MS, Di Blanco YE, Pereira JA, Paviolo A, Pérez IJ. 2009. Time partitioning favors the coexistence of sympatric crab-eating foxes (*Cerdocyon thous*) and pampas foxes (*Lycalopex gymnocercus*). *Journal of Mammalogy,* **90**(2): 479-490.

Fox JW. 2004. Modelling the joint effects of predator and prey diversity on total prey biomass. *Journal of Animal Ecology,* **73**(1): 88-96.

Gao W, Yang ZJ. 1991. The relationship of mixed flock of birds in the artificial larch forest in winter. *Chinese Journal of Zoology,* **26**(4): 9-12. (in Chinese)

Gao W, Li WC, Lü JT. 1997. The niche and competition of three woodpeckers. *Journal of Northeast Normal University: Natural Science Edition,* (1): 78-81. (in Chinese)

Gao X, Alvo M, Chen J, Li G. 2008. Nonparametric multiple comparison procedures for unbalanced one-way factorial designs. *Journal of Statistical Planning and Inference,* **138**(8): 2574-2591.

Gong HS. 1994. The observation of breeding ecology of Golden-breasted Fulvetta (*Alcippe chrysotis*). *Sichuan Journal of Zoology,* **13**(2): 89. (in Chinese)

Guillemain M, Fritz H, Guillon N, Simon G. 2002. Ecomorphology and coexistence in dabbling ducks: the role of lamellar density and body length in winter. *Oikos,* **98**(3): 547-551.

Gustafsson L. 1988. Foraging behaviour of individual Coal Ttis, Parus-Ater, in relation to their age, sex and morphology. *Animal Behaviour,* **36**(3): 696-704.

Hardin G. 1960. The competitive exclusion principle. *Science,* **131**(3409): 1292-1297.

Hespenheide HA. 1973. Ecological inferences from morphological data. *Annual Review of Ecology and Systematics,* **4**(1): 213-229.

Hill BG, Lein MR. 1988. Ecological relations of sympatric black-capped and mountain chickadees in southwestern Alberta. *The Condor,* **90**(4): 875-884.

Huang Y, Wu WG, Huang SM. 1988. The breeding babit of Grey-hooded Fulvetta (A.cinereiceps). *Chinese Wildlife,* **42**(2): 13-15. (in Chinese)

Kaifu K, Miller MJ, Aoyama J, Washitani I, Tsukamoto K. 2013. Evidence of niche segregation between freshwater eels and conger eels in Kojima Bay, Japan. *Fisheries Science,* **79**(4): 593-603.

Kalinoski R. 1975. Intra-and interspecific aggression in House Finches and House Sparrows. *The Condor,* **77**(4): 375-384.

Landmann A, Winding N. 1993. Niche segregation in high-altitude Himalayan chats (Aves, Turdidae): does morphology match ecology? *Oecologia,* **95**(4): 506-519.

Langkilde T, Shine R. 2004. Competing for crevices: interspecific conflict influences retreat-site selection in montane lizards. *Oecologia,* **140**(4): 684-691.

Lara C, Martínez-García V, Ortiz-Pulido R, Bravo-Cadena J, Loranca S, Córdoba-Aguilar A. 2011. Temporal-spatial segregation among hummingbirds foraging on honeydew in a temperate forest in Mexico. *Current Zoology,* **57**(1): 56-62.

Lara C, Martínez-García V, Ortiz-Pulido R, Bravo-Cadena J, Loranca S, Córdoba-Aguilar A. 2011. Temporal-spatial segregation among hummingbirds foraging on honeydew in a temperate forest in Mexico. *Current Zoology,* **57**(1): 56-62.

Lee PY, Wang LJ, Hsu HC, Chou LS, Chen CC. 2010. Habitat selection among nesting, foraging, and singing sites of the Gray-cheeked Fulvetta Alcippe morrisonia in northeastern Taiwan. *Ornithological Science,* **9**(2): 135-140.

Levin SA. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *The American Naturalist,* **104**(939): 413-423.

Li L, Zhang L, Yin JX, Liu ZC, Liu H, Wan DM. 2013. Coexistence mechanism of two species passerines in man-made nest boxes. *Acta Ecologica Sinica,* **13**(1): 150-158. (in Chinese)

Li W, Zhou W, Zhang XY, Cao M, Zhang RG. 2006. Spring foraging sites of three pheasants at Nanhua part in Ailaoshan National Nature Reserve. *Zoological Research*, **27**(5): 495-504. (in Chinese)

Liu DY, Wang JX, Lv PY, Chen YY. 1988. Comprehensive report on scientific exploration of the Ailaoshan Nature Reserve. *In*: Xu YC, Jiang HJ. Comprehensive Survey of Ailaoshan Nature Reserve. Kunming: Yunnan Ethnic Press, 1-10. (in Chinese)

Liu LH, Chen XC, Chu H, Sun JC, Zhang XA, Zhao L. 2013. Ecomorphological explanations of passerines coexistence in alpine meadow. *Zoological Research*, **34**(3): 160-165. (in Chinese)

Liu NF, Li Y, Liu JZ. 1989. Studies of interspecific relationship between great tit and willow tit. *Zoological Research*, **10**(4): 277-284. (in Chinese)

Liu ZS, Chao LR, Li ZG, Li T, Wang XM. 2005. Winter habitat selection of blue eared pheasant (*Crossoptilon auritum*) in Helan Mountain, China. *Chinese Journal of Zoology*, **40**(2): 38-43. (in Chinese)

Loveridge AJ, Macdonald DW. 2003. Niche separation in sympatric jackals (*Canis mesomelas* and *Canis adustus*). *Journal of Zoology*, **259**(2): 143-153.

Lucherini M, Reppucci JI, Walker RS, Villalba ML, Wurstten A, Gallardo G, Iriarte A, Villalobos R, Perovic P. 2009. Activity pattern segregation of carnivores in the high Andes. *Journal of Mammalogy*, **90**(6): 1404-1409.

Macarthur RH. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology*, **39**(4): 599-619.

Martin TE. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? *Ecology*, **82**(1): 175-188.

Martínez-Freiría F, Lizana M, Do Amaral JP, Brito JC. 2010. Spatial and temporal segregation allows coexistence in a hybrid zone among two Mediterranean vipers (*Vipera aspis* and *V. latastei*). *Amphibia-Reptilia*, **31**(2): 195-212.

Mazerolle MJ. 2013. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c), http://CRAN.R-project.org/package= AICcmodavg.

Miles DB, Ricklefs RE, Travis J. 1987. Concordance of ecomorphological relationships in three assemblages of passerine birds. *The American Naturalist*, **129**(3): 347-364.

Munday PL, Jones GP, Caley MJ. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. *Ecology*, **82**(8): 2177-2189.

Nakashizuka T. 2001. Species coexistence in temperate, mixed deciduous forests. *Trends in Ecology and Evolution*, **16**(4): 205-210.

Pagen RW, Thompson III FR, Burhans DE. 2002. A comparison of point-count and mist-net detections of songbirds by habitat and time-of-season. *Journal of Field Ornithology*, **73**(1): 53-59.

Quillfeldt P, Masello JF, Navarro J, Phillips RA. 2013. Year-round distribution suggests spatial segregation of two small petrel species in the South Atlantic. *Journal of Biogeography*, **40**(3): 430-441.

R Core Team. 2013. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing

Rappole JH, Winker K, Powell GVN. 1998. Migratory bird habitat use in southern Mexico: Mist Nets versus Point Counts. *Journal of Field Ornithology*, **69**(4): 635-643.

Richards SA, Nisbet RM, Wilson WG, Possingham HP. 2000. Grazers and diggers: exploitation competition and coexistence among foragers with different feeding strategies on a single resource. *The American Naturalist*, **155**(2): 266-279.

Salewski V, Bairlein F, Leisler B. 2003. Niche partitioning of two Palearctic passerine migrants with Afrotropical residents in their West African winter quarters. *Behavioral Ecology*, **14**(4): 493-502.

Schoener TW. 1974. Resource partitioning in ecological communities. *Science*, **185**(4145): 27-39.

Schoener TW. 1983. Field experiments on interspecific competition. *The American Naturalist*, **122**(2): 240-285.

Schuett GW, Hardy DL, Greene HW, Earley RL, Grober MS, Van Kirk EA, Murdoch WJ. 2005. Sympatric rattlesnakes with contrasting mating systems show differences in seasonal patterns of plasma sex steroids. *Animal Behaviour*, **70**(2): 257-266.

Song YJ. 1983. Study of breeding habit of the Coal Tit (Parus ater). *Acta Ecologica Sinica*, **3**(4): 399-407. (in Chinese)

Svenning JC. 1999. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology*, **87**(1): 55-65.

Traba J, Acebes P, Malo JE, García JT, Carriles E, Radi M, Znari M. 2013. Habitat selection and partitioning of the Black-bellied Sandgrouse (*Pterocles orientalis*), the Stone Curlew (*Burhinus oedicnemus*) and the Cream-coloured Courser (*Cursorius cursor*) in arid areas of North Africa. *Journal of Arid Environments*, **94**: 10-17.

Tschapka M. 2004. Energy density patterns of nectar resources permit coexistence within a guild of Neotropical flower-visiting bats. *Journal of Zoology*, **263**(1): 7-21.

Vidus-Rosin A, Lizier L, Meriggi A, Serrano-Perez S. 2012. Habitat selection and segregation by two sympatric lagomorphs: the case of European hares (*Lepus europaeus*) and Eastern cottontails (*Sylvilagus floridanus*) in northern Italy. *Acta Theriologica*, **57**(4): 295-304.

Wang XF, Tang SF, Gao PL. 1988. The mountain climate of mid-north section of the Ailao Mountains. *In*: Xu YC, Jiang HJ. Comprehensive Survey of Ailaoshan Nature Reserve. Kunming: Yunnan Ethnic Press, 24–34. (in Chinese)

Ward-Campbell BMS, Beamish FWH, Kongchaiya C. 2005. Morphological characteristics in relation to diet in five coexisting Thai fish species. *Journal of Fish Biology*, **67**(5): 1266-1279.

Wen ZZ, Wang QL, Sun RY. 1998. Study of interspecific relationship of the herons. *Chinese Journal of Ecology*, **17**(1): 27-34. (in Chinese)

Wiens JJ, Graham CH. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**: 519-539.

Wu F, Yang XJ. 2008. Application of point count method in forest birds survey. *Chinese Journal of Ecology*, **27**(12): 2240-2244. (in Chinese)

Wu F, Yang XJ, Yang JX. 2010. Additive diversity partitioning as a guide to regional montane reserve design in Asia: an example from Yunnan Province, China. *Diversity and Distributions*, **16**(6): 1022-1033.

Yang L, Yang XJ. 2004. The Avifauna of Yunnan, China. Vol. 2 Passeriformes. Kunming: Yunnan Science and Technology Press. (in Chinese)

Yang XN, Zhu L, Hao G, Wen AX, Sun YH. 2012. Niche separation and coexistence of two species of tits at Wawushan. *Chinese Journal of Zoology*, **47**(4): 11-18. (in Chinese)

Ye F, Huang CM, Li HH. 2006. Study on spartial niche of seven species of colonial breeding egrets and herons of Fangcheng, Guangxi Autonomous Region. *Sichuan Journal of Zoology*, **25**(3): 577-583. (in Chinese)

Zhao L, Zhang XA. 2004. Nest-site selection and competition coexistence of Horned Larks and Small Skylarks. *Zoological Research*, **25**(3): 198-204.

(in Chinese)

Zheng GM. 1995. Ornithology. Beijing: Beijing Normal University Press. (in Chinese)

Zheng GM. 2002. A Checklist on the Classification and Distribution of the Birds of the World. Beijing: Science Press. (in Chinese)

Zheng GM. 2011. A Checklist on the Classification and Distribution of the Birds of China. 2nd ed. Beijing: Science Press. (in Chinese)

Zhou F. 1989. Study of breeding ecology of Grey-cheeked Fulvetta (*Alcippe morrisonia*). *Chinese Wildlife,* **52**(6): 54-57. (in Chinese)

Zhou F, Fang HL. 2000. On the interspecific niche relationship between two species of wren warbler. *Zoological Research,* **21**(1): 52-57. (in Chinese)

Zhu X, Zhang LX, Liang J, Xuan ZC. 1998. Spatial niche and interspecific relationships of Ardeidae Birds in Taigongshan Hill, Zhejiang. *Zoological Research,* **19**(1): 45-51. (in Chinese)