Breeding Biology of Two Coexisting Laughingthrush Species in Central China

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ABSTRACT

The coexistence of ecologically similar species is widespread in nature and has fascinated the evolutionary biologists for a long time. In order to avoid direct competition, closely related bird species that breed alongside each other are expected to use different habitats characteristics for nesting. We looked for possible differences in breeding ecology of two bird species, the plain laughingthrush *Garrulax davidi concolor* and Elliot's laughingthrush *Trochalopteron elliotii* in lianhuashan, try to figure out the mechanisms permit stable coexisting of these two species, and hypothesized that the different nesting site selection favours coexisting of these two species. We determined the breeding time, reproductive success and nesting characteristics through field works, our results revealed highly difference in nest height above the ground and different preference for nesting plants between the two species. However, the nest predation rate and breeding success were not different significantly. Our study suggested that the space segregation of nesting site contribute to the extensive stable coexistence of these two species.

INTRODUCTION

Why the coexistence of ecologically similar and close related species is widespread in nature? In several decades of studies, a good deal of theoretical and empirical evidences proposed hypotheses and theories to make clear this question (Gause, 1934; Begon *et al.*, 1996; Tokeshi, 1999; Chesson, 2000; Mikami *et al.*, 2004; Zeng and Lu, 2009; Lu *et al.*, 2011). The principle of competitive exclusion states that if two species occupy truly identical niches, one is expected to supplant the other (Gause, 1934; Mikami *et al.*, 2004). Various hypotheses have been proposed to explain apparent contradictions of this principle, including subtle but real differences in ecological niches, inter-year fluctuations in environmental conditions, responses to frequent disturbances, and male-male repulsion (Begon *et al.*, 1996, Tokeshi, 1999; Chesson, 2000; Mikami *et al.*, 2004). Ecological niche theory predicts that potential competition between ecologically similar and often closely related organisms may be mitigated through mechanisms to segregate such species in the dimensions of: breeding season, foraging microhabitat, nesting site and/or diet (Pianka, 1981; Chesson, 2000; Lu *et al.*, 2011). In order to avoid direct competition, closely related bird species that breed alongside each other are expected to use different habitats characteristics for nesting (Lu *et al.*, 2009; Laughlin *et al.*, 2013).

Nesting habitat partitioning involving different uses of space, which can play an important role in determining the coexistence of species (Martin, 1988; Mikula *et al.*, 2014). Knowledge of such mechanisms is vital to understand phenotypic diversification and ecological speciation (Sommer and Worm, 2002; Bolnick and Fitzpatrick, 2007; Lu *et al.*, 2011).

Laughingthrush is the most diverse genus within the family Leiothrichidae with at least 40 species in China (Dickinson, 2003). Many species coexsting in the mountains of southwest and central China, but little is known on the mechanisms that permit such coexistence. The plain laughingthrush *Garrulax davidi concolor* (PL) occurs widely in shrub-dominated habitats in both cultivated and uncultivated areas between 800-2600 m above sea level in northern China (Lei and Lu, 2006; Liu and Sun, 2018). Elliot's laughingthrush *Trochalopteron elliotii* (EL) occurs widely in shrubs and mixed coniferous-deciduous forest at 800-4200 m a.s.l. of southwestern and central China (Lei and Lu, 2006; Liu and Sun, 2016). Both species are sexually monomorphic and socially monogamous, have similar life history (Liu and Sun, 2016, 2018). At Lianhuashan National Nature Reserve, southern Gansu Province, central China, above mentioned two species are seemingly prominent equally in the local passerine breeding community and lived fair population size, but the mechanisms that permit their coexistence are not apparent. To figure out the possible mechanisms behind this, and get better understanding of the diversification of laughingthrush species, we conducted a series of field studies on the breeding ecology in these two species.

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We predicted that: (1) interspecific competition result in significant difference in reproductive success between the two species; (2) the different preference for nesting plant species favours the coexisting of these two species.

