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Trophic niche partitioning between two Rock Nuthatches (*Sitta tephronota* & *Sitta neumayer*) in a contact zone in Iran

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Abstract

Two sympatric nuthatch species, *Sitta tephronota* and *S. neumayer*, provided the exemplar case of character displacement when the term was coined. The two species are quite similar morphologically but have diverged from one another in sympatry, presumably because of competition-driven selection favoring the partitioning of food resources. However, actual diet partitioning has never been shown. Here, we report the dietary composition of the two species by analyzing items recovered from the gastrointestinal tract. We found that *S. tephronata* fed predominantly on Coleopterans, Hemipterans and Orthopterans with the most important seed plants taken being *Amygdalus lycioides, Ficus carica* and Fabaceae, whereas, *S. neumayer* fed mainly on Coleopterans, Hemipterans and Lepidopteran, with *A. lycioides*, Fabaceae and *Tritium aestivum* as the most important plants taken. To determine whether the two species partition prey into different sizes, we examined two mostly abundant insect preys (Hemipterans and Coleopterans) and measured head length for Hemipterans and mandible size for Coleopterans as proxies for prey body size. We found a significant relationship between bird body size and prey size, as *S. tephronata*, which is larger, captured larger bugs and beetles. We also measured the ability of each species to crack seeds of different hardness, finding that *S. tephronata* takes larger and harder seeds than *S. neumayer*. Analyses of trophic niche breadth and overlap showed (1) that trophic niche breadth for *S. neumayer* was wider than that for *S. tephronata;* (2) overall trophic niche overlap was considerably high but (3) overlap in the size of the most frequently consumed insects was low, suggesting that the species may be partitioning resources by prey size. We conclude that the relative body size of consumed prey is an important axis of niche partitioning and may have driven character displacement in associated trophic traits, allowing the stable coexistence of the two species.

Introduction

The mechanisms that enable closely related, ecologically similar species to coexist remain a topic of intense study in community ecology (Atienzar, Belda & Barba, 2013). Theory has long held that stable coexistence of species within a community is possible only when the species do not overlap too strongly in the use of limited resources (Hutchinson, 1957; MacArthur & Levins, 1967; Wang, Zhang & Wang, 2005). This suggests that closely related species with similar ecological requirements should diverge from one another in morphological, ecological and physiological traits (Brown & Wilson, 1956; Grant, 1975). This phenomenon of divergence is called character displacement and may be most readily manifested in those morphological traits that are functionally relevant to divergence in resource use (Grant, 1975; Pfennig & Pfennig, 2012). Divergence consistent with competition-driven character displacement has been documented across many different systems (Brown & Wilson, 1956; Losos, 2000; reviewed in Schluter, 2000; Grant & Grant, 2002; Dayan & Simberloff, 2005; Grant & Grant, 2006, 2010; Pfennig & Pfennig, 2012; reviewed in Stuart & Losos, 2013; Stuart *et al.*, 2014; Tobias *et al.*, 2014). However, the evidence for the exemplar case of character displacement, the case that first described the phenomenon, remains incomplete. When Brown & Wilson (1956) coined the term, their first example was a pair of Rock Nuthatch species from the Zagros Mountains of Iran: *S. tephronota* and *S. neumayer* (Vaurie, 1950; Grant, 1975). The two species are nearly indistinguishable in allopatry, but have clearly diverged in body size and bill length in sympatry (Vaurie, 1950; Grant, 1975; see Table 1 for summary statistics), and authors have proposed that such divergence in morphology is due to adaptation to diet partitioning between the two species (Vaurie, 1950; Grant, 1975; see Table 1 for summary statistics). Although Grant (1975) showed that the species differ in the hardness and size of the seeds they ate, this data are not sufficient to explore the possibility of the differences in diet between both species in sympatric zone. Here, to redress this knowledge gap, we investigate trophic niche partitioning between the two nuthatch species.

Materials and methods

Study area

The easternmost range edge of *S. tephronota* reaches the Tien Shan Mountains in China, and the western edge lies in Iran. The westernmost distribution of *S. neumayer* is in Bosnia and Greece and the eastern end of its distribution is in Iran, creating a region of sympatry with *S. tephronata* in Iran's Zagros Mountains (Vaurie, 1950; Grant, 1975). The Zagros Mountains stretch 1400 km from Uremia Lake in northwest Iran to the Strait of Hormuz in southeast Iran (Darvishzadeh, 2003) (Fig. 1). The mountain range has a maximal width of 250 km and the highest peak is Mount Dena, 4409 m high (Darvishzadeh, 2003). This region has a Mediterranean climate with dry summers, receiving most of its rainfall in winter and spring (Darvishzadeh, 2003). Oak woodland (*Quercus* spp.) is the predominant floral community in the mountainous area.

