

# Coping with extremes: convergences of habitat use, territoriality, and diet in summer but divergences in winter between two sympatric snow finches on the Qinghai-Tibet Plateau

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## Abstract

On the Qinghai-Tibet Plateau, extreme environmental conditions have imposed intense selective pressure on the evolution of phenotypic traits of wild animals. To date, limited information is available on behavioral and ecological traits concerning niche differentiation among sympatric animals on the Qinghai-Tibet Plateau, especially during winter when the environments are most severe. Here, we studied the seasonal variations in habitat occurrence, territorial behavior, and diet in two sympatric snow finches (the white-rumped snow finch, *Onychostruthus taczanowskii*, WRSF; and the rufous-necked snow finch, *Pyrgilauda ruficollis*, RNSF) to determine convergence and divergence of ecological traits in such severe climatic conditions. Our results showed that: (i) WRSF occupied rural areas as a dominant species throughout the annual cycle while RNSF occupied the rural areas in summer and then shifted to human-occupied areas in winter and spring; (ii) WRSFs exhibited robust aggressive behavior and territoriality during winter relative to RNSFs; (iii) the diets of both species varied with the season but did not vary between species except that WRSF ate significantly more seeds but RNSF consumed more starchy material derived from human food waste during winter. Therefore, the separations in the spatial niche and territoriality between WRSF and RNSF, especially in winter, may contribute to alleviating the pressure of interspecific competition, and promoting the coexistence of the two sympatric snow finches in the extreme environments on the Qinghai-Tibet Plateau.

**Key words:** diet, habitat use, Qinghai-Tibet Plateau, snow finch, territorial behavior

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[Correction added on 14 August 2020, after first online publication: The orientation of Figure 3 has been changed from landscape to portrait.]

## INTRODUCTION

Extreme climatic conditions impose intense selective pressures on the genotypic and phenotypic evolution of animals (Møller 2011; Wingfield *et al.* 2011, 2017; Qu *et al.* 2013; Bailey & Van 2016; Natarajan *et al.* 2016; Van *et al.* 2017; Zhu *et al.* 2018; Delgado *et al.* 2019; Hao *et al.* 2019). Some phenotypic traits are highly flexible such as seasonal variations in behavioral ecology involved in intraspecific or interspecific competition (Sih *et al.* 2004). However, others are conserved such as hematological features (Bijlsma & Loeschcke 2005). How animals express optimal ecological and behavioral strategies to maximize fitness and respond to the seasonality of extreme environmental conditions is not well understood. Furthermore, how closely related animals that have co-evolved sympatrically in habitats with extreme environmental conditions express the divergent or convergent traits of territorial behavior, habitat use, and diet, in relation to competitive adjustments and/or niche differentiation (Li *et al.* 2008, 2012; Lu *et al.* 2009, 2011a; Zeng & Lu 2009b; Brambilla *et al.* 2018, 2019) remain largely unexplored. Answers to these questions are critical goals to uncover the optimal ecological and evolutionary strategy of animals in extreme environmental conditions.

Predictions from classical ecological theory suggest that closely related sympatric species in adaptive radiations should exhibit great phenotypic divergence, and thus low niche overlap (Rundell & Price 2009; Tobias *et al.* 2013; Deleón *et al.* 2014). Nonetheless, closely related species may also face significant and contrasting challenges such as the intensity of interspecific competition due to several shared traits through common ancestry (Schluter 2000; Laiolo 2017). Spatiotemporal variations in niches, along with the changes in resource availability, should be a crucial ecological strategy to alleviate competition, and then to maintain local or regional coexistence for closely related species (Zeng & Lu 2009b; Lu *et al.* 2011a; Deleón *et al.* 2014). For example, four sympatric Darwin's ground finch species in the Galapagos islands prefer to use overlapping resources under benign conditions (in time and space), but then revert to resources for which their morphologies for foraging are best adapted during periods of food limitation (Deleón *et al.* 2014).

The interspecific relationships between closely related, co-occurring species may vary with the life-history stage. Therefore, the mechanisms of coexistence detected only in one stage may be insufficient for understanding the potential mechanisms for coexistence in others (Moll & Brown 2008). For the majority of bird species, the

perturbation resistance potential (PRP, a measure of how well prepared an individual is to cope with perturbations of the environment superimposed on demands of the predictable, or seasonal changes in environment; Wingfield *et al.* 2017) is decreased in winter relative to summer because of the low cumulative energetic resources and reserves (Dubowy 1988; Wingfield *et al.* 2017). In particular, such resource limitations in winter from extreme environmental conditions would, in turn, intensify the energetic costs of interspecific and intraspecific competition.