MATERIALS AND METHODS

Study area

Our studies conducted at Badu village of Lianhuashan National Natural Reserve (34°40′67″N, 103°30′84″E), in Gansu Province, Central China. The average annual temperature in the reserve is 5.1-6.0°C, with recorded extremes of 34°C and -27.1°C, on the study area at an altitude of 2100 m a.s.l., the climate is semi-arid. The local shrubs are principally willows *Salix* spp., berberis *Berberis* spp., Rosaceae *Cotoneaster* spp., *Rosa* spp., *Malus* spp., and Chinese aralis *Aralia chinensis*, dominated by crabapple *Malus baccata*, rose *Rosa davidii*, Chinese buckthorn *Rhamnus utilis*, seabuckthorn *Hippophae rhamnoides* and dahurian buckthorn *Rhamnus parvifolia*. Spruce *Picea asperata* is the only cultivated species. The grey-backed shrike *Lanius tephronotus*, Siberian chipmunk *Eutamias sibiricus* and spotted nutcracker *Nucifraga caryocatactes* are main local nest predators.

Data collection

We could accurately distinguish nests of the two laughingthrush species as EL lays spotted eggs while PL lays unspotted blue eggs. We carried out investigations in Lianhuashan from March to end of August in three consecutive breeding seasons (2013 to 2015) within an 80 ha study area. We employed systematic searching methods to find nests in the bushes after the birds established territories and paired. We measured the distance from each nest to the nearest stream (categorized as < 20 m, 20-50 m, 50-100 m and > 100 m); species, height and crown diameter of the nesting plant (to 0.1 m); nest height above the ground (to 0.1 m). In three seasons, we determined these variables in 44 nests of PL and 54 of EL separately. We checked nests every two days, and designated the first-egg date as the clutch initiation time, we also identified the date of clutch completion, the clutch size, the date of start of incubation, the date of hatching, measured fresh egg mass and chick body mass at 10 days of age (to 0.01 g) with an electrical balance, egg length and width (to 0.01 mm) with calipers, and determined the nestling period (days). We determined chick body mass at 10 days old as breeding success to avoid the artificial early fledging and compare reproductive output between two species. Nest fate was determined for 44 nests of PL, and 53 nests of EL, categorized as 0 for depredation and one for success. All animal procedures were approved by the Institutional

Animal Care and Use Committee of the Institute of Zoology, Chinese Academy of Sciences.

Statistical analysis

T-tests were used to assess differences in nest height (above the ground), height and crown diameter of shrubs in which nests were placed, chick body mass at 10 days of age and incubation period between two species. Chi-square tests were applied where data were characterised as frequencies. Generalized linear model (binomial distribution and logit link) were employed to identify the factors distinguishing the two species and nest fate. Potential explanatory factors included distance of nest site to the nearest stream, nesting plant species, nesting plant height and nest height above the ground. All statistical tests were performed with SPSS software, values are presented as Mean±SD, all probabilities are two-tailed, and the significance level $P = 0.05$.

RESULTS

Breeding ecology

Variables of breeding ecology, especially clutch size and fledged young number in PL (2-4 eggs, 2-4 fledglings) and EL (3-4 eggs, 3-4 fledglings) were similar to each other (Table I). The PL started breeding as early as late March, the earliest nest we found contained 2 eggs in April 8th, 2015, the latest nest contained 4 eggs were found in August 11th 2013, the majority of nests were found in June; the EL started breeding on late April, the earliest nest we found contained 1 greenish-blue egg with reddish-brown spots in broad end on April 25th, 2014, the latest nest contained 3 eggs were found in July 20th 2015, the majority of nests were found in May and June. The breeding season of two species were overlapped in May, June and July (Fig. 1). The shape of nests in both species were open-cupped, both male and female nesting, after nest built, there is an empty period about 7 days, after then, in PL one unspotted blue egg laid per day, only female incubation start on the clutch completion time, clutch size from 2 to 4 (Table I). In EL, one spotted greenish-blue egg laid per day, biparental incubation started on the clutch completion time, clutch size from 3 to 4 (Table I). In both species, incubation period lasted for 14 days (Table I), and nestling period lasted about 15 days with biparental provisioning, and the parents continued provisioning and guarding the fledged young. During our study for three years, number of fledged nestlings was equal to clutch size in both species if the nest had not been predated, no brood reduction was observed. The clutch size, average egg length, chick

body mass at 10 days age and incubation period were not significantly different between two species (Table I). Nest predation rate in PL was 35.4%, EL was 36.2%.

Table I.- Breeding ecology in two laughingthrush species: the plain laughingthrush *Garrulax davidi* and Elliot's laughingthrush *Trochalopteron elliotii* overlapped at Lianhuashan.