Table 1 Mean ± SD and range of bill measurements in *S. tephronota* (n = 49) and *S. neumayer* (n = 32)

	S. tephronota		*S. neumayer*	
Variable	Mean (mm) ± SD	Range (mm)	Mean (mm) ± SD	Range (mm)
Bill Length (BL)	18.83 ± 1.12	16–20.9	15.52 ± 0.93	13.3–16.7
Bill Depth (BD)	6.08 ± 0.24	5.5–6.6	4.32 ± 0.22	4–4.9
Bill Width (BW)	5.89 ± 0.30	5.1–6.7	4.6 ± 0.26	4.1–5.2

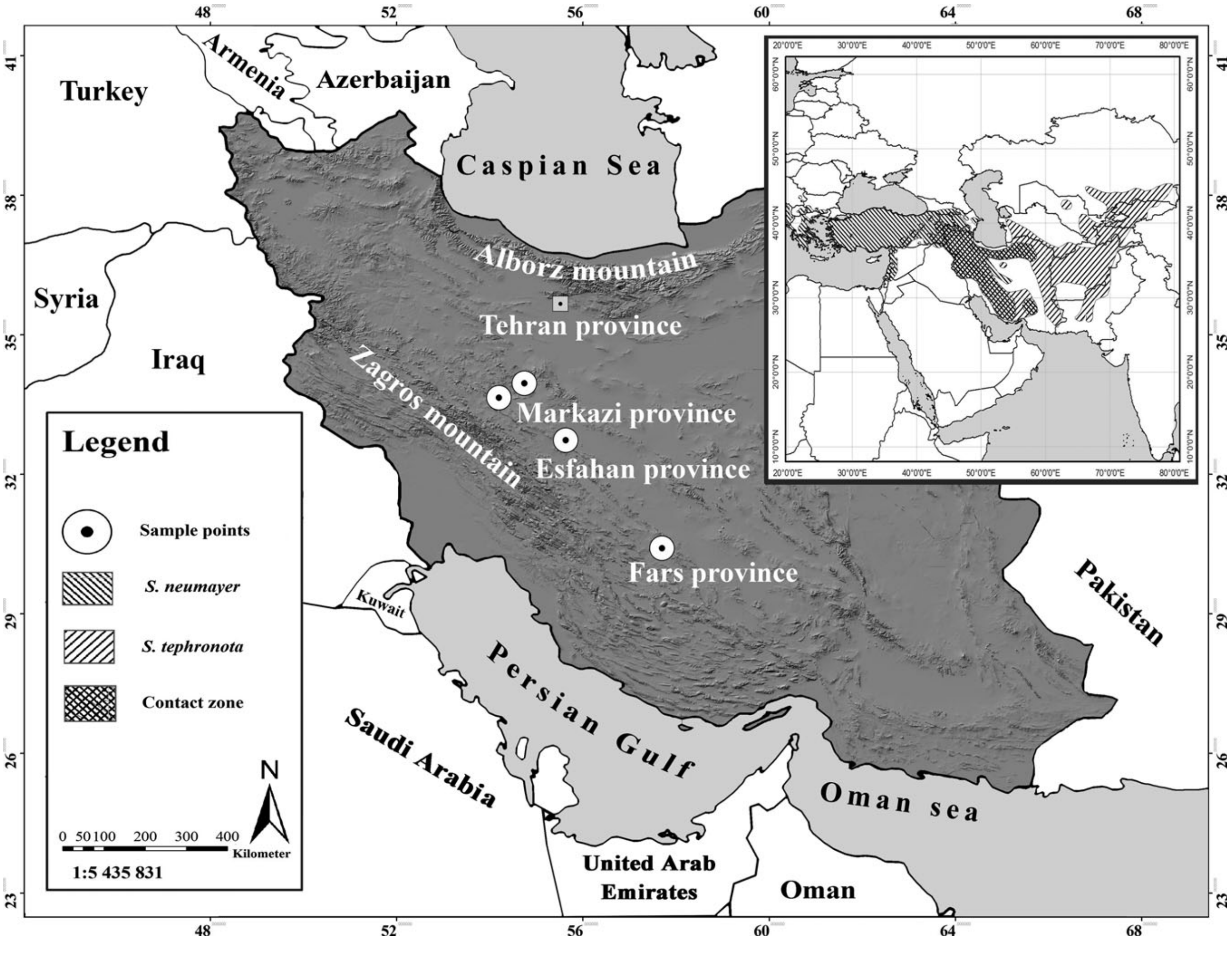

Figure 1 Sampling points of *S. tephronota* and *S. neumayer* in part of their sympatric zone along the Zagros Mountains, Iran.