The Qinghai-Tibet Plateau has the typical features of extreme environmental conditions, for example, hypobaric hypoxia, low ambient temperature, high winds, intense ultraviolet radiation (Thompson *et al.* 2000; Richardson *et al.* 2003; Wang *et al.* 2008), and dramatic seasonal fluctuation of gross primary production (Kato *et al.* 2004). Therefore, the Qinghai-Tibet Plateau provides fewer available resources for organisms, especially in winter, and leads to stronger interspecific and intraspecific competition for species with similar ecological requirements (Lu *et al.* 2011a). In the last three decades, many aspects of avian phenotypic traits have been determined, including flying performance and related morphology (Sun *et al.* 2016), standard metabolic rate (Deng & Zhang 1990), acute stress response (Li *et al.* 2008, 2012, 2020), and reproductive ecology on the Qinghai-Tibet Plateau in spring and summer (Lu *et al.* 2009, 2011a,b,c; Zeng & Lu 2009b; Tang *et al.* 2017; Wang & Lu 2018). These studies suggested that bird species underwent significant phenotypic changes in morphology, physiology, and behavior under the selection pressure of extreme environmental conditions of the Qinghai-Tibet Plateau. However, to date, no studies have been carried out, nor are any data available on niche differentiation such as habitat use, territoriality, and diet for these birds during the severe environmental conditions of winter. This is especially relevant to corresponding convergent and divergent traits between closely related and sympatric species.

The snow finch complex (Passeridae: *Montifringilla*, *Pyrgilauda*, and *Onychostruthus*) is native to the Qinghai-Tibet Plateau and surrounding areas occupying the elevational range from 2300 up to 5300 m (del Hoyo *et al.* 2017). The snow finches evolved approximately 2–2.25 million years ago as a result of environmental change during the Qinghai-Tibet Plateau uplift (Qu *et al.* 2006). Most of the snow finch taxa in the narrow niche of the Qinghai-Tibet Plateau are separated either by altitude or habitat differences (Fu *et al.* 1998; Lu *et al.* 2009). Only two species are distributed almost sympatrically year-round,

the white-rumped snow finch, *O. taczanowskii* (WRSF), and the rufous-necked snow finch, *Pyrgilauda ruficollis* (RNSF), (Zhang 1982; Lu *et al.* 2009). Both the WRSF and RNSF are ground-nesting species and have similar breeding phenology and reproductive biology (Arthur *et al.* 2008; Lu *et al.* 2009; del Hoyo *et al.* 2017), and similar acute stress responses during winter relative to other seasons (Li *et al.* 2020). In summer, relatively large interspecific differentiation in morphological and behavioral traits between the species is believed to promote their co-occurrence. For example, WRSFs have larger body sizes and are behaviorally dominant with resource-rich territories relative to RNSFs, while small-sized RNSFs shift to those suboptimal territories with less resources (Arthur *et al.* 2008; Lu *et al.* 2009; Zeng & Lu 2009a).

Here, we aimed to determine the features of individual territoriality, diet, and habitat use in WRSF and RNSF across an annual cycle, and we further explored the coexistence mechanisms of the two species under the extreme environmental conditions of the Qinghai-Tibet Plateau. We expected that the two sympatric species would exhibit the convergence in ecological features (i.e. territoriality, diet, and habitat use) and thus restrict niche overlap as adaptations to the seasonality of extreme environmental conditions. Specifically, (i) the larger species, WRSF would express intense territorial activity and more aggressive behavior throughout the annual cycle relative to RNSF, the smaller species; (ii) spatio-temporal niche differentiation between WRSF and RNSF is associated with habitat and food availability driven by strong selective pressures of interspecific competition in such harsh environments, especially in winter; (iii) both WRSF and RNSF would express shared behavior and diet in summer, stemming from common ancestry, when resources are more abundant in the annual cycle.

## MATERIALS AND METHODS

### Animals and study locations

Free-living adult WRSFs and RNSFs were studied at Qinghai Lake (37°02.216'N 99°44.293'E, Elevation, 3215 m), Wenquan (35°24.258'N 99°25.876'E, Elevation, 3946 m), and Huashixia (35°06.345'N 98°51.390'E, Elevation, 4106 m), Qinghai Province, China. Samples were collected in the spring (April 17 to May 25; the early breeding stage), summer (July 2 to August 26; the late breeding and the pre-basic molt stages), and winter seasons (January 23 to February 10; the wintering stage) of 2008.