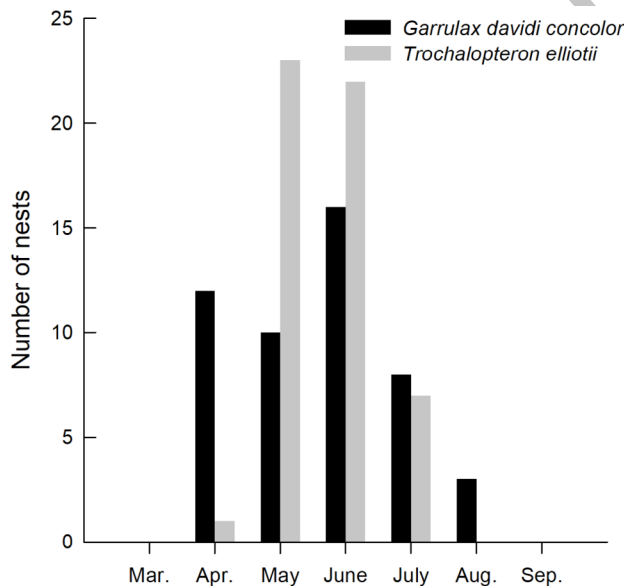| Variables	Species	Mean±SD	N
Clutch size	*G. d. concolor*	3.21±0.54	19
	G. elliotii	3.39±0.50	18
Fresh egg mass (g)	*G. d. concolor*	5.36±0.44	54
	G. elliotii	5.57±0.38	59
Egg length (mm)	*G. d. concolor*	26.85±1.06	58
	G. elliotii	27.13±1.00	59
Egg width (mm)	*G. d. concolor*	19.53±0.45	58
	G. elliotii	19.98±0.49	59
Nestling body mass at 10 days age (g)	*G. d. concolor*	33.27±3.74	37
	G. elliotii	34.69±2.95	31
Incubation period (d)	*G. d. concolor*	13.93±0.83	14
	G. elliotii	14.15±0.69	13

Fig. 1. The number of nests found in each month during the breeding season of the plain laughingthrush *Garrulax davidi concolor* and Elliot's laughingthrush *Trochalopteron elliotii*.

Table II.- Number of nests found on different nesting plants in two sympatric laughingthrush species at Lianhuashan Nature Reserve, Gansu China: the plain laughingthrush *Garrulax davidi* and Elliot's laughingthrush *Trochalopteron elliotii*.

Nesting plant species	Nests of PL	Nests of EL	Chi	P
Chinese buckthorn, *Rhamnus utilis*	20	14	0.291	> 0.05
Crabapple *Malus, baccata*	7	7	0.172	> 0.05
Rose, *Rosa davidii*	4	8	2.288	> 0.05
Seabuckthorn, *Hippophae rhamnoides*	8	0	6.142	0.013
Dahurian buckthorn, *Rhamnus parvifolia*	7	0	7.098	0.008
Spruce, *Picea asperata*	2	4	1.224	0.404
Others	6	11	3.262	0.107

Table III.- Results of generalized linear model analysis showing that which factors of nesting site selection can distinguish the two species: the plain laughingthrush *Garrulax davidi* and Elliot's laughingthrush *Trochalopteron elliotii* overlapped at Lianhuashan.

Potential explanatory factors	Chi	P
Distance from nearest stream	4.838	0.184
Nesting plant species	1.994	0.158
Nest height above the ground	11.06	0.001

Nest-site selection

Nest heights above the ground in PL 1.18±0.38 m (n=54), were highly significantly lower than in EL 1.57±0.47 m (n=44, P < 0.001; Fig. 2). No significant difference was found in nesting plant height (PL: 2.35±0.67 m, n=54; EL: 2.55±0.73 m, n=44; t=1.417, P > 0.05) and crown diameter of nesting plant (PL: 1.33±0.54, n=54; EL: 1.53±0.62, n=44; t=1.732, P > 0.05). PL and EL selected 10 and 13 plant species for nesting, respectively. Percentages of the three most frequently selected species (crabapple *M. baccata*, rose *R. davidii*, Chinese buckthorn *Rosa utilis*; PL: 66.0%; EL: 57.4%, Table II). Similarly, no significant difference existed between the two species in number of nests placed in spruce *Picea asperata* (PL, 3.7%; EL, 9.1%) but the PL selected the seabuckthorn *Hippophae rhamnoides* (13.0%) and dahurian buckthorn *Rhamnus parvifolia* (14.8%) significantly more often than the EL did (Table II). EL selected other plant species more (25% opposite 11.1% nests, Table III). The nest

height were not depend on the clutch initiation date in both species (PL: F=1.147, n=54, P=0.401; EL: F=1.302, n=44, P=0.257), as well as the nesting plant species (PL: F=0.856, n=54, P=0.651; EL: F=0.880, n=44, P=0.632). The differences in nest height between PL and EL were not explained by the seasonal differences (P=0.782).
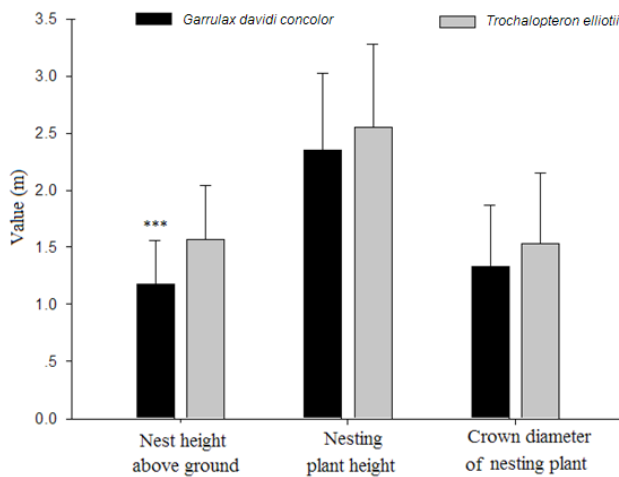

Fig. 2. The relative location of nests of the plain laughingthrush *Garrulax davidi concolor* and Elliots laughingthrush *Trochalopteron elliotii* (*** above the bar indicates highly significant difference).

DISCUSSION

Clutch size expresses great variations in the genus *Garrulax*, the minimum clutch size is two eggs and maximum clutch size ranges from three to seven eggs in most subtropical and tropical species (Ali and Ripley, 2002; Lu *et al*., 2008). The mean clutch size and number of fledged young in three other high-altitude breeders *viz*., the brown-cheeked laughingthrush *T. henrici*, endemic to Tibet plateau (2.5: 2-3 eggs, 2-3 fledglings, Lu *et al*., 2008), the giant laughingthrush *G. maximus* (2.2: 2-3 eggs, 1 fledglings, Wang *et al*., 2010) and the snowy-cheeked laughingthrush *G. sukatschewi* (3.2: 2-5 eggs, 2-3 fledglings, Wang *et al*., 2011). The results showed that the clutch size and number of fledged young decreased with altitude in *Garrulax* species. Laughingthrush invest more energy in fewer offsprings at higher altitude. This pattern has also been reported in other avian species (Blackburn, 1991; Badyaev, 1997). The unspotted blue colour egg in PL was similar to the giant laughingthrush and the snowy-cheeked laughingthrush (Wang *et al*., 2010; 2011), but the greenish-blue egg in EL spotted with broad end is similar to the spotted laughingthrush *G. ocellatus* (Ali and Ripley, 2002). EL displayed biparental incubation, similar to the giant laughingthrush and the snowy-cheeked

laughingthrush (Jiang *et al*., 2007; Wang *et al*., 2010, 2011). Incubation period lasted for 14 days in both PL and EL, similar to the snowy-cheeked laughingthrush (Wang *et al*., 2011) and shorter than the brown-cheeked laughingthrush (Lu *et al*., 2008).

Breeding time of two species expressed asynchronous, but PL bred as early as the end of March. We found just one nest of EL at the end of April in 2014; 3 nests of PL in August (and none of EL); this suggests EL terminates breeding earlier than PL, and that PL breeds earlier and has a longer breeding season than EL; the breeding time is therefore segregated in the two laughingthrush species. The breeding time reported for another EL population (80 days, Jiang *et al*., 2007) is consistent with our observations at lianhuashan (83 days), the brown-cheeked laughingthrush breeding from early May to late August (Lu *et al*., 2008). Two other *Garrulax* species *viz*., the giant laughingthrush and snowy-cheeked laughingthrush occur at our study site, Lianhuashan. Outside the breeding season, these two species lived in flocks at 2100 m a.s.l., along with the PL and EL, but during the breeding season, the giant laughingthrush and snowy-cheeked laughingthrush both upgraded to higher altitude and both breeding during May and June (Wang *et al*., 2010; 2011). The brown-cheeked laughingthrush, another species living in Tibet Plateau, breed from early May to late August (Lu *et al*. 2008). These results from different laughingthrush species indicate breeding time divergence in the genus *Garrulax*.

The nest height above the ground in PL is significantly lower than in EL, a lower placement could protect the nests from prevailing wind and reduce physiological costs of thermoregulation for incubating and nestlings, especially under harsh spring weather (Zerba and Morton, 1983; Lu *et al*., 2011). Different selection of nesting plant species suggests different preferences for nesting plants. The giant laughingthrush and snowy-cheeked laughingthrush as the two congeners occur together with the birds under study during non-breeding season, while in spring, they upgrade to higher altitude to breed. Such was also observed in the white-winged snowfinch *Montifringilla nivalis* and the scarlet rosefinch *Carpodacus erythrinus* express competitive exclusion (Zeng and Lu, 2009; Lu *et al*., 2009, 2011). The giant laughingthrush, nesting in coniferous forests at altitude of 2850-2950 m, mainly selected spruce *Picea asperata* and dragon spruce *Abies chensiensis* for nesting at about 4.0 m higher than both PL and EL (Wang *et al*., 2010). The snowy-cheeked laughingthrush at altitude of 2800-2900 m, mainly nesting in spruce *Picea asperata* at 2.4 m above the ground (Wang *et al*., 2011), that was higher than the PL and EL. Another resident in Tibet, the brown-cheeked laughingthrush breeding at 3900-4150 m

a.s.l., mainly nested in roses and barberry about 1.3 m above the ground (Lu *et al*., 2008), rather intermediate to the PL and EL. Studies carried out in a nursery of young spruce *Picea asperata* in Zhuoni population of EL showed that the birds nested on the small Spruce more often, and nesting at height 1.50 m above the ground (Jiang *et al*., 2007), is very similar to our results, indicating varying selection of nesting species among populations. The study indicates that the nest site location and nesting plant selection in the species of genus *Garrulax* varies suggesting a leaning towards vertical spatial distribution. The nest height were not depend on the clutch initiation date in both species, as well as the nesting plant species. The differences in nest height between PL and EL were not explained by the seasonal differences.

For the fiercely competition to breeding resource and territory, Interspecific aggression was commonly observed in similar body sized sympatric congeners (Martin and Martin, 2001; Sedláček *et al*., 2004; Zeng and Lu, 2009; Lu *et al*., 2009), in our study, although the body mass ratio of two laughingthrush species is 1.04, lower than stable critical values that have been suggested as necessary to allows sympatry in closely related species (Farlow and Pianka, 2002), the interspecific aggression is very rare, during our field work, only twice were observed, unless the two species try to nest on the same shrubs at the same time in breeding season.

Reduction of fitness in subordinate individuals caused by interspecific competition has been frequently reported in similar-sized sympatric congeners (Connell, 1983; Wellborn, 2002; Lu *et al*., 2011), the related species will partition limited resources more efficiently and reduce fitness costs (Bothwell *et al*., 2015). In our two study species, however, clutch size and breeding success were not significantly different. Nest predation reduces avian fitness as the predation risk influences the nest site selection such as microhabitat selection and space location of nests in breeding birds (Martin, 1993; Latif *et al*., 2012). In our study, the nest fate was identified with the nesting plant selection rather than other variables, as the most nests were placed mainly on six nesting plants. The hypothesis which proposes that nest predation being an important influence on the evolution of nest spatial distribution (Martin, 1993) does not explain our study system which is similar to studies on two coexisting Rosefinch species (*C. rubicilloides* and *C. eos*, Lu *et al*., 2011).

A study of morphological divergence in *Garrulax* has proposed that the competitive exclusion principle may explain the evolution and distribution of *Garrulax* species, and argues that the genus originated in the Southwest China (Cheng, 1982). Phylogenetic analysis of *Garrulax* species and allies based on mitochondrial and nuclear DNA sequences argues against this. Our results of breeding ecology and niche segregation in the studied species; and other reported species suggest no character displacement (Brown and Wilson, 1956) occurring in these species. We propose that the influence of competitive exclusion on distribution patterns of *Garrulax* species is weak.

Overall, the nest height were not depend on the clutch initiation date in both species, as well as the nesting plant species. The differences in nest height between PL and EL were not explained by the seasonal differences. The vertical spatial distribution of nest and different preference for nesting plants favours the stable coexistence of the plain laughingthrush *G. davidi* and Elliot's laughingthrush *T. elliotii*. The study about the niche segregation between these two similar species would be an interesting investigation.

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Statement of conflicts of interest
The authors have declared no conflicts of interest.

REFERENCES

Ali, S. and Ripley, S.D., 2002. *Handbook of the birds of India and Pakistan together with those of Bangladesh, Nepal, Sikkim, Bhutan, and Sri Lanka: Laughingthrushes to the Mangrove Whistler*, 2nd ed. Oxford University Press, Oxford, UK.

Badyaev, A.V., 1997. Avian life history variation along altitudinal gradients: an example with cardueline finches. *Oecologia*, **111**: 365–374. https://doi.org/10.1007/s004420050247

Begon, M., Harper, J.L. and Townsend, C.R., 1996. *Ecology: Individuals, populations and communities*. 3rd edn. Blackwell Science, Oxford.

Blackburn, T., 1991. An interspecific relationship between egg size and clutch size in birds. *Auk,* **108**: 973–977.

Bolnick, D.I. and Fitzpatrick, B.M., 2007. Sympatric speciation: Models and empirical evidence. *Annu. Rev. Ecol. Evol. Syst*., **38**: 459–487. https://doi.

org/10.1146/annurev.ecolsys.38.091206.095804

Bothwell, E., Montgomerie, R., Lougheed, S.C. and Martin, P.R., 2015. Closely related species of birds differ more in body size when their ranges overlap—in warm, but not cool, climates. *Evolution*, **69**: 1701–1712. https://doi.org/10.1111/evo.12706

Brown, W.L. and Wilson, E.O., 1956. Character displacement. *System. Zool.,* **5**: 49-64. https://doi.org/10.2307/2411924

Cheng, T.H., 1982. On the evolution of *Garrulax* (Timaliinae), with comparative studies of the species found at the center and those in the periphery of the distributional range of the genus. *Acta Zool. Sin.,* **28**: 205–209.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, **31**: 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Connell, J.H., 1983. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *Am. Natural*, **122**: 661–696. https://doi.org/10.1086/284165

Dickinson, E.C., 2003. *The Howard and Moore complete checklist of the birds of the World*. 3rd edn. Princeton University Press, Princeton, NJ:

Farlow, J.O. and Pianka, E.R., 2002. Body size overlap, habitat partitioning, and living-space requirements of terrestrial vertebrate predators: Implications for large-theropod paleoecology. *Histor. Biol.*, **16**: 21–40. https://doi.org/10.1080/0891296031000154687

Gause, G.J., 1934. *The struggle for existence*. Williams and Wilkins, Baltimore.

Jiang, Y.X., Zhu, Y.Z. and Sun, Y.H., 2007. Notes on reproductive biology of Elliot's Laughingthrush at Zhuoni, Gansu. *Sichuan. J. Zool.*, **26**: 555-556.

Latif, Q.S., Heath, S.K. and Rotenberry, J.T., 2012. How avian nest site selection responds to predation risk: testing an adaptive peak hypothesis. *J. Anim. Ecol.,* **81**: 127-138. https://doi.org/10.1111/j.1365-2656.2011.01895.x

Laughlin, A.J., Istvan, K. and Fred, J.A., 2013. Habitat partitioning and niche overlap of two forest thrushes in the Southern Appalachian Spruce-Fir Forests. *Condor*, **115**: 394-402. https://doi.org/10.1525/cond.2013.110179

Lei, F.M. and Lu, T.C., 2006. *China endemic birds*. Science Press, Beijing, China.

Liu, P.F. and Sun, Y.H., 2016. Sexual size dimorphism and assortative mating in Elliot's Laughingthrush *Trochalopteron elliotii*. *Ardea*, **104**: 177-181. https://doi.org/10.5253/arde.v104i2.a2

Liu, P.F. and Sun, Y.H., 2018. Sexual size dimorphism

and assortative mating in the plain laughingthrush *Garrulax davidi concolor*. *Wilson J. Ornithol.,* **130**: 510-512. https://doi.org/10.1676/16-031.1

Lu, X., Gong, G. and Zeng, X., 2008. Reproductive ecology of brown-cheeked laughing thrushes (*Garrulax henrici*) in Tibet. *J. Field. Ornithol.,* **79**: 152-158. https://doi.org/10.1111/j.1557-9263.2008.00157.x

Lu, X., Ke, D.H., Zeng, X.H. and Yu, T.L., 2009. Reproductive ecology of two sympatric Tibetan snowfinch species at the edge of their altitudinal range: response to more stressful environments. *J. Arid Environ.*, **73**: 1103–1108. https://doi.org/10.1016/j.jaridenv.2009.06.011

Lu, X., Guo, G. and Ma, X., 2011. Niche segregation between two alpine Rosefinches: to coexistence in extreme enviroments. *Evol. Biol.*, **38**: 79-87. https://doi.org/10.1007/s11692-010-9102-7

Luo, X., Qu, Y.H., Han, L.X., Li, S.H. and Lei, F.M., 2009. A phylogenetic analysis of Laughingthrushes (Timaliidae: *Garrulax*) and allies based on mitochondrial and nuclear DNA sequences. *Zool. Scrip.,* **38**: 9-22. https://doi.org/10.1111/j.1463-6409.2008.00355.x

Martin, T.E., 1988. On the advantage of being different: Nest predation and the coexistence of bird species. *Proc. natl. Acad. Sci. USA.,* **85**: 2196–2199. https://doi.org/10.1073/pnas.85.7.2196

Martin, T.E., 1993. Nest predation and nest sites: New perspectives on old patterns. *BioScience,* **43**: 523–532. https://doi.org/10.2307/1311947

Martin, P.R. and Martin, T.E., 2001. Behavioral interactions between two coexisting wood warblers (Parulidae:*Vermivora*): experimental and empirical tests. *Ecology,* **82**: 207–218. https://doi.org/10.1890/0012-9658(2001)082[0207:BIBCSS]2.0.CO;2

Mikami, O.K., Masanori, K. and Masakado, K., 2004. A new hypothesis for species coexistence: male–male repulsion promotes coexistence of competing species. *Pop. Ecol.,* **46**: 213-217. https://doi.org/10.1007/s10144-004-0189-5

Mikula, P., Hromada, M., Albrecht, T. and Tryjanowski, P., 2014. Nest site selection and breeding success in three Turdus thrush species coexisting in an urban environment. *Acta Ornithol.,* **49**: 83-92. https://doi.org/10.3161/000164514X682913

Pianka, E.R., 1981. Competition and niche theory. In: *Theoretical ecology: principles and applications* (eds. R.M. May), Blackwell, Oxford, UK, pp. 114–141

Sedláček, O., Fuchs, R. and Exnerová, A., 2004. Redstart

Phoenicurus phoenicurus and Black Redstart *P. ochruros* in a mosaic urban environment: neighbours or rivals? *J. Avian Biol.,* **35**: 336-343. https://doi.org/10.1111/j.0908-8857.2004.03017.x

Sommer, U. and Worm, B., 2002. *Ecological studies 161: Competition and coexistence*. Springer, Berlin. https://doi.org/10.1007/978-3-642-56166-5

Tokeshi, M., 1999. *Species coexistence: Ecological and evolutionary perspectives*. Blackwell Science, Oxford.

Wang, J., Jia, C.X., Tang, S.H., Fang, Y. and Sun, Y.H., 2011. Breeding biology of the snowy-cheeked laughingthrush *Garrulax sukatschewi*. *Wilson J. Ornithol.,* **123**: 146-150. https://doi.org/10.1676/10-052.1

Wang, J., Jia, C.X., Tang, S.H., Fang, Y. and Sun, Y.H., 2010. Breeding of the giant laughingthrush *Garrulax maximus* at Lianhuashan, Southern Gansu, China. *Wilson J. Ornithol.,* **122**: 388-391. https://doi.org/10.1676/09-057.1

Wellborn, G.A., 2002. Trade-off between competitive ability and antipredator adaptation in a freshwater amphipod species complex. *Ecology,* **83**: 129–136. https://doi.org/10.1890/0012-9658(2002)083[0129:TOBCAA]2.0.CO;2

Zeng, X.H. and Lu, X., 2009. Interspecific dominance and asymmetric competition with respect to nesting habitats between two Snowfinch species in a high-altitude extreme environment. *Ecol. Res.,* **24**: 607–616. https://doi.org/10.1007/s11284-008-0530-0

Zerba, E. and Morton, M.L., 1983. The rhythm of incubation from egg laying to hatching in mountain white-crowned sparrows. *Ornis Scand.,* **14**: 188–197. https://doi.org/10.2307/3676152