In the sympatric zone, individuals of each species can be found together, and, with the possible exception of the Kerman region in southeastern Iran, the species are equally abundant (Vaurie, 1950). The foraging and nesting activities of both species are more or less restricted to the ground and surfaces of cliffs and rock faces, often in steep ravines (Grant, 1975).

Sampling period

Our sampling effort spanned May–July 2011 and May–July 2012 and focused on Zagros contact zone in the mountainous provinces of Markazi, Isfahan and Fars (Fig. 1). With permission from the Department of the Environment of Iran, we used a mist net to collect 81 specimens total: 49 *S. tephronota* (30 male, 19 female) and 32 *S. neumayer* (19 male, 13 female).

Analyses of gastrointestinal tract contents

From each specimen, we dissected the gastrointestinal tract, preserving it in 96% ethanol and then dissected out the contents. We identified plants and insects through a stereomicroscope (Magnification 6.3–400) using morphological identification keys (Bey-Bienko, 1954, 1964, 1967; Harza, 1975; Triplehorn & Johnson 2005). We calculated the following summary statistics for the gut contents: (1) percent frequency for each taxon (%f), where a particular prey category was expressed as the number of occurrences of the category, divided by total occurrences for all categories, multiplied by 100; (2) percent occurrence (%oc), defined as the number of occurrences of the particular prey category, divided by the total gastrointestinal tract samples, times 100; and (3) percent volume (%vol), where percent volume of a particular prey category was expressed as the volume of that prey category divided by the total volume of all prey, times 100 (following Andreas *et al.*, 2013). To that end, excess preservation fluid was initially removed with absorbent paper and then all the gut material belonging to a focal order was poured in a 10-mL cylindrical tube (graduated cylinder). Due to how small the stomach contents were, displacement per milliliter of water in the tube was recorded.

Percent frequency (%f) indicates the relative importance of the particular prey categories according to the frequencies in which they were consumed; percent occurrence (%oc) indicates the relative importance of the particular categories among the total gastrointestinal tract; percent volume (%vol) describes the proportion of the volume represented by each particular prey category in the set of gastrointestinal tract samples analyzed (Andreas, *et al.*, 2013).

Trophic niche breadth were estimated using Levin's index B (Levins, 1968; Krebs, 1999), from the proportion p_j of all prey categories in the diet (equation 1). To calculate the overlap either in food type or in prey size, we used Horns index R_0 (Krebs, 1999) (equation 2). Krebs (1999) suggests that the best measure of niche overlap is Morisita's index (Krebs, 1999) because it has nearly zero bias at all sample sizes and when there are a large number of taxa. However, Morisita's index requires that resources be expressed as a count of individuals. Because we do not have counts, we used the next best measure of overlap: Horn's index (Krebs, 1999).

$$B = \frac{1}{\Sigma p_j^2} \tag{1}$$

$$R_0 = \frac{\Sigma(p_{ij} + p_{ik}) \log(p_{ij} + p_{ik}) - \Sigma p_{ij} \log p_{ij} - \Sigma p_{ik} \log p_{ik}}{2 \log 2} \tag{2}$$

B ranges from 0 to n, where n is the number of prey categories, and large B reflects a large trophic niche breadth; p_j is the fraction of total diet items in category j. R_0 (equation 2) estimates niche overlap for species j and k, where p_{ij} is the fraction of the total diet taken up by resource i for species j, and p_{ik} is the same fraction for species k.

Measurement of head and mandibles of bugs (Hemiptera) and beetles (Coleoptera) as the most frequently prey in the diet of *S. tephronota* and *S. neumayer*

Morphological differences in bird beak shape and size between the two *Sitta* species (Grant, 1975; see Table 1 for summary statistics) suggest that they may partition prey resources by prey size.

Hemipteran bugs and Coleopteran beetles were the two prey categories with the highest percent frequency (%f) in the gut contents of both bird species. Thus, to determine whether the two species partition these prey into different size categories to facilitate coexistence, we measured the head length of bugs and the mandible lengths of beetles as proxies for body size (Gould, 1966; Eberhard *et al.*, 1998; Kawano, 2002; Pizzo *et al.*, 2006), using a stereomicroscope and Dino capture software.

We divided bugs in two size categories according to head length (Large Bugs >3 mm, Small Bugs <2 mm). Beetles were divided in two size categories according to the length of the mandibles (Large Mandibles >2 mm, Small Mandibles <1 mm). We chose these size bins because both the bug heads and beetle mandibles were bimodally distributed for size (Table 2). Among the maximum height, width and length of head, head length for bugs and length of the mandibles for beetles is a good proxy (Kawano, 2002).

Table 2 Mean ± SD and range of insects measurements (bugs and beetles) in *S. tephronota* (*n* = 49) and *S. neumayer* (*n* = 32)

	S. tephronota		*S. neumayer*	
Variable	Mean (mm) ± SD	Range (mm)	Mean (mm) ± SD	Range (mm)
Head length of bugs	3.41 ± 0.28	3.96–2.98	1.14 ± 0.44	1.35–1.01
Length of the mandibles	2.56 ± 0.22	2.95–2.24	1.22 ± 0.22	2.03–1.02

We also used Correspondence Analysis (CA) to test whether the two *Sitta* species differ in diet composition of Hemipterans and Coleopterans, the most abundant orders in gut contents.

Measurement of seed hardness

Both bird species eat seeds. They each carry a seed to flat but pitted rocks, place the seed in a pit, and use their bill to hammer the seed until it cracks open, thereby allowing the kernel to be extracted and consumed (Grant, 1975). Grant (1975) measured the dimension and hardness of cracked seed cases by both species in sympatric zone in Iran, Shiraz county. We wished to continue this work, determining whether the two species still partition seed resources by seed hardness and dimension, for comparison with Grant's findings. During field observations (6 months of direct observation in the Zagros Mountains sympatric zone across 2 years), we collected seeds specimens from the same plant species that we observed were cracked and eaten by both bird species. Then, we measured length, width and diameter of these seeds using digital calipers. We also measured the hardness of each seed species using a hardness-measuring machine [Metal Industry, Tehran, Iran; Universal test machine, Santam; Santam Machine Controller (v4.16)] (Fig. 2). We measured hardness by applying a gradually increasing force to the seeds until they cracked. This method is not strictly appropriate since a bird cracks a seed by delivering a blow to it with its bill, but it is likely sufficient for comparative purposes here. Because both species place seeds into pitted rocks and then hammer those seeds with their bills, we used a lever that mimics rock crevices (Fig. 2).

Results

Dietary composition

In both species, there is not sexual dimorphism in bill shape and we find no inter-sexual differences in dietary composition within each species. We note that in the gut contents of both species, some food items (e.g. insect eggs and plant fragments) could not be identified to taxon as they were largely digested. In addition, some gravel and a small amount of soil were found in the gut contents. We did not consider these to be food items. Both species breed from February to March, so they were done breeding by the time of our study. Thus, we do not have data regarding temporal variation in diet and diet overlap. We describe the diet of both species, which was composed of both insects and plants, in detail below.

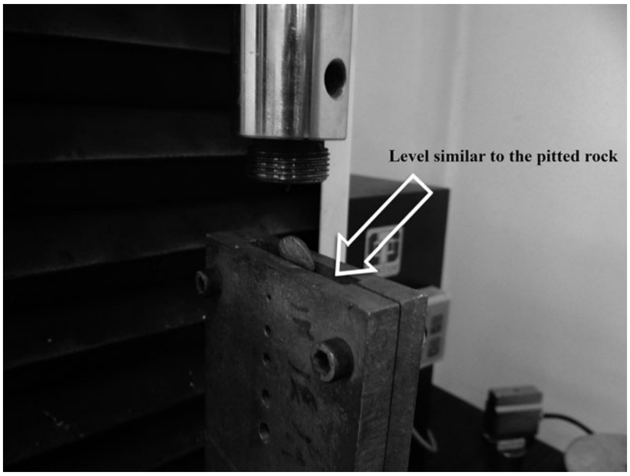

Figure 2 Hardness measurements, using our lab apparatus, of *A. scoparia* seeds that we observed were cracked by *S. tephronota* in the field.

S. tephronota (Eastern Rock Nuthatch)

Insects

In 49 gut samples for *S. tephronota*, we found that the prey consumed most often are Coleoptera (%f: 40.21, %oc: 75.51, %vol: 26.92), Hemiptera (%f: 25, %oc: 46.93, %vol: 37.17) and Orthoptera (%f: 16.30, %oc: 30.61, %vol: 15.38) (Fig. 3). Within the Coleoptera, the most frequently consumed prey were Carabidae (20%) and Curculionidae (20%). Within the Hemiptera the most frequently consumed prey (%f) were Scutelleridae (*Eurygaster integriceps,* 49.75%) and Pentatomidae (35.5%). For Orthoptera, the most frequently taken prey were Acrididae (28%) and Tettigoniidae (8%).

Plants

The most frequent seeds eaten by *S. tephronota* are *A. lycioides* (%f: 64.57, %oc: 51.02, %vol: 46.15), *F. carica* (%f: 10.81, % oc: 8.16, %vol: 19.23%) and Fabaceae (%f: 10.81, % oc: 8.16, %vol: 3.84) (Fig. 4).

S. neumayer (Rock Nuthatch)

Insects

In 32 gut samples for *S. neumayer,* the most frequent prey were Hemiptera (%f: 34.78, %oc: 50, %vol: 42.10), Coleoptera (%f: 30.43, %oc: 43.75, %vol: 26.31) and Diptera (% f: 17.39, %oc: 25, %vol: 18.42) (Fig. 3).

Plants

The most frequent plants in *S. neumayer* are *A. lycioides* (%f: 47.36, %oc: 28.12, %vol: 54.54) Fabaceae (%f: 26.31, % oc:15.62, %vol: 9.09) and *T. aestivum* (%f: 15.78, %oc: 9.37, %vol: 18.18) (Fig. 4).

Size differences in insect prey taken by the two *Sitta* species

The most obvious differences in diet composition between the *Sitta* species was in the body sizes of bug and beetle prey (Fig. 5). Since the prey size data were not normally distributed, we used a non-parametric test, the Mann–Whitney *U*-test, to test the null hypothesis that there is not a difference in the size of insect prey taken by both species. The Mann–Whitney *U*-test showed significant differences between bird species in bug head

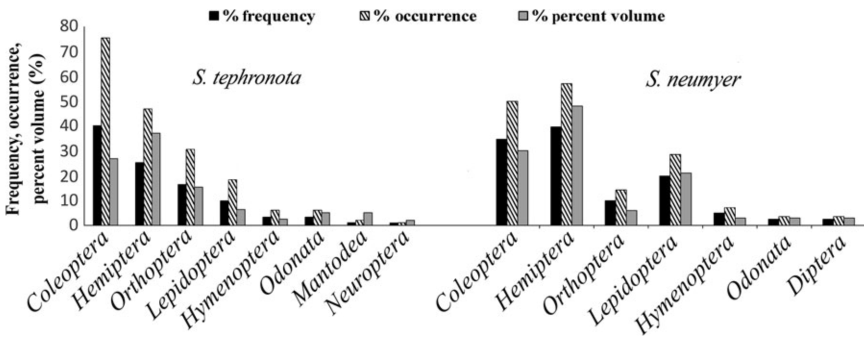

Figure 3 Insect family composition in the guts of *S. tephronata* and *S. neumayer* (n = 49, n = 32).

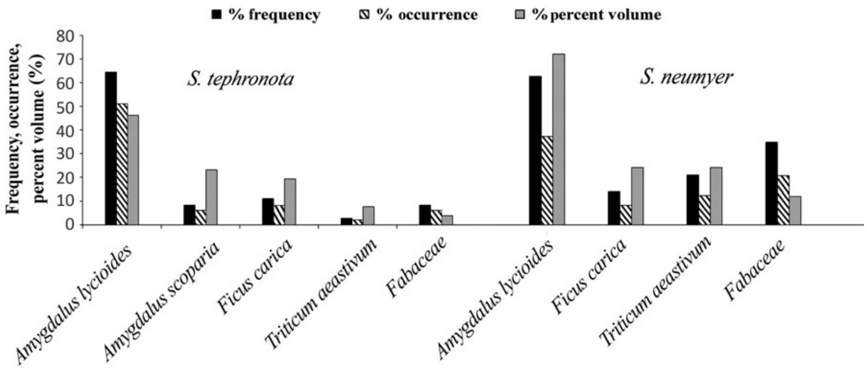

Figure 4 Plants compositions in the guts of in *S. tephronata* and *S. neumayer* (n = 49, n = 32). Figure 4. Plants compositions in the guts of in *S. tephronata* and *S. neumayer* (n = 49, n = 32).

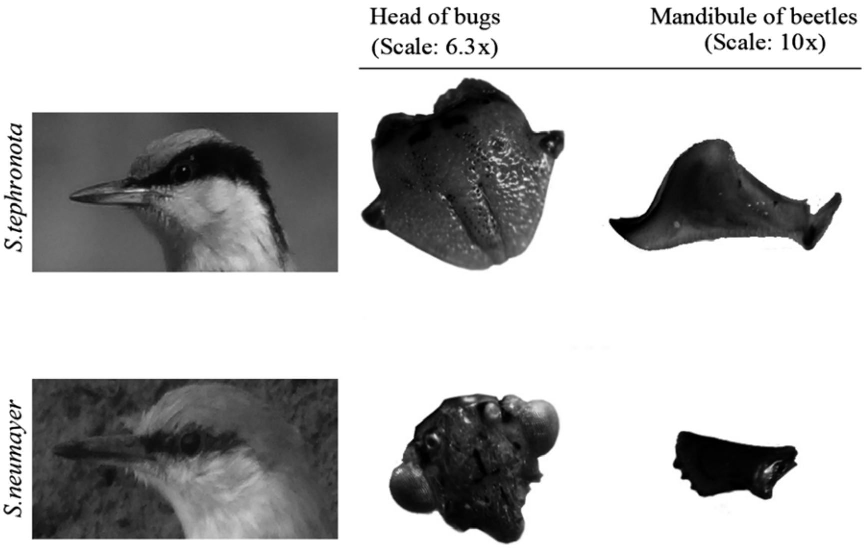

Figure 5 Representative bug heads and beetle mandibles in the diet of *S. tephronota* and *S. neumayer* in the Zagros Mountains. For each prey type, images are to scale, and represent the mean size for that prey.

length (N = 38, Mann–Whitney U-test = 610, P-value < 0.01) and beetle mandible length (N = 30, Mann–Whitney U-test = 829, P-value < 0.02). *S. tephronota* took small Hemipterans and Coleopterans rarely (Hemiptera head length <2 mm, %f: 11.26; Coleoptera mandible length <1 mm, %f: 15.78), focusing instead on larger Hemiptera and Coleoptera

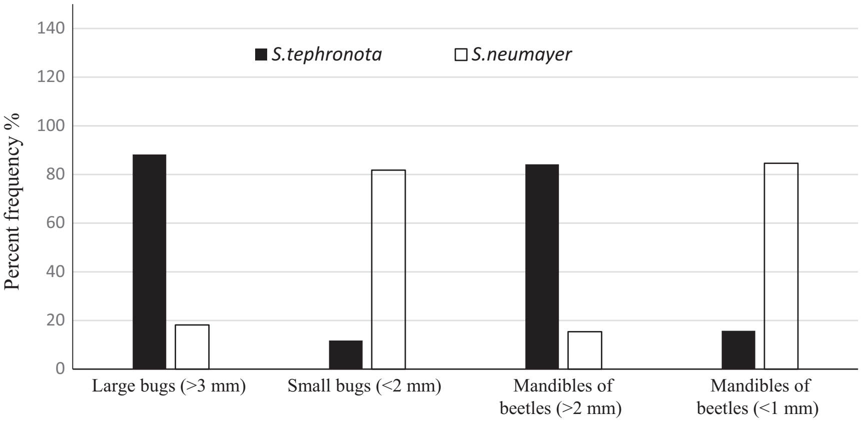

Figure 6 Percent frequency of Hemiptera with long and short heads and Coleopteras with large and small mandibles in the diet of *S. tephronota* and *S. neumayer*. These traits are proxies for insect body size.

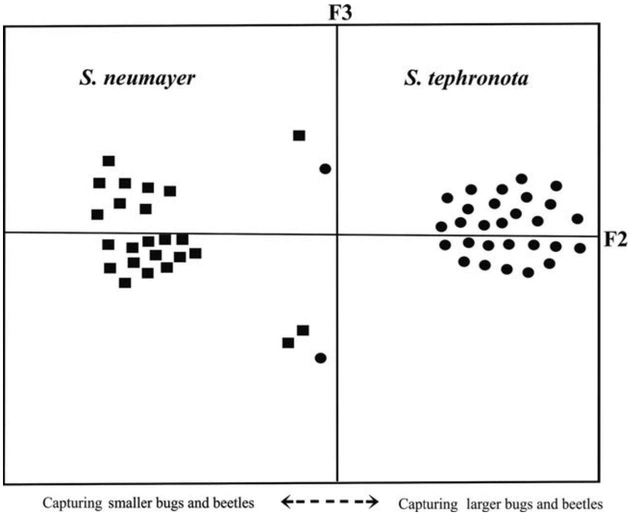

Figure 7 Distribution of the *S. neumayer* (square points) and *S. tephronota* (circle points) according to prey size eaten (bugs and beetles) [second (F2) and third (F3) axes of Correspondence Analysis (CA) of the measurement insect's matrix].

(Hemiptera head length >3 mm, %f: 88.23; Coleoptera mandible length >2 mm, %f: 84.21) (Fig. 6).

In contrast, *S. neumayer* took fewer larger Hemiptera and Coleopteran (Hemiptera head length >3 mm, %f: 18.18; Coleoptera mandibles length >2 mm, %f: 15.38), taking smaller Hemiptera and Coleoptera instead (Hemiptera head length <2 mm, %f: 81.88; Coleoptera mandibles length <1 mm, %f: 84.61) (Fig. 6).

Correspondence Analysis (CA) of the head size and mandible length for Hempiterans and Coleopterans (two most abundant insects in diet of both species) indicated that the first three axes accounted for 88% of variance. The results of ordination revealed a clear separation in size of insects preferred by the two species. *S. neumayer* mostly consumed small insects, whereas *S. tephronota* mostly ate large insects.

Table 3 Trophic niche breath expressed as Levin's index. Result computed from percent frequency (%f), percent volume (%vol) and percent occurrence (%oc)

	%f	%vol	%oc
S. tephronota	0.372	0.517	0.384
S. neumayer	0.585	0.509	0.543

Trophic niche overlap and niche breadth

Trophic niche breadth, calculated using Levin's niche breadth index B, for %f, %vol and %oc, respectively, are reported in Table 3. Trophic niche breadth for *S. neumayer* was broader than that for *S. tephronata* (Table 3), resulting in a trophic niche overlap value for the two species (Horns index R_0), that was considerably high (Table 4). However, overlap in the size of the most frequently consumed prey, Coleopterans and Hemipterans was low (Table 4).

Seed hardness of seeds typical in the *S. tephronota* and *S. neumayer* diets

The hardness of seeds cracked and eaten by birds (mean of multiple seeds per plant (three seeds per plant), multiple plant species; Table 5) in the field was significantly different across bird species (P-value < 0.02, Mann–Whitney U-test = 6, N = 10). Seeds exploited by *S. tephronota* were also larger than those exploited by *S. neumayer* (P-value < 0.01, Mann–Whitney U-test = 12, N = 10) (Table 5).

Discussion

High niche overlap in insect prey composition but low niche overlap in insect prey size

One likely axis of niche partitioning between the two *Sitta* species may be food resources, as this axis has been suggested

Table 4 Trophic niche overlap of diet composition (expressed as Horn's index) based on percent frequency (%f) and percent volume (%vol) and percent occurrence (%oc) and trophic niche overlaps expressed as Horn's index (values reported in brackets), for %f, sub-setting the prey data to only the prey taken most frequently: Hemiptera and Coleoptera

	S. tephronota			*S. neumayer*		
	%f	%vol	%oc	%f	%vol	%oc
S. neumayer	0.775 (0.420)	0.779	0.936	–	–	–
S. tephronota	–	–	–	0.775 (0.420)	0.779	0.936

Table 5 Measurements of seed cases cracked by *S. tephronota and S.neumayer* and seed hardness, measured as the force required to crack a seed

	N	Kgf	Length $\bar{X}$ ± SD (Range)	Width $\bar{X}$ ± SD (Range)	Depth $\bar{X}$ ± SD (Range)
Sitta tephronota					
Amygdalus lycioides	11	14.03	15.20 ± 0.02 (14.86–15)	10.13 ± 0.21 (9.66–10.50)	6.22 ± 0.18 (5.90–7.59)
A. scoparia	6	22.86	17.90 ± 0.41 (16.80–18.82)	10.26 ± 0.32 (9.67–10.50)	7.71 ± 0.10 (7.46–7.79)
A. commonis	3	26.40	24.40 ± 0.14 (23.80–24.80)	16.48 ± 0.43 (15.92–16.95)	10.99 ± 0.20 (10.93–11.31)
Juglans regia	3	21.32	31.30 ± 0.71 (30.26–32.08)	26.85 ± 0.82 (25.95–28.02)	26.27 ± 0.14 (25.57–26.88)
Celtis cacusica	3	17.31	8.53 ± 0.08 (8.46–8.65)	8.10 ± 0.28 (7.73–8.42)	7.59 ± 0.27 (7.58–8.24)
Prunus armeniaca	3	19.70	23.67 ± 0.08 (23.57–23.77)	17.62 ± 0.61 (16.77–18.17)	11.52 ± 0.90 (10.57–12.74)
P. persica	2	122.27	29.59 ± 1.33 (28.26–30.93)	25.53 ± 1.09 (26.63–24.44)	20.95 ± 0.83 (20.06–21.85)
Sitta neumayer					
A. lycioids	3	13.74	14.57 ± 0.51 (14.12–15.30)	9.50 ± 0.24 (9.30–9.85)	6.24 ± 0.04 (6.18–6.29)
Prunus sp.	2	10.85	12.65 ± 0.45 (12.20–13.10)	10.87 ± 0.57 (10.30–11.44)	6.62 ± 0.01 (6.52–6.73)
Gundelia tournefortii	3	10.20	7.65 ± 0.07 (8.20–7.01)	7.31 ± 0.14 (7.80–6.80)	6.85 ± 0.23 (7.40–6.30)

Kgf, kilogram force.

to be the most important axis for coexistence in many cases (e.g. Grant, 1999; Sebastiano *et al.*, 2012), and difference in prey size is an important factor in trophic niche partitioning in closely related sympatric species (Freeman & Lemen, 2007; Andreas *et al.*, 2013). We found that the trophic niche breadth of *S. neumayer* was wider than that for *S. tephronata* and that the two nuthatch species do overlap strongly in prey composition, which would suggest that they do not partition resources. However, we did find considerable prey partitioning when we considered prey size instead; the larger *S. tephronota* used larger prey items, whereas the smaller *S. neumayer* used smaller prey items. This is consistent with other findings, in which prey size tends to be directly proportional to predator size, and larger predators take large preys (van der Meij & Bout, 2004; Herrel *et al.*, 2005). Our results are consistent with a character displacement hypothesis, which is further supported by morphological results found by Grant (1975). Those studies found body size divergence in the same direction as prey size divergence: *S. tephronota* is significantly larger, which may be adaptive for the observed capturing and feeding of larger prey in this study.

High niche overlap in consumed plants, but partitioning in seed dimension and hardness

Both bird species fed on similar plant species (Figs 3 and 4), so trophic niche overlap was high. However, the dimension and hardness of seeds taken were significantly different between the two species (Table 5), suggesting that the two species may also partition seed resources.

The ratios of bill depth/bill length as well as bill width/bill length significantly differ between the two species (Grant, 1975, an outcome commonly observed in co-occurring, closely related bird species. As suggested above, beak size and shape divergence may facilitate partitioning of food resources according to food size (Schluter, 2000; Okuzaki, Takami & Sota, 2010). In *S. tephronota*, the bill is considerably thicker and longer than that of *S. neumayer*. Larger bills correspond to stronger bite force (Cornwallis, 1975; van der Meij & Bout, 2004, 2006; Herrel, *et al.*, 2005; Measey *et al.*, 2011), so a larger bill may allow *S. tephronota* to crack harder seeds and capture larger insects compared to *S. neumayer*, which is consistent with our data (Table 5).

Conclusion

Resource partitioning to reduce competition between sympatric congener species can occur along the axes of space, diet, and time (Lu, Gong & Ma, 2011; De Leon *et al.*, 2014). The two nuthatches in this study are found in the same habitats in their contact zone in Zagros Mountains, where they both feed on similar insect and plant foods. Their niche overlap in dietary composition (insects and plant materials) is high, but the two species exploit food items in different sizes and hardness, which correlates well with their substantial differences in bill dimensions and body size (Grant, 1975). While it has long been thought that divergence in body size and beak traits enables the two species to coexist (Grant, 1975), this is the first evidence suggesting that the two species do indeed feed on different insect prey sizes, perhaps reducing competition (Grant & Grant, 2006; Atienzar *et al.*, 2013). Our findings are consistent with character displacement and provide new data supporting the exemplar case of character displacement.

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