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RESEARCH ARTICLE

Overlap and selection of dust-bathing sites among three sympatric montane galliform species

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ABSTRACT

Niche theory predicts that, to avoid interspecific competitive exclusion, ecologically similar bird species in sympatry should reduce habitat use overlap, especially when shared resources are limiting in an environment. Dust-bathing sites represent a distinctive behavior-specific habitat, differing from other habitats as they are used for short durations and infrequently. However, we have little understanding of selection, potential interspecific overlap, and partitioning of dust-bathing sites among sympatric species. In this study, we examined overlap and selection of dust-bathing sites of 3 sympatric montane galliform species on the Qinghai-Tibet Plateau: Blood Pheasant (*Ithaginis cruentus*), Szechenyi's Partridge (*Tetraophasis szechenyii*), and White Eared-Pheasant (*Crossoptilon crossoptilon*). We identified dust-bathing scrapes and measured habitat characteristics of dust-bathing sites along 10 transects established in Gexigou National Nature Reserve, Sichuan Province, China, from April to August in 2015. In total, we identified 105 dust-bathing scrapes and established 58 dust-bathing site quadrats. More than one-third of dust-bathing scrapes and ~20% of dust-bathing sites were used by multiple species. The 3 species showed no significant differences in the dimensions or soil particle size distributions of their dust-bathing scrapes, nor did we find that habitat features of dust-bathing sites differed significantly among the 3 species (all pairwise overlap indices >0.6). All 3 species preferred surrounding fir forests with dense tree and shrub strata, good concealment that could provide sufficient protection from predators and precipitation, and sparse grass cover with suitable substrates containing finer soil particles for better dust-bathing. Our results suggest that the 3 sympatric galliform species had similar habitat requirements that led to overlap in selection for dust-bathing sites. We recommend further monitoring of temporal use of dust-bathing sites by the 3 galliform species to test potential temporal partitioning mechanisms that may minimize competition between heterospecific and conspecific individuals.

Keywords: dust-bathing sites, ground-dwelling birds, habitat overlap, habitat selection, Phasianidae, species coexistence

Chevauchement et sélection des sites de bain de poussière chez trois espèces montagnardes de galliformes sympatriques

RÉSUMÉ

La théorie des niches prédit que pour éviter l'exclusion compétitive interspécifique, les espèces d'oiseaux sympatriques dont l'écologie est similaire devraient réduire le chevauchement de l'utilisation de l'habitat, particulièrement lorsque les ressources communes sont limitantes dans l'environnement. Les sites de bain de poussière représentent un habitat distinct spécifique au comportement qui diffère des autres car ils sont utilisés pour de courtes durées et de façon non fréquente. Toutefois, nos connaissances sont limitées concernant la sélection, le chevauchement interspécifique potentiel et la répartition des sites de bain de poussière parmi les espèces sympatriques. Dans cette étude, nous avons examiné le chevauchement et la sélection des sites de bain de poussière chez trois espèces montagnardes de galliformes sympatriques sur le plateau Qinghai-Tibet : *Ithaginis cruentus*, *Tetraophasis szechenyii* et *Crossoptilon crossoptilon*. Nous avons identifié les grattages de bain de poussière et mesuré les caractéristiques de l'habitat des sites de bain de poussière le long de 10 transects établis dans la réserve naturelle nationale de Gexigou, dans la province du Sichuan, en Chine, entre avril et août 2015. Au total, nous avons identifié 105 grattages de bain de poussière et établi 58 quadrats de sites de bain de poussière. Plus d'un tiers des grattages et

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~20 % des sites de bain de poussière étaient co-utilisés par plusieurs espèces. Les trois espèces ne présentaient aucune différence significative dans les dimensions des grattages de bain de poussière ou la répartition granulométrique du sol, et nous n'avons pas trouvé non plus que les caractéristiques de l'habitat différaient significativement entre les trois espèces lorsque tous les indices de chevauchement par paires étaient > 0,6. Les trois espèces préféraient les forêts de sapins avec des strates arborescente et arbustive denses, une bonne dissimulation pouvant offrir une protection suffisante contre les prédateurs et les précipitations, de même qu'une couverture herbacée clairsemée avec des substrats propices contenant des particules de sol plus fines pour mieux se baigner. Nos résultats suggèrent que les trois espèces de galliformes sympatriques se chevauchent en sélectionnant des sites de bain de poussière selon des besoins en habitat similaires. Nous recommandons plus de suivi de l'utilisation temporelle des sites de bain de poussière par ces trois espèces pour tester les mécanismes potentiels de partition temporelle qui peuvent minimiser la compétition entre les individus hétérospécifiques et les congénères.

Mots-clés : site de bain de poussière, oiseaux terricoles, chevauchement d'habitats, sélection d'habitats, Phasianidés, coexistence des espèces

INTRODUCTION

How sympatric species use resources in their shared environment has been of interest to community ecologists for many decades. Niche theory predicts that ecologically similar species living in sympatry should reduce overlap in resource use to minimize interspecific competition (Gause 1934, Hardin 1960, Chesson 2000). Numerous studies have reported that ecologically similar bird species partition habitats, such as nesting sites (Martin et al. 2004, Hanane 2015), foraging sites (Hasui et al. 2009, Lara et al. 2015), and roosting sites (Hayward and Garton 1984). Such habitat partitioning has been suggested to be an important mechanism for reducing interspecific competition and facilitating species coexistence (Schoener 1974, Alley 1982). However, it is sometimes possible for sympatric bird species to select similar habitats or allow overlap in habitats, if they show daily (Lara et al. 2011) or seasonal differences (Cotton 1998) in using the same habitats that they depend on.

Dust-bathing is a self-cleaning behavior performed by many galliform species (del Hoyo et al. 1994), and is characterized by a sequence of preening acts while tossing and rubbing the body in the bathing substrate (e.g., dust, sand, or peat; Kruijt 1964, van Liere et al. 1991, González-García 1994). The behavior helps individuals to keep their plumage in good condition by removing stale lipids (van Liere and Bokma 1987, van Liere et al. 1991) and dislodging ectoparasites under feathers (Martin and Mullens 2012), contributing to functions such as insulation, flight, and signaling (Middleton 1991). It may also maintain social or pair cohesