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ORIGINAL ARTICLE

Nestedness of bird assemblages in the karst forest fragments of southwestern Guangxi, China

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Abstract The limestone region in southwestern Guangxi contains the most typical karst landforms in the world. Due to their destruction, the original forests mainly survive in nature reserves in the form of fragmented areas. From June 2009 to September 2010 we conducted an investigation of 13 relatively isolated habitats or sites, selected from each of the 13 nature reserves in southwestern Guangxi, with the least amount of anthropological activity and the largest presence of the original vegetation, in order to study the distribution of birds on forest fragments. The distribution patterns of the birds and the factors which affect them were analyzed by using the "BINMATNEST" software and the Spearman's rank correlation analysis, to determine: 1) whether nested patterns of birds in the karst area of southwestern Guangxi exist or not and 2) which factors are correlated with the nested patterns and the effect of these factors on forming nested patterns. The results show that the birds had statistically significant nested patterns in the karst area and the specificity of the habitat of the birds had a significant effect on the nested patterns. We suggest possible reasons for these results, based on the characteristics of the seasonal tropical rain forests in the study area and on neutral theory. We also urgently recommend that close attention be paid to the protection of the diversity of the environment for birds in all fragmented habitats.

Keywords birds, nestedness, habitat fragmentation, karst area, neutral theory

Introduction

Habitat fragmentation is always a current issue in research by conservation biologists and ecologists (Lord and Norton, 1990; Robinson et al., 1995; Crooks et al., 1999; Fahrig, 2003; Castellón and Sieving, 2006; Ewers and Didham, 2007). Including birds, many species are affected by fragmented habitats (Andrén, 1994b; Herkert, 1994; Souza and Brown, 1994; Lens et al., 2002). During the last two decades, a number of studies have been conducted on, such as, species richness and abundance on fragmented habitats (Terborgh et al., 2001), the minimum living area of birds (Winter and Faaborg, 1999) and birds migration between fragmented habitats (Wiens, 1994). As well, the pattern of species distribution on fragmented habitats has been widely researched, where nested analysis is the most common method to investigate species distribution patterns on various fragmented habitats (Blake, 1991; Honnay et al., 1999; Lomolino and Perault, 2000; Lindenmayer et al., 2002, 2003; Fischer and Lindenmayer, 2005; Wethered and Lawes, 2005; Feeley et al., 2007). One of the patterns that has been identified is the nestedness of insular biotas; isolated communities often form nested subsets, with species on species-poor islands constituting subsets of those present on richer islands (Patterson and

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Atmar, 1986). A group of species assemblages is said to be completely nested when the all species making up smaller biotas are also found in all larger ones. It has been shown that nested structures are widely present in all organisms and habitat islands (Wright et al., 1998). To account for nested patterns of species distribution, four general hypotheses have been proposed: 1) passive sampling (Andrén, 1994a; Nielsen and Bascompte, 2007), 2) selective extinction (Patterson, 1984; Lomolino, 1996), 3) selective colonization (Cook and Quinn, 1995; Conroy et al., 1999; Mac Nally et al., 2002) and 4) habitat nestedness (Blake, 1991; Calmé and Desrochers, 1999; Honnay et al., 1999). As passive sampling hypothesis is related to the diversity between species and sampling effect, the others are related to habitat features and species life-history traits.

The most typical karst landscape in the world is found in southwestern Guangxi of China. Karst environments are fragile and very sensitive to human impact and very difficult to restore when destroyed (Tuyet, 2001; Shu et al., 2009). Many of the original local tropical forests have been damaged to varying degrees, causing the forest area and the number of small forest stands to continue to decline, resulting in a shrinkage of species habitat areas (Wu, 2009). At present, the best protected forest areas are in nature reserves in the form of habitat fragments, hence it is a huge challenge to protect species diversity, including birds. Nested analysis of species communities is of special importance in species protection (Patterson, 1987), offering a new perspective on their protection (Chen and Wang, 2004). We have studied distribution patterns of birds in fragmented habitats of the karst area of southwestern Guangxi to explore: 1) if nested patterns of birds in the karst area of southwestern Guangxi exist or not, 2) the factors which are correlated with a nested pattern and the effect of factors on the formation of these nested patterns and 3) some suggestions for the protection of bird species diversity in this karst area.

Study area and methods

Study area and sampling design

The karst area is located at 105°29′–108°6′E and 22°9′–23°41′N in the southwest of the Guangxi Zhuang Autonomous Region in China (Fig. 1), adjacent to the Socialist Republic of Vietnam. This area includes nine cities and counties, i.e., the counties Long'an of Nanning city, Jiangzhou, Fusui, Daxing, Tiandeng and Longzhou of Chongzuo city as well as the counties Jingxi, Debao and Napo of Baise city. The total area covers about 1300 km^2 (Table 1), of which 56% is of a karst landform. This area is the most typical karst landscape in the world and a global biodiversity hotspot (Myers et al., 2000), with rich north tropical biological karst resources. The karst area of southwestern Guangxi is the most important site of global significance among other biodiversity hotspots in China (Chen, 1993). The major landform of southwestern Guangxi is the typical limestone, besides the shale and sandstone landscape. The area is located south of the tropic of cancer and has a north tropical monsoon climate, with an average annual temperature of 18 to 22°C and rainfall of 1100 –1500 mm. The vegetation is mainly that of a north tropical forest, with small areas of subtropical evergreen broad-leaved forests. Because of rapid social and economic development, the original forest vegetation has deteriorated considerably. The remainder of the original forest vegetation is largely preserved in nature reserves in the form of fragmented areas.

There are 13 nature reserves in the study area (Nonggang, Chunxiu, Qinglongshan, Bangliang, Diding, Encheng, Xialei, Gulongshan, Longhushan, Laohutiao, Banli, Bapen and Huanglianshan Nature Reserves), from which 13 relatively isolated fragmented areas with less human intervention and well-forested area were selected as our study sites, numbered by size from 1 to 13. Site 3 is in the Sino-Vietnam border area and fragments on both sides of the border were selected as one site. Because of its continuous forest, only the result of our bird survey, conducted on the Guangxi side, was used, but the entire area on both sides of the border was treated as a whole area.

Bird survey

The cover of the study area is dominated by six vegetation types: 1) tropical rain forest, 2) broad-leaved forest, 3) shrub-forest, 4) shrub-grass, 5) farmland and 6) wetland. At each site, line transect method was used for bird survey. Two transect lines were sampled on the wetland, farmland and shrub-grass respectively and four transect lines were sampled on the rain forest, broad-leaved forest and shrub-forest respectively. The main area was covered by these transect lines. During the survey the length and direction of each transect line were adjusted according to the shape and size of each

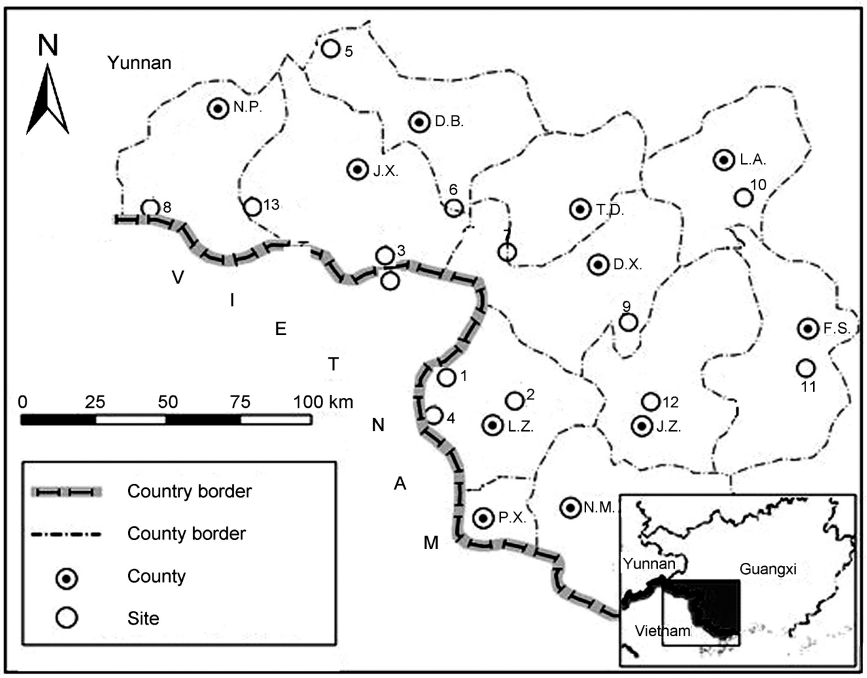

Fig. 1 Map of the limestone area in southwestern Guangxi with sites surveyed. N.P. = Napo; D.B. = Debao; L.A. = Long'an; J.X. = Jingxi; T.D. = Tiandeng; D.X. = Daxing; F.S. = Fusui; L.Z. = Longzhou; J.Z. = Jiangzhou; P.X. = Pingxiang; N.M. = Ningming. For the nature reserve numbers, see information in Table 1.

Table 1 Habitat features of the 13 sites

Habitat fragment	Nature reserve	Area (km^2)	Distance to nearest larger fragment (m)	Vegetation richness
1	Qinglongshan nature reserve	57.2	18.7	1100
2	Nonggang nature reserve *	54.2	7.5	1340
3	Bangliang nature reserve	50.7	20.4	956
4	Chunxiu nature reserve	44.3	20.3	900
5	Huanglianshan nature reserve	43.6	7.5	1166
6	Gulongshan nature reserve	40.5	34.9	1065
7	Xialei nature reserve	35.4	52.1	1004
8	Laohutiao nature reserve	31.1	22.7	520
9	Encheng nature reserve	28.7	34.9	927
10	Longhushan nature reserve	22.5	10.2	870
11	Bapen nature reserve	20.6	37.1	231
12	Banli nature reserve	16.8	15.2	550
13	Diding nature reserve	11.5	17.1	1000

* Refers to a national nature reserve, the others are regional nature reserves.

site in order to obtain accurate results.

This study was conducted between June 2009 and September 2010. Days with persistent rain and strong winds were avoided, for under those conditions it would be difficult to record birds. Bird surveys were carried out by using 8 × 42 binoculars from 06:00–10:00 and from 15:00–18:00 local time. Observation points along each 1500 m transect line were arranged and birds observed on both sides of transect and habitat type was recorded at each site. In order to survey the birds accurately in the shrubs, we set 3 m × 5 m mist nets on the edge of the shrubs. Three or five mist nets were set for 3–5 days as a group between 06:00 and 18:00. The mist nets were checked every hour and any

birds trapped were recorded and then released. Considering that raptors and water birds are strong flyers with the ability to migrate between fragmented areas, the study was only conducted on resident and breeding birds while omitting raptors and water birds from our survey at each site.

Habitat features

Three habitat variables, area, isolation and vegetation richness of a habitat are commonly considered to greatly affect the distribution pattern of birds (Lomolino and Perault, 2000; Fischer and Lindenmayer, 2005; Wethered and Lawes, 2005; Wang et al., 2010). For our study, three factors are selected as habitat features: area, distance to the nearest larger fragmented area and vegetation richness. We interpreted the distance to the nearest larger fragment as the straight line distance between one fragment and the nearest larger fragment. Vegetation richness is the number of plant species at each fragment, the data was obtained from the scientific survey report of each reserve and several references (Liang et al., 1985; Xie et al., 1994). Google Earth Pro 5.1 was used to evaluate the area and the distance between fragments and vegetation richness was obtained from survey data and a few references (Liang et al., 1985; Xie et al., 1994).

Species life-history traits

Bird life-history traits have also been proved to affect bird distribution patterns (Cook and Quinn, 1995; Kadmon, 1995; Fischer and Lindenmayer, 2005; Feeley et al., 2007; Wang et al., 2010). The activity ability and body size of birds, and habitat specificity were used to analyze the nested pattern of the birds. The activity ability is interpreted as the mobility of a given species, defined as the dispersal ratio ("dp"; Woinarski, 1989) and calculated for each bird by dividing its mean wing length (mm) by the cubic root of its mean mass (g) (Fischer and Lindenmayer, 2005); the larger the "dp" value, the stronger the mobility of a bird. The body size of birds was obtained from the record of specimens at Guangxi University, Guangxi Academy of Sciences and *The Avifauna of Yunnan China*, *The Avifauna of Guizhou*, *Fauna Sinica Aves* and several references (Zhou and Jiang, 2008; Alström et al., 2010). Habitat specificity refers to the number of habitat types (six habitat types in the current landscape) where each bird species lives. For example, the habitat specificity of one species only found in one habitat type was given the value 1, which meant the species has a narrow distribution range and vice versa.

Data analysis

Quantification of nestedness

Based on the data of our bird survey, sites were initially sorted by species richness which determines the ordering of rows, while fragments were sorted by their size, determining the ordering of columns. Given these procedures, a binary code "1/0" was used to show presence/absence of species in each fragment. In the end, a presence-absence matrix was constructed for birds (see Supplementary Table S1).

Species nestedness is currently calculated with the nestedness temperature T, used in the algorithm implemented by the calculator BINMATNEST (binary matrix nestedness temperature calculator; Rodríguez-Gironés and Santamaria, 2006). T provides a standardized measure of matrix disorder by assessing the deviation of an observed matrix from the completely nested. T thus ranges from 0 for a completely nested matrix to 100 for one that is completely disordered (Boecklen, 1997; Wright et al., 1998). The calculator first computes an isocline of perfect order, which is a curve in a completely nested matrix of the same size. BINMATNEST creates three null models to compute the temperature of each random matrix and returns the proportion of matrices with temperature lower than or equal to the temperature of the input matrix. Among these, null model 3 was considered to be able to avoid the effect of passive sampling (Rodríguez-Gironés and Santamaria, 2006; Moore and Swihart, 2007).

Spearman's rank correlation analysis

The effect of habitat features and species life-history traits on forming a nested pattern was evaluated by a Spearman's rank correlation analysis (Fernández-Juricic, 2004; Schouten et al., 2007).

We used Microsoft Excel 2003 for data calculation and arrangement and other statistical analyses from SPSS 17.0. We followed the usual convention that $p < 0.05$ means statistically significant differences, $p < 0.01$ means strongly significant differences and $p > 0.05$ signifies non-significant differences.

Results

Bird composition

A total of 248 bird species were recorded, belonging to 42 families and 9 orders, including 191 Passeriformes bird species from 30 families. The number of bird species in each fragment ranges between 113 and 183 (see Supplementary Table S1). Among these, 25 bird species, such as the White Wagtail (*Motacilla alba*), Rufous-necked Scimitar Babbler (*Pomatorhinus ruficollis*), Red-whiskered Bulbul (*Pycnonotus jocosus*), Barn Swallow (*Hirundo rustica*), Spotted Dove (*Streptopelia chinensis*), Greater Coucal (*Centropus sinensis*) and so on were recorded in all fragments; 42 bird species were only found in one fragment, while 181 bird species were recorded in more than one fragment.

Habitat features

The habitat features of the 13 fragments were recorded as data. The sampling sites ranged from 11.5 to 57.2 km^2 in size. The distance of each fragment to the nearest larger fragment was between 7.5 and 52.1 m; the vegetation richness of each fragment was between 231 and 1340 species (Table 1).

Life-history features

It can be seen from Table 2 that bird body weight ranged from 5 to 1400 g, body length was between 81 and 885 mm, the "dp" value ranged from 14.22 to 52.58 and habitat specificity from 1–5; most birds were found in habitat types 2 and 3.

Result of nestedness

The results of the nestedness are shown by BINMATNEST. The nestedness temperature T of bird communities in southwestern Guangxi was 39.78°C. The degree of nestedness for all three models shows highly significant differences ($p < 0.001$). These results show that birds in the karst area of southwestern Guangxi have nested patterns (Table 3).

Determinants of nestedness

Spearman's rank correlation coefficients indicate that the three habitat features (area: $r = 0.121$, $p > 0.05$; distance to the nearest larger fragment: $r = 0.115$, $p > 0.154$; vegetation richness: $r = 0.055$, $p > 0.05$) and the three life-history traits (body weight: $r = 0.026$, $p > 0.05$; body length: $r = 0.069$, $p > 0.05$; dp: $r = 0.062$, $p > 0.05$) had no significant effect on bird nestedness. The only factor correlated with bird nestedness was bird habitat specificity ($r = 0.339$, $p < 0.01$). For more details please see Table 4.

Discussion

As with nested patterns of birds at other fragmented habitats (or islands) (Blake et al., 1991; Davidar et al., 2002; Amparo Lázaro et al., 2005; Fischer and Lindenmayer, 2005; Feeley et al., 2007; Louzada et al., 2010; Wang et al., 2010; 2011), we obtained similar result, i.e., strongly nested pattern in bird assemblages in the karst area of southwestern Guangxi. Our result provides further proof that statistically significant nestedness is common (Wright et al., 1998) and is present in almost all types of biological groups and fragmented habitats (islands).

However, from the results of Spearman's rank correlation analysis, we conclude that none of the three habitat features (area, distance to nearest larger fragment, vegetation richness) was statistically significant ($p > 0.05$), despite the fact that "area" has always been considered to be statistically significant to nested patterns of species (Lomolino and Perault, 2000; Fischer and Lindenmayer, 2005; Wethered and Lawes, 2005). Isolation is not significant to generating nestedness probably because the range of isolation is small in our study. Although the habitat features were not significant in the nested patterns, this does not mean that habitat features do not affect bird assemblages. Single factor cannot affect the distribution pattern of the birds (Schoener and Schoener, 1983a, 1983b). The following reasons should be considered for analyzing the results.

Our study area, i.e., the karst area of southwestern Guangxi, is in a northern tropical area where the main vegetation consists of seasonal tropical rain forests and some broad-leaved forests. On the large scale, fragments are distributed in the region about 2310000 km^2, hence differences between fragmented habitats in this large scale landscape can be expected. Some fragments had good protection with a high proportion of a rain forest (e.g. fragments 2, 3, 7, 10–13), but the vegetation of other fragments consisted mainly of broad-leaved forests (e.g. fragments 1, 4–6, 8, 9).

Table 2 Life-history traits of bird species in southwestern Guangxi

Species	Body weight (g)	Body length (mm)	Wing length (mm)	dp	Habitat specificity
Chinese Francolin (*Francolinus pintadeanus*)	365.0	320	145	20.29	3
Spotted Dove (*Streptopelia chinensis*)	182.0	322	159	28.06	4
Large Green-billed Malkoha (*Phaenicophaeus tristis*)	117.5	502	150	30.63	2
Common Coucal (*Centropus sinensis*)	266.6	184	217	33.72	4
Lesser Coucal (*Centropus bengalensis*)	99.8	330	160	34.49	3
Common Kingfisher (*Alcedo atthis*)	27.2	165	70	23.28	1
White-throated Kingfisher (*Halcyon smyrnensis*)	89.6	265	117	26.15	2
Barn Swallow (*Hirundo rustica*)	15.6	171	109	43.62	4
Red-rumped Swallow (*Hirundo daurica*)	20.6	180	117	42.68	4
White Wagtail (*Motacilla alba*)	21.2	181	90	32.52	4
Scarlet Minivet (*Pericrocotus flammeus*)	29.2	205	100	32.47	3
Red-whiskered Bulbul (*Pycnonotus jocosus*)	30.7	194	86	27.47	4
Chinese Bulbul (*Pycnonotus sinensis*)	35.5	190	90	27.38	4
Black Bulbul (*Hypsipetes leucocephalus*)	54.6	237	121	31.89	3
Long-tailed Shrike (*Lanius schach*)	58.3	261	105	27.08	3
Red-billed Blue Magpie (*Urocissa erythrorhyncha*)	170.8	555	190	34.24	3
Taiwan Whistling Thrush (*Myophoneus caeruleus*)	184.0	303	173	30.42	2
Hwamei (*Garrulax canorus*)	68.4	233	93	22.74	3
Rufous-necked Scimitar Babbler (*Pomatorhinus ruficollis*)	25.1	190	74	25.27	5
Rufous-capped Babbler (*Stachyris ruficeps*)	9.6	109	52	24.47	5
Grey-cheeked Fulvetta (*Alcippe morrisonia*)	16.0	136	63	25.00	3
Yellow-bellied Prinia (*Prinia flaviventris*)	7.4	136	44	22.58	4
Common Tailorbird (*Orthotomus sutorius*)	8.0	113	45	22.50	5
Japanese White-eye (*Zosterops japonicus*)	10.5	104	55	25.12	3
Great Tit (*Parus major*)	13.7	129	67	28.00	5
Hair-crested Drongo (*Dicrurus hottentottus*)	88.8	311	172	38.55	2
Crested Myna (*Acridotheres cristatellus*)	125.2	243	138	27.59	3
Fork-tailed Sunbird (*Aethopyga christinae*)	6.2	103	49	26.67	3
Silver Pheasant (*Lophura nycthemera*)	1400.0	885	250	22.35	3
White-breasted Waterhen (*Amaurornis phoenicurus*)	246.0	322	170	27.13	3
White-throated Bulbul (*Alophoixus pallidus*)	50.8	235	110	29.70	2
Green-winged Bulbul (*Hypsipetes mcclellandii*)	40.3	232	106	30.92	2
Grey Bushchat (*Saxicola ferrea*)	12.3	136	64	27.73	3
Hill Prinia (*Prinia atrogularis*)	10.6	163	46	20.94	3
Plain Prinia (*Prinia inornata*)	9.9	149	45	20.96	3
Black-throated Tit (*Aegithalos concinnus*)	6.4	100	48	25.85	3
Black-naped Oriole (*Oriolus chinensis*)	78.3	247	152	35.53	3
Red Junglefowl (*Gallus gallus*)	990.0	633	224	22.48	3
Indian Cuckoo (*Cuculus micropterus*)	103.0	324	189	40.32	2
Drongo Cuckoo (*Surniculus lugubris*)	37.2	254	136	40.74	2
House Swift (*Apus nipalensis*)	26.6	139	132	44.22	3
Sooty-headed Bulbul (*Pycnonotus aurigaster*)	48.7	211	97	26.56	3
Magpie Robin (*Copsychus saularis*)	38.4	204	96	28.46	3
Hainan Blue Flycatcher (*Niltava hainanus*)	13.9	138	69	28.70	3
Black-naped Monarch (*Hypothymis azurea*)	12.5	143	72	31.02	3
Striated Yuhina (*Yuhina castaniceps*)	13.0	130	56	23.82	2
Plain Flowerpecker (*Dicaeum concolor*)	6.8	81	46	24.28	3
Blue Rock Thrush (*Monticola solitarius*)	49.4	211	120	32.70	3
Grey-chinned Minivet (*Pericrocotus solaris*)	17.3	181	84	32.48	2
Collared Finchbill (*Spizixos semitorques*)	40.5	196	90	26.21	2

Table 2 (Continued)

Species	Body weight (g)	Body length (mm)	Wing length (mm)	dp	Habitat specificity
Chestnut Bulbul (*Hemixos castanonotus*)	34.7	206	101	30.97	3
Black-throated Laughingthrush (*Garrulax chinensis*)	91.0	230	110	24.46	2
Orange-bellied Leafbird (*Chloropsis hardwickii*)	33.5	185	90	27.92	2
Dollarbird (*Eurystomus orientalis*)	131.7	264	185	36.36	2
Large-billed Crow (*Corvus macrorhynchos*)	525.6	475	326	40.40	3
Great Barbet (*Megalaima virens*)	190.2	333	140	24.34	2
Black-winged Cuckoo Shrike (*Coracina melaschistos*)	37.6	227	117	34.92	2
Blyth's Leaf Warbler (*Phylloscopus reguloides*)	7.6	104	60	30.52	3
Crow-billed Drongo (*Dicrurus annectans*)	60.5	269	142	36.17	2
Silver-eared Mesia (*Leiothrix argentauris*)	26.0	168	76	25.65	2
Red-billed Leiothrix (*Leiothrix lutea*)	21.5	142	66	23.74	2
Larger white-rumped Swift (*Apus pacificus*)	37.5	178	176	52.58	3
Ring-necked Pheasant (*Phasianus colchicus*)	1135.0	747	232	22.24	2
Chinese Bamboo Partridge (*Bambusicola thoracica*)	271.0	308	131	20.24	3
Grey-headed Woodpecker (*Picus canus*)	144.7	304	150	28.57	2
Rosy Minivet (*Pericrocotus roseus*)	19.1	186	88	32.92	2
Rusty-capped Fulvetta (*Alcippe dubia*)	20.0	146	62	22.84	2
White-bellied Yuhina (*Yuhina zantholeuca*)	12.5	118	67	28.87	2
White-browed Rufous (Piculet *Sasia ochracea*)	8.5	89	55	26.95	3
Bianchi's Warbler (*Seicercus valentini*)	7.3	110	54	27.84	3
Small Niltava (*Niltava macgrigoriae*)	11.0	128	64	28.78	3
Yellow-bellied Sunbird (*Cinnyris jugularis*)	7.5	107	51	26.05	2
Ashy Wood Swallow (*Artamus fuscus*)	40.0	178	127	37.14	3
Emerald Dove (*Chalcophaps indica*)	121.0	233	139	28.10	2
White-throated Fantail (*Rhipidura albicollis*)	11.0	177	78	35.07	2
Blue-winged Siva (*Minla cyanouroptera*)	18.0	151	64	24.42	3
Spectacled Laughingthrush (*Eudynamys scolopaceus*)	218.0	427	202	33.56	3
Yellow-billed Bay Woodpecker (*Blythipicus pyrrhotis*)	117.0	254	135	27.60	2
Striped Tit Babbler (*Macronous gularis*)	10.7	123	54	24.51	3
Rufous Woodpecker (*Celeus brachyurus*)	92.0	230	120	26.58	2
Fujian Niltava (*Niltava davidi*)	24.8	170	91	31.20	3
Sulphur-breasted Warbler (*Phylloscopus ricketti*)	7.0	97	57	29.80	2
Bar-winged Flycatcher Shrike (*Hemipus picatus*)	9.4	139	64	30.33	3
Red Turtle Dove (*Streptopelia tranquebarica*)	111.3	231	138	28.69	2
Golden-throated Barbet (*Megalaima franklinii*)	81.8	217	98	22.58	2
Grey-headed Canary Flycatcher (*Culicicapa ceylonensis*)	10.4	120	62	28.40	3
Crimson Sunbird (*Aethopyga siparaja*)	7.0	137	55	28.75	2
Common Cuckoo (*Cuculus canorus*)	100.8	332	228	48.99	2
Speckled Piculet (*Picumnus innominatus*)	12.8	103	57	24.37	2
Plumbeous Water Redstart (*Rhyacornis fuliginosus*)	16.5	119	72	28.28	1
Sultan Tit (*Melanochlora sultanea*)	40.6	195	105	30.55	2
Short-tailed Wren Babbler (*Napothera brevicaudata*)	27.0	146	66	22.00	2
Black-headed Babbler (*Stachyris nigriceps*)	18.0	117	60	22.89	3
Eurasian Hoopoe (*Upupa epops*)	75.9	274	148	34.96	2
Crested Kingfisher (*Ceryle rudis*)	302.0	398	188	28.02	1
Lesser Racket-tailed Drongo (*Dicrurus remifer*)	46.3	543	158	44.00	2
Snowy-browed Flycatcher (*Ficedula hyperythra*)	8.4	103	59	29.02	2
Plaintive Cuckoo (*Cacomantis merulinus*)	29.2	232	113	36.70	1
Great Pied Woodpecker (*Picoides major*)	73.4	250	134	32.00	2
Pygmy Wren Babbler (*Pnoepyga pusilla*)	11.5	87	47	20.82	3

Table 2 (Continued)

Species	Body weight (g)	Body length (mm)	Wing length (mm)	dp	Habitat specificity
Black-crested Bulbul (*Pycnonotus melanicterus*)	31.6	193	87	27.52	2
Lesser Pied Kingfisher (*Megaceryle lugubris*)	93.0	290	136	30.02	1
Oriental Yellow-eyed Babbler (*Chrysomma sinense*)	23.3	182	69	24.16	2
Brown-breasted Bulbul (*Pycnonotus xanthorrhous*)	31.8	194	88	27.78	2
White-bellied Green Pigeon (*Treron sieboldii*)	290.0	300	173	26.14	2
White-rumped Munia (*Lonchura striata*)	10.5	109	50	22.83	3
Crested Bunting (*Melophus lathami*)	22.0	140	79	28.19	3
Blackbird (*Turdus merula*)	102.0	271	150	32.10	3
Spotted Munia (*Lonchura punctulata*)	15.0	116	54	21.90	3
Pale Blue Flycatcher (*Niltava unicolor*)	19.0	168	84	31.48	2
Yellow-cheeked Tit (*Parus spilonotus*)	18.3	137	76	28.84	3
Gray Treepie (*Dendrocitta formosae*)	99.1	368	141	30.47	2
Ashy Drongo (*Dicrurus leucophaeus*)	46.8	271	143	39.68	2
Franklin's Prinia (*Prinia hodgsonii*)	6.1	110	45	24.63	3
Gould's Sunbird (*Aethopyga gouldiae*)	6.8	145	55	29.03	2
Tree Sparrow (*Passer montanus*)	21.2	139	68	24.57	3
Scarlet-backed Flowerpecker (*Dicaeum c.cruentatum*)	6.6	88	48	25.59	2
Azure-winged Magpie (*Pica pica*)	232.4	450	209	33.99	3
Blue-and-white Flycatcher (*Cyanoptila cyanomelana*)	10.5	170	61	27.86	2
Eastern Crowned Warbler (*Phylloscopus coronatus*)	9.0	116	61	29.33	2
White-rumped Shama (*Copsychus malabaricus*)	26.4	243	89	29.89	2
Blue-throated Barbet (*Megalaima asiatica*)	86.7	229	100	22.59	2
White-browed Laughingthrush (*Garrulax sannio*)	67.5	228	97	23.82	3
Ashy Lauthingthrush (*Garrulax cineraceus*)	52.0	226	87	23.31	2
White-winged Magpie (*Urocissa whiteheadi*)	260.0	450	211	33.06	3
Yellow-bellied Warbler (*Seicercus superciliaris*)	6.5	100	49	26.26	2
Dark-crowned Prinia (*Prinia rufescens*)	7.1	108	42	21.85	3
Spot-necked Babbler (*Stachyris striolata*)	26.4	152	63	21.16	3
Grey-bellied Tesia (*Tesia cyaniventer*)	8.5	82	49	24.01	2
Nonggang Babbler (*Stachyris nonggangensis*)	35.5	165	89	27.08	3
Black Drongo (*Dicrurus macrocercus*)	49.5	276	143	38.95	3
Chestnut-crowned Warbler (*Seicercus castaniceps*)	5.0	96	51	29.82	2
Long-tailed Broadbill (*Psarisomus dalhousiae*)	60.0	257	100	25.54	2
Asian Paradise Flycatcher (*Terpsiphone paradisi*)	27.7	300	92	30.41	2
White-tailed Warbler (*Phylloscopus davisoni*)	6.2	104	53	28.85	2
White-bellied Jungle Babbler (*Pellorneum albiventre*)	17.0	140	53	20.61	2
Limestone Leaf Warbler (*Phylloscopus calciatilis*)	5.6	95	53	29.85	2
White-tailed Blue Robin (*Cinclidium leucurum*)	23.0	174	91	32.00	2
Golden Babbler (*Stachyris chrysaea*)	8.0	108	48	24.00	2
Velvet-fronted Nuthatch (*Sitta frontalis*)	13.1	116	74	31.39	2
Gould's Fulvetta (*Alcippe brunnea*)	19.5	135	60	22.29	2
Red-winged Crested Cuckoo (*Clamator coromandus*)	88.4	380	158	35.47	2
Large Scimitar Babbler (*Pomatorhinus hypoleucos*)	85.0	257	96	21.83	2
Malabar Pied Hornbill (*Anthracoceros albirostris*)	786.1	788	300	32.51	2
Golden Mountain Thrush (*Zoothera dauma*)	127.0	285	163	32.43	2
Chestnut-tailed Starling (*Sturnia malabaricua*)	44.0	196	103	29.18	3
Blue-rumped Pitta (*Pitta soror*)	110.0	229	108	22.54	2
Dusky Warbler (*Phylloscopus fuscatus*)	8.8	118	61	29.55	3
Olive-backed Pipit (*Anthus hodgsoni*)	21.7	153	83	29.76	4
Brown Shrike (*Lanius cristatus*)	31.9	192	89	28.06	2

Table 2 (Continued)

Species	Body weight (g)	Body length (mm)	Wing length (mm)	dp	Habitat specificity
Yellow-breasted Green Magpie (*Cissa hypoleuca*)	156.2	328	143	26.55	2
Grey-backed Thrush (*Turdus hortulorum*)	75.0	240	129	30.59	3
Brown-chested Jungle Flycatcher (*Rhinomyias brunneata*)	17.0	150	80	31.11	2
Two-barred Greenish Warbler (*Phylloscopus plumbeitarsu*)	7.6	108	58	29.50	3
Black-necked Tailorbird (*Orthotomus atrogularis*)	5.9	115	43	23.80	2
Red-headed Trogon (*Harpactes erythrocephalus*)	97.0	341	154	33.52	2
Oriental White-eye (*Zosterops palpebrosus*)	8.9	100	51	24.61	3
Large Hawk Cuckoo (*Cuculus sparverioides*)	147.5	388	236	44.67	2
Fire-breasted Flowerpecker (*Dicaeum ignipectus*)	6.9	83	49	25.74	2
Black-throated Sunbird (*Aethopyga saturate*)	5.5	141	53	30.03	3
Orange-headed Ground Thrush (*Zoothera citrine*)	55.0	205	113	29.71	2
Brown-breasted Flycatcher (*Muscicapa muttui*)	13.5	125	75	31.50	2
Large Niltava (*Niltava grandis*)	36.4	204	103	31.08	2
Verditer Flycatcher (*Eumyias thalassina*)	17.7	156	86	33.00	2
Asian House Martin (*Delichon dasypus*)	11.7	113	111	48.89	3
Vivid Niltava (*Niltava vivida*)	21.0	145	82	29.72	2
Mountain Tailorbird (*Orthotomus cuculatus*)	6.9	112	46	24.16	2
Oriental Turtle Dove (*Streptopelia orientalis*)	238.0	331	198	31.95	2
Hill Blue Flycatcher (*Niltava banyumas*)	14.3	144	71	29.25	2
Bronzed Drongo (*Dicrurus aeneus*)	29.2	235	127	41.24	2
Russet Sparrow (*Passer rutilans*)	22.0	135	75	26.77	3
Fairy Pitta (*Pitta nympha*)	59.5	189	119	30.48	2
Grey-crowned Woodpecker (*Picoides canicapillus*)	25.3	154	95	32.36	2
Red-winged Shrike Babbler (*Pteruthius flaviscapis*)	36.0	169	83	25.14	2
Black-capped Kingfisher (*Halcyon pileata*)	96.3	277	126	27.49	3
Rusty-cheeked Scimitar Babbler (*Pomatorhinus erythrogenys*)	69.1	228	91	22.18	2
White-spectacled Warbler (*Seicercus affinis*)	5.0	110	50	29.24	2
Little Spiderhunter (*Arachnothera longirostra*)	13.5	147	67	28.14	2
Pin-tailed Green Pigeon (*Treron apicauda*)	230.0	381	154	25.13	1
Silver-breasted Broadbill (*Serilophus lunatus*)	30.2	170	84	26.97	2
Dusky Crag Swallow (*Ptyonoprogne concolor*)	18.0	125	105	40.06	1
Large Cuckoo Shrike (*Coracina novaehollandiae*)	109.2	312	180	37.66	2
Brown-rumped Minivet (*Pericrocotus divaricatus*)	22.2	192	94	33.45	2
Short-billed Minivet (*Pericrocotus brevirostris*)	19.0	185	87	32.60	2
Yellow-bellied Bulbul (*Alophoixus flaveolus*)	54.2	219	104	27.48	2
Grey-backed Shrike (*Lanius tephronotus*)	47.1	231	100	27.69	2
Slaty-blue Flycatcher (*Ficedula tricolor*)	9.4	113	60	28.43	2
Streak-breasted Jungle Babbler (*Pellorneum ruficeps*)	24.5	155	67	23.07	2
Grey-cheeked Warbler (*Seicercus poliogenys*)	6.0	105	51	28.07	2
Broad-billed Warbler (*Seicercus hodgsoni*)	6.0	102	47	25.87	2
Rufous-faced Warbler (*Abroscopus albogularis*)	5.0	96	48	28.07	2
Red-tailed Laughingthrush (*Garrulax milnei*)	81.5	253	96	22.14	2
Barred Buttonquail (*Turnix suscitator*)	74.0	161	87	20.72	2
Spectacled Laughingthrush (*Garrulax perspicillatus*)	123.6	290	123	24.69	3
Lesser Necklaced Laughingthrush (*Garrulax pectoralis*)	133.5	300	135	26.41	2
Grey-headed Parrotbill (*Paradoxornis gularis*)	27.0	175	80	26.67	3
Slaty-breasted Banded Rail (*Gallirallus striatus*)	140.0	256	126	24.27	2
Black-collared Starling (*Gracupica nigricollis*)	164.0	285	164	29.96	3
Little Pied Flycatcher (*Ficedula westermanni*)	7.2	108	58	30.04	2
Chinese Babax (*Babax lanceolatus*)	63.0	239	90	22.62	2

Table 2 (Continued)

Species	Body weight (g)	Body length (mm)	Wing length (mm)	dp	Habitat specificity
Burmese Shrike (*Lanius collurioides*)	31.7	190	87	27.49	2
Streaked Spiderhunter (*Arachnothera magna*)	33.1	188	91	28.34	2
Silver-backed Spinetail Swift (*Hirundapus cochinchinensis*)	95.0	190	168	36.82	2
Vinous-throated Parrotbill (*Paradoxornis webbianus*)	10.2	120	54	24.90	2
Zitting Cisticola (*Cisticola juncidis*)	8.2	105	51	25.29	3
Water Rail (*Rallus aquaticus*)	160.0	270	130	23.95	2
Brownish-flanked Bush Warbler (*Cettia fortipes davidiana*)	10.8	116	53	23.98	2
Lesser Cuckoo (*Cuculus poliocephalus*)	54.8	255	160	42.12	2
Blue-winged Leafbird (*Chloropsis cochinchinensis*)	24.0	169	81	28.08	1
Eurasian Jay (*Garrulus glandarius*)	159.3	336	180	33.20	2
Yellow-browed Warbler (*Phylloscopus inornatus*)	6.5	100	50	26.79	3
Blue-breasted Quail (*Coturnix chinensis*)	62.0	120	70	17.69	3
Small Buttonquail (*Turnix sylvatica*)	46.0	110	66	18.42	2
Himalayan Greenfinch (*Carduelis sinica*)	20.0	123	81	29.84	3
Brown Crake (*Amaurornis akool*)	184.0	277	127	22.33	2
Spectacled Barwing (*Actinodura ramsayi*)	39.0	177	83	24.48	2
Ruddy-breasted Crake (*Porzana fusca*)	76.0	220	110	25.97	2
Rufous-bellied Woodpecker (*Picoides hyperythrus*)	47.2	203	122	33.76	2
Richard's Pipit (*Anthus richerdi*)	30.3	178	97	31.11	2
Tree Pipit (*Anthus trivialis*)	23.2	147	86	30.15	2
Long-tailed Minivet (*Pericrocotus ethologus*)	16.9	190	90	35.07	2
Tiger Shrike (*Lanius tigrinus*)	28.9	170	84	27.37	2
Hill Myna (*Gracula religiosa*)	211.0	280	163	27.38	2
Stonechat (*Saxicola torquata*)	13.0	129	67	28.49	3
Giant Babax (*Babax waddelli*)	74.5	143	130	30.90	2
Pale-rumped Warbler (*Phylloscopus proregulus*)	6.5	93	51	27.33	3
Buff-bellied Warbler (*Phylloscopus subaffinis*)	6.7	99	53	28.11	2
Grey Laughingthrush (*Garrulax maesi*)	112.7	290	134	27.74	2
Blue-tailed Bee-eater (*Merops philippinus*)	93.0	295	134	29.58	2
Forest Wagtail (*Dendronanthus indicus*)	17.6	165	79	30.37	3
White-shouldered Starling (*Sturnia sinensis*)	45.0	187	103	28.96	3
Silky Starling (*Sturnus sericeus*)	77.6	207	120	28.13	3
Chestnut-headed Fulvetta (*Alcippe castaneceps*)	8.5	107	55	26.95	2
Brown Hill Prinia (*Prinia polychroa*)	7.8	127	47	23.70	3
Yellowish-bellied Bush Warbler (*Seicercus superciliaris*)	9.0	107	42	20.19	2
Pale-footed Bush Warbler (*Cettia pallidipes*)	9.8	117	48	22.43	2
Brown Bush Warbler (*Bradypterus luteoventris*)	12.4	127	51	22.03	2
Green-backed Tit (*Parus monticolus*)	18.1	125	67	25.52	3
Watercock (*Gallicrex cinerea*)	380.0	385	103	14.22	2
Green Imperial Pigeon (*Ducula badia*)	487.5	433	228	28.97	1
Chestnut-capped Babbler (*Timalia pileata*)	23.0	165	62	21.80	2
Japanese Bush Warbler (*Cettia diphone*)	23.4	148	73	25.52	2
Brown-breasted Hill Partridge (*Arborophila brunneopectus*)	310.0	220	130	19.21	3
Flavescent Green Bulbul (*Pycnonotus flavescens*)	33.8	206	87	26.91	2
White-crowned Forktail (*Enicurus leschenaultia*)	45.0	250	109	30.64	2
Crimson-winged Liocichla (*Liocichla phoenicea*)	50.0	221	91	24.70	3
Black-chinned Yuhina (*Yuhina nigrimenta*)	11.0	120	58	26.08	2
Black-headed Sibia (*Heterophasia melanoleuca*)	36.0	195	90	27.26	2

Table 3 Nestedness of the bird matrix

Null model	*p* value	Mean temperature (°C)	Variance
1	< 0.01	70.71	2.26
2	< 0.01	62.43	3.45
3	< 0.01	57.61	2.70

Note: Nestedness temperature 39.78°C.

The investigations of tropical forests by Hubbell (2005a; 2005b; 2006) show that it is difficult to explain the diversity often observed in these species-rich communities. Hubbell and other ecologists have proposed the neutral theory (Hubbell, 1979, 2001, 2005a, 2006; Hubbell and Foster, 1983, 1986). They argued that the number of species in a community of a tropical forest is greater than in other forests. Based on our study of the 13 fragment habitats, the number of species in seasonal tropical rain forests was beyond its carrying capacity; for example, fragment 13 had the smallest area, but its number of birds was greater than that of some larger fragments. That "area" was not significant in our study may be the reason for this result.

Habitat specificity was statistically significant to nested patterns of birds. Because vegetation in seasonal tropical rain forest is often unique, with special and a greater variety of habitats, compared with broad-leaved forests, the habitat choice for birds provide for greater differences. Some tropical birds are mainly found in fragments 2, 3 and 13, consisting of larger tropical forests; these include the Red-headed Trogon (*Harpactes erythrocephalus*), Long-tailed Broadbill (*Psarisomus dalhousiae*), Black-throated Sunbird (*Aethopyga saturate*), Little Spiderhunter (*Arachnothera longirostris*) and others. In contrast, some birds can adapt to and are found in several habitats, such as the White Wagtail (*Motacilla alba*), Red-whiskered Bulbul (*Pycnonotus jocosus*), Spotted Dove (*Streptopelia chinensis*), as well as other birds. Simultaneously it should be noted that the result, that vegetation richness was not significant on nested bird patterns, might be a function of the vegetation in each fragment. Seasonal tropical rain forests have larger food resources and provide more habitat types for greater numbers of bird species, especially the high specificity species.

Among the three bird life-history traits, only habitat specificity was statistically significant on nested bird patterns. Because many species have a bias in favor of one type of habitat and not all types of habitats are randomly found in each fragment, there are nested habitat patterns, hence the nest pattern of habitats caused the nest pattern of species (Calmé and Desrochers, 1999). Different species select different habitats; low habitat specific species can adapt more readily to different kinds of habitat, including large and small fragments. In contrast, high habitat specific species only live in large fragmented habitats.

However, our study have some limitations, for example, the analysis methods for the quantification of nestedness have been developed rapidly, although BINMATNEST remains popular, some other rigorous programs, such as NODF and BR, have also been developed recently. So, it is necessary for us to have further study on bird assemblages of southwestern Guangxi and better to confirm the nested result.

In other words, birds have significant nested patterns in the karst area of southwestern Guangxi by our analysis. In these nested patterns, large habitat fragments always have a high richness vegetation and heterogeneity, i.e., more species, which need strong protection (Zhang, 2008). But many studies, including ours, also prove that even species distributions have significant nestedness; the total number of species in several small fragments was often greater than that of one large fragment, with the same area, as the total area of the small fragments (Beckon, 1993; Cook, 1995; Skaggs and Boecklen, 1996). Hence, for the protection of the diversity of birds in the karst area of southwestern Guangxi, we advocate that, while close attention should also be paid to large fragmented habitats, rich in vegetation, but even more care should be lavished on the kinds of species found in the smaller fragmented habitats, i.e. in the nature reserves.

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Table 4 Correlation coefficients of habitat features and life-history traits of birds

	Habitat features			Life-history traits			
	Area	Distance to the nearest larger fragment	Vegetation richness	Body weight	Body length	dp	Habitat specificity
r	0.121	0.115	−0.055	0.026	0.069	0.062	0.339**
p	0.694	0.707	0.859	0.848	0.281	0.332	< 0.01

** $p < 0.01$

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Supplementary material

Available on Chinese Birds website, links at http://www.chinesebirds.net, including

Table S1

桂西南喀斯特地区斑块生境中鸟类群落嵌套结构分析

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摘要：桂西南喀斯特地区拥有世界上发育最典型的溶岩地貌。由于遭到破坏，原生性较强的森林都以斑块形式存在于各保护区中。在桂西南喀斯特地区内的13个自然保护区中，分别选择一块人为干扰较小、植被原生性较强且相对隔离的生境斑块，于2009年6月至2010年9月对各生境斑块中的鸟类组成进行调查。使用BINMATNEST软件分析该地区斑块生境中鸟类群落的分布格局，探求桂西南喀斯特地区斑块生境中的鸟类群落是否存在嵌套性分布，以及影响嵌套性格局形成的因素及其对鸟类群落嵌套性分布的影响。结果表明，桂西南喀斯特地区斑块生境中的鸟类群落分布符合嵌套性结构，对选择的3种斑块特征因子和4种生活特征因子使用Spearman矩阵相关性分析，只有生境专属性因子对鸟类群落的嵌套结构影响显著，结合研究地的季雨林生境特征和中性理论分析了可能的原因。对桂西南喀斯特地区的鸟类多样性保护提出了全面重视的保护策略。

关键词：鸟类，嵌套结构，斑块生境，喀斯特，中性理论