### Animal sampling

All birds were captured opportunistically using mist nets. To reduce possible variation in diet due to daily biological rhythms, all the birds in winter and spring (short day-length), and summer (long day-length) were sampled from 0800 to 1300 hours and 0700 to 1200 hours, respectively. After capture, birds were transferred into a wireframe cage for territorial and social behavior observations. Birds sampled for stomach collection were immediately humanely euthanized with isoflurane inhalation followed by decapitation (spring: WRSF,  $n = 8$ ; RNSF,  $n = 15$ ; summer: WRSF,  $n = 7$ ; RNSF,  $n = 7$ ; winter: WRSF,  $n = 11$ ; RNSF,  $n = 17$ ). Stomachs (ventriculus) were placed on aluminum foil and frozen in liquid nitrogen until they could be moved to a  $-80^{\circ}\text{C}$  storage freezer.

### Territoriality and social behavior

Territoriality and sociality were assessed through both individual counts from January 23 to August 9 in 2008 from either human-occupied sites or rural areas. Human-occupied sites were categorized as any collecting location within 50 meters of a paved roadway with more than one building, and rural sites were categorized as those areas with no roadway and no single building within 50 meters. We considered those birds that occurred within 50 meters of anthropogenic environments as human commensalism. For territoriality and sociality, simulated territorial intrusion (STI) (Mukai *et al.* 2009) experiments were conducted at Qinghai Lake and Wenquan during winter (March 5 to 24, 2008). Previous studies showed that many avian species also exhibited territorial behavior in non-breeding periods, such as in winter (Wingfield 1994; Pinxten *et al.* 2000; Hau *et al.* 2004). In brief, an individual WRSF or RNSF was captured off-site and transported to the STI location in a wireframe cage (30 cm  $\times$  30 cm  $\times$  25 cm). The cage was then placed on the ground in the center of the caged bird's territory, in a clearly visible and unobstructed position. Behavioral responses from surrounding conspecific individuals were recorded by the same observer for the following 10 min focusing on latency to approach within 5 m of the cage, time spent within 5 m of the cage, and the number of contact with the cage (WRSFs in rural areas:  $n = 10$ ; RNSF:  $n = 20$ , including 14 tests in urban areas and 6 tests in rural areas). The shorter distance of closest approach, shorter response latency, more time spent in 5 m of the cage, and more physical contacts with the cage indicated a species with a robust aggressive behavior (Mukai *et al.* 2009).

In addition, we also attempted to census the number of individuals from both the target species (conspecific) and non-target species (heterospecific, including any other bird species that happened to be present) within 10 m of the center of the observational area (based on those observations of human-occupied sites that were randomly selected). The number of observations in different seasons were: spring: WRSF,  $n = 15$ ; RNSF,  $n = 20$ ; summer: WRSF,  $n = 9$ ; RNSF,  $n = 8$ ; winter: WRSF,  $n = 13$ ; RNSF,  $n = 19$ . Because WRSFs have been reported to exclude heterospecific songbirds from their territory, we noted territorial encounters (i.e. physical attack, face-offs, and jump-flight, etc., measures for interspecific and intraspecific competition; Gochfeld 1979).

## Diet

Stomachs were dissected, and contents were assayed under light microscopy. Contents were classified by an overall count of individual items found in the stomach itemized as seeds, grass, starchy, insects, or grit (to aid digestion of hard seed and insect material). The starchy material included a variety of amorphous starchy masses, many of which were likely the partially digested remains of anthropogenically sourced food items (bread, rice, processed food items, etc.) at human-occupied sites. Starchy masses were discrete conglomerations of unidentifiable matter. No starchy mass was larger than 5 mm in diameter, and we did not count or include diffuse masses of non-distinct material. The counts of stomach content for each individual were transformed into percentages for further analysis.

## Statistical analysis

We used the Chi-square test to determine whether the occurrence (rural or human-occupied habitat) differed between the number of observations of WRSF and RNSF in a certain season. We examined the seasonal differences of territoriality (conspecific and heterospecific counts), contents in the stomach (seeds, grass, starchy material, insects, and grit) in WRSF or RNSF using Kruskal–Wallis one-way analysis of variance (ANOVA), and species differences of these variables in a certain season using a Mann–Whitney  $U$  test. We examined the effects of STI (the distance of the closest approach, latency to approach, the time within 5 m, and times of contact with the cage) between species in winter using independent sample  $t$ -tests. Differences between pairs of means were identified by Bonferroni-adjusted post hoc tests based on model-

predicted estimated marginal means. Effect sizes were estimated using *Cohen's d* for Chi-square and  $U$  tests and partial omega-squared ( $\omega^2$ ) for ANOVA to measure the strength of statistically significant differences between groups (Elis 2010). All tests were performed using SPSS Statistics 21.0 software (IBM, New York, USA). Differences were considered significant at  $P < 0.05$ . All data are presented as means  $\pm$  SEM.

## RESULTS

### Comparisons of habitat occupation across seasons and between species

In summer, both the WRSFs and RNSFs occurred in rural areas. In winter and spring, RNSFs exhibited behavior shifts toward human-occupied areas, whereas WRSFs remained in the rural areas (Table 1).

### Comparisons of territoriality across seasons and between species

Both WRSFs and RNSFs exhibited significant seasonal variations in conspecific counts (Table 2). Post hoc tests showed that both species had less conspecific counts in winter relative to those during spring (WRSF:  $P < 0.001$ ; RNSF:  $P < 0.001$ ), and RNSFs had less conspecific counts in summer than those during spring ( $P < 0.001$ ; Fig. 1a). RNSFs exhibited a significant seasonal variation in heterospecific counts but WRSFs did not (Table 2). Post hoc tests showed that RNSFs had more heterospecific counts in winter relative to those during spring ( $P = 0.005$ ) and summer periods ( $P < 0.001$ ; Fig. 1b).

In winter and spring, RNSFs had significantly more conspecific and heterospecific counts compared with WRSFs (Table 2; Fig. 1). In winter, social behavior of WRSFs showed significantly robust conspecific aggressive responses such as showing smaller distance of closest approach ( $t_{1,18} = 5.523$ ,  $P < 0.001$ ; Fig. 2a), shorter response latency ( $t_{1,18} = 9.643$ ,  $P < 0.001$ ; Fig. 2b), more time spent in 5 m ( $t_{1,9.5} = -7.726$ ,  $P < 0.001$ ; Fig. 2c), and more physical contacts with the cage ( $t_{1,9.0} = -3.207$ ,  $P = 0.011$ ; Fig. 2d) to STIs with decoys compared to RNSFs.

### Comparisons of diet across seasons and between species

Among all types of stomach contents, insects and grit were found in both species, and seeds in WRSFs and grass

**Table 1** The season-dependent occurrence (in rural or human-occupied habitat) of the white-rumped snow finch (*Onychostruthus taczanowskii*, WRSF) and the rufous-necked snow finch (*Pyrgilauda ruficollis*, RNSF) during spring, summer, and winter (*n* represents the number of observations) and statistical results of Chi-square tests are given on the right of the table

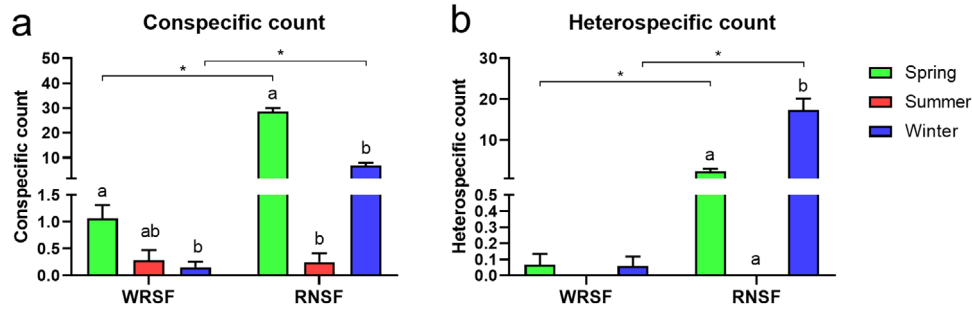
Season	WRSF			RNSF			$\chi^2$	<i>P</i> value	<i>Cohen's d</i>
	<i>n</i>	Urban (%)	Rural (%)	<i>N</i>	Urban (%)	Rural (%)			
Spring	15	0	100	20	95	5	31.172	<b>&lt;0.001</b>	<b>5.707</b>
Summer	10	0	100	8	0	100	n.a.		
Winter	13	0	100	20	80	20	19.319	<b>&lt;0.001</b>	<b>2.377</b>

*Cohen's d* is a measure of effect size. Significant factors (*P* < 0.05) and large size effects (*Cohen's d* > 0.8) are shown in bold type.

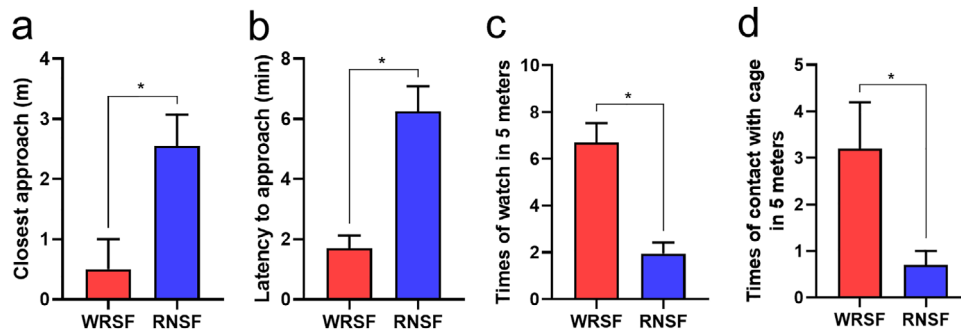
**Table 2** Comparisons of territoriality (conspecific and heterospecific counts) and diet (seeds, grass, starchy material, insects, and grit in the stomach) in the white-rumped snow finch (*Onychostruthus taczanowskii*, WRSF) and the rufous-necked snow finch (*Pyrgilauda ruficollis*, RNSF) among different seasons by Kruskal–Wallis ANOVA, and comparisons of those variables between species in a certain season by Mann–Whitney *U* test are given to the right of the table

Type of variable	Response variable	Species	df	$\chi^2$	<i>P</i> value	$\omega^2$	Season	df	<i>Z</i> value	<i>P</i> value	<i>Cohen's d</i>
Territoriality	<b>Conspecific count</b>	WRSF	2,32	9.503	<b>0.009</b>	<b>0.279</b>	Spring	1,33	−5.027	<b>&lt;0.001</b>	<b>5.349</b>
		RNSF	2,44	34.828	<b>&lt;0.001</b>	<b>0.825</b>	Summer	1,15	0.151	1.000	0.303
							Winter	1,30	−4.058	<b>&lt;0.001</b>	<b>1.741</b>
	<b>Heterospecific count</b>	WRSF	2,39	0.651	0.722	−0.018	Spring	1,34	−2.779	<b>0.025</b>	<b>1.123</b>
		RNSF	2,48	22.186	<b>&lt;0.001</b>	<b>0.456</b>	Summer	1,20	0.001	1.000	N.A.
							Winter	1,33	−4.248	<b>&lt;0.001</b>	<b>1.780</b>
Diet	<b>Seeds in stomach</b>	WRSF	2,22	9.565	<b>0.008</b>	<b>0.317</b>	Spring	1,19	0.443	0.697	−0.320
		RNSF	2,32	4.77	0.092	<b>0.086</b>	Summer	1,11	−1.286	0.234	<b>0.666</b>
							Winter	1,24	2.437	<b>0.015</b>	<b>−0.958</b>
	<b>Grass in stomach</b>	WRSF	2,23	0.606	0.739	−0.002	Spring	1,21	1.660	0.294	0.193
		RNSF	2,36	12.722	<b>0.002</b>	<b>0.128</b>	Summer	1,12	1.000	0.710	<b>−0.535</b>
							Winter	1,26	−1.508	0.175	0.459
	<b>Insects in stomach</b>	WRSF	2,23	20.563	<b>&lt;0.001</b>	<b>0.738</b>	Spring	1,21	−0.855	0.466	<b>0.628</b>
		RNSF	2,36	20.994	<b>&lt;0.001</b>	<b>0.382</b>	Summer	1,12	1.214	0.259	<b>−0.691</b>
							Winter	1,26	−0.804	0.817	N.A.
	<b>Starchy material in stomach</b>	WRSF	2,23	2.811	0.245	−0.009	Spring	1,21	−0.209	0.875	0.339
		RNSF	2,36	8.78	<b>0.012</b>	<b>0.096</b>	Summer	1,12	−0.105	1.000	0.389
							Winter	1,26	−2.305	<b>0.025</b>	<b>0.706</b>
	<b>Grit in stomach</b>	WRSF	2,23	14.837	<b>0.001</b>	<b>0.761</b>	Spring	1,21	3.422	<b>&lt;0.001</b>	<b>−1.866</b>
		RNSF	2,36	22.013	<b>&lt;0.001</b>	<b>0.689</b>	Summer	1,12	1.348	0.209	<b>−0.946</b>
							Winter	1,26	1.788	0.073	<b>−0.961</b>

Partial omega-squared ( $\omega^2$ ) and *Cohen's d* are measures of effect size for Kruskal–Wallis tests and Mann–Whitney *U* test, respectively. Significant factors (*p* < 0.05) and medium ( $\omega^2$  > 0.06; *Cohen's d* > 0.5) or large size effects ( $\omega^2$  > 0.14; *Cohen's d* > 0.8) are shown in bold type.



**Figure 1** Comparisons of conspecific (a) and heterospecific counts (b) in the white-rumped snow finch (*Onychostruthus taczanowskii*, WRSF) and the rufous-necked snow finch (*Pyrgilauda ruficollis*, RNSF) during spring, summer, and winter periods. The Y-axis shows the average values of either conspecific or heterospecific individuals. Groups with different letters are significantly different from one another season ( $P < 0.05$ ), and with an asterisk is significantly different between species in a certain season ( $P < 0.05$ ).



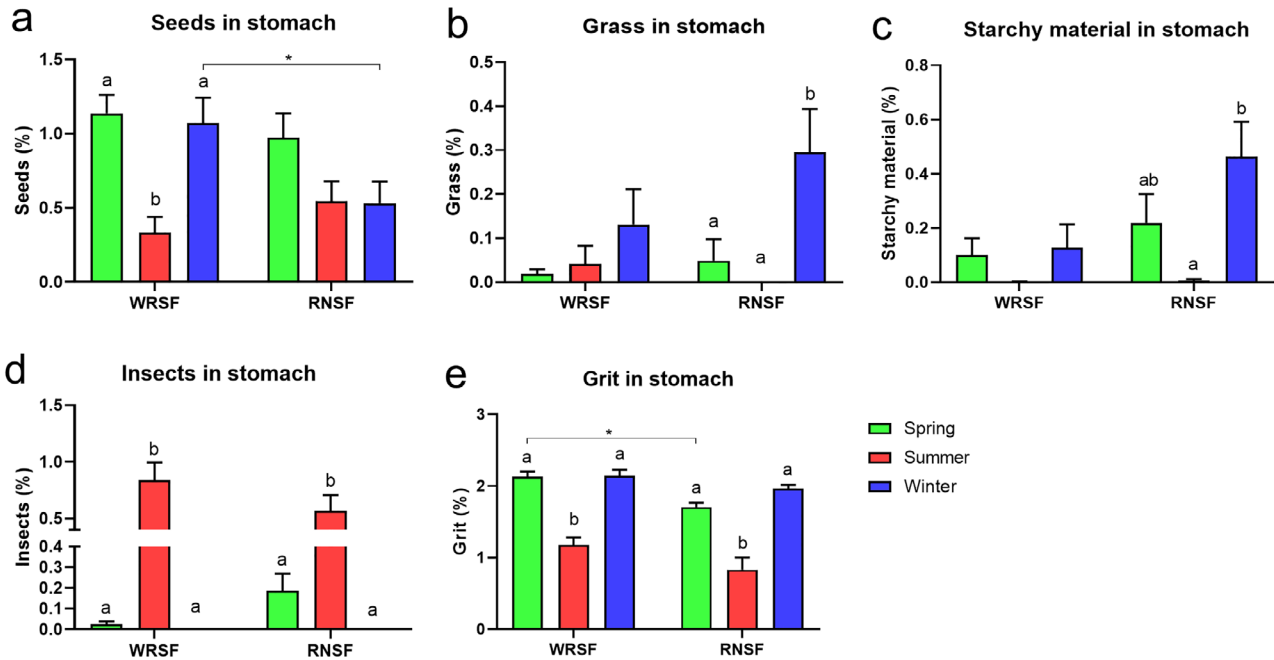
**Figure 2** Comparisons of the effects of a simulated territorial intrusion (STI) for 10 min between the white-rumped snow finch (*Onychostruthus taczanowskii*, WRSF) and the rufous-necked snow finch (*Pyrgilauda ruficollis*, RNSF) during winter. (a) Closest approach (m), (b) latency to approach (min), (c) time in 5 m (min), (d) times of contact with the cage. Groups with different letters are significantly different from one another ( $P < 0.05$ ).

and starchy material in RNSFs varied significantly with the season but seeds in RNSFs and grass and starchy material in WRSFs did not (Table 2). Post hoc results showed RNSFs ate significantly more grass during winter relative to spring ( $P = 0.006$ ) and summer ( $P = 0.016$ ) and more starchy material during winter relative to summer ( $P < 0.012$ ). WRSFs ate less seeds during summer relative to winter ( $P = 0.016$ ) and spring ( $P = 0.017$ ). Both RNSFs and WRSFs ate more insects during summer relative to winter (RNSF:  $P < 0.001$ ; WRSF:  $P < 0.001$ ) and spring (RNSF:  $P = 0.022$ ; WRSF:  $P = 0.005$ ), and had less grit in stomach during summer relative to winter (RNSF:  $P = 0.001$ ; WRSF:  $P = 0.001$ ) and spring (RNSF:  $P = 0.019$ ; WRSF:  $P = 0.005$ ; Fig. 3). There were no differences in stomach contents between species except that RNSFs ate fewer seeds in winter and had less grit in the stomach compared with WRSFs (Table 2; Fig. 3).

## DISCUSSION

### Habitat occupation and territoriality

In summer, both WRSFs and RNSFs were widely distributed in rural areas and had less heterospecific counts relative to other seasons, indicating that there was spatial niche differentiation between species. The results agree with the previous findings showing that larger-sized WRSFs occupied the resource-rich habitats while small-sized RNSFs only occurred in marginal habitats (Zeng & Lu 2009b). By contrast, in winter and spring, RNSFs aggregated and moved to human-occupied habitats, while WRSFs remained in rural areas. At these times, RNSFs exhibited more counts of congener and heterogeneity relative to WRSFs. Generally, for species with similar ecology, competition tends to become increasingly intensive in more stressful conditions (Tokeshi 1999; Zeng & Lu



**Figure 3** Comparisons of type of diet during spring, summer, and winter periods in the white-rumped snow finch (*Onychostruthus taczanowskii*, WRSF) and the rufous-necked snow finch (*Pyrgilauda ruficollis*, RNSF). Stomach contents include (a) seeds, (b) grass, (c) starchy material, (d) insects, and (e) grit. Groups with different letters are significantly different from one another season ( $P < 0.05$ ), and with an asterisk is significantly different between species in a certain season ( $P < 0.05$ ).

2009b). When the available resources get scarcer in winter, WRSFs outcompeted RNSFs in rural areas while RNSFs exhibited seasonal behavior shift toward human-occupied areas where resources (e.g. food from human waste) and shelters were less intensely competitive. This distinction of intrinsic properties for the two species was also supported by the phenomenon that WRSFs have significantly greater flight initiation distance relative to RNSFs in response to equal human intrusions (Zhang *et al.* 2016). However, unlike some competitively subordinate species that shrink their spatial niche (Tarjuelo *et al.* 2017; Reif *et al.* 2018), small-sized RNSFs as an opportunistic species escaped from rural habitats to avoid the competitor, while large-sized WRSFs occurred in rural habitats throughout an annual cycle.

We found that RNSF had remarkably reduced territoriality against their congeners and heterospecifics relative to WRSF in winter and spring. Our result indicates that RNSF could endure more intense intraspecific competition and encounter more uncertain heterospecific competitors with its range-shifting in winter. In the field, we did observe some other species such as Eurasian tree sparrow (*Passer montanus*) and horned lark (*Eremophila alpestris*) foraging sympatrically with the RNSFs in win-

ter. This is partly because sufficient and relatively stable resources in human-occupied environments attract various birds so they can endure such extreme harsh winters of the Qinghai-Tibet Plateau. Although we did not determine the degree of resource overlap between the RNSFs and other bird species, minimal interspecific competition may be expected in human-occupied areas where resources are abundant and/or not limiting under the influence of human activity (Dubowy 1988; Peiman & Robinson 2010). Given that urban RNSFs in the wintering stage can take advantage of human food resources and buildings for shelter, they may be shielded from the harsh conditions of the surrounding environment.

Rural WRSFs during winter exhibited robust aggressive behaviors associated with territorial defense (Fig. 2) and behaved as the dominant competitor over the RNSF throughout the annual cycle. Considering behavioral strategy related to the coping styles (Sih *et al.* 2004) in a stable environment, it appears that WRSF is a “proactive” species (more aggressive) tending to dominate and out-compete RNSF, a “reactive” species (less aggressive but able to adjust behavior to changes), resulting in asymmetric competition. Based on seasonal variations in the habitat occurrence and territoriality, we confirmed the

phenomenon of the co-existence of these two sympatric species exhibiting spatiotemporal niche differentiation as adaptations to the seasonality of extreme environmental conditions. Given the greater survival pressure in winter, we argue that the enlarged space segregation between closely related species may be a better adaptive strategy of alleviating interspecific competition for adapting to the extreme environmental conditions of the Qinghai-Tibet Plateau.

### Feeding habit

The seasonal variations in feeding habits of both species indicated that the partitioning of food resources varied with respect to the seasonality of available food resources, that is, more insects during summer, and more grass, starchy material, or seeds during winter. Both the higher proportion of grit content in the stomach of WRSF and RNSF during winter and spring contributed to enhancing the ability of mechanical digestion (Kleyheeg *et al.* 2018). We verified that both species were typically omnivorous in diet and adopted similar feeding strategies (Table 2), which is further supported by previous studies showing that there were no species differences in mass-corrected liver and stomach, and intestine length (Liu & Zhao 2016). However, in winter, WRSF depended more on seeds, but RNSF depended more on starchy materials. This difference may result from the availability of starchy materials and indicate a reduction in dietary overlap for the two species when food resources were in short supply (Dunbar 1978). RNSF shift their habitat range to human-occupied areas where they can take advantage of potential food resources from humans. Therefore, we propose that the separations in the spatial niche and behavioral type may contribute to alleviating the pressure of interspecific competition during the extreme environmental conditions of winter. Therefore, spatial niche partition over different seasons deriving from morphology and behavior-dependent asymmetric competition between WRSF and RNSF may be essential for facilitating the co-occurrence on the Qinghai-Tibet Plateau without apparent feeding niche differentiation (Laiolo *et al.* 2015).

A previous study showed that both WRSF and RNSF were still at an unstable-coexistence phase on the Qinghai-Tibet Plateau (Zeng & Lu 2009b). The direct aggressive interactions between the two species may further result in the skewness in habitat and resource use from the asymmetrical competition (Persson 1985). Our results indicate that human-occupied habitats have a significant influence on the survival of RNSF and the maintenance of the WRSF-RNSF guild. Further investigations on how

WRSF-RNSF behaviorally interact and what are the potential physiological mechanisms of life-history strategy (especially in winter *versus* summer) in both species, and whether WRSF can eventually eliminate RNSF from a specific area (i.e. competitive exclusion) will be crucial for understanding the competition and coexistence mechanisms of these two closely related sympatric species in such a severe environment of the Qinghai-Tibet Plateau.

### CONCLUSION

As predicted, WRSF and RNSF expressed a suite of distinct convergences and divergences in behavior-related habitat use, territoriality, social behavior, and diet, across different seasons. In spring and summer, despite both species having a similar diet, WRSFs had stronger territoriality, which enables them proactively to occupy the resource-rich habitats relative to RNSFs. In winter, WRSFs remained in the rural areas by exhibiting robust territorial behaviors and relying more on seeds, while RNSFs exhibited behavior shifts toward human-occupied sites by avoiding interspecific competitors and relying more on food resources from humans. Therefore, the coexistence of the two species is manifest in divergent traits of behavioral strategy of habitat use, territoriality, and diet across seasons between the WRSF and RNSF, suggesting temporal and spatial niche differentiation between closely related species. Alternatively, convergence in feeding habits indicates that there are highly conserved ecological traits in the two species. Therefore, separations in the spatial niche and territoriality between WRSF and RNSF in winter may contribute to alleviating the pressure of interspecific competition, promoting the coexistence of the two sympatric snow finches under the extreme environments on the Qinghai-Tibet Plateau.

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## CONFLICT OF INTEREST

The authors declare that they have no competing interests.

## ETHICS DECLARATIONS

This study was conducted in accordance to the Institutional Committee for Animal Care and Use of Institute of Zoology, Chinese Academy of Sciences, China; the University of Washington; and the University of California, Davis; and was carried out under the auspices of scientific collecting permits issued by the Departments of Wildlife Conservation (Forestry Bureau) of Qinghai Province, China.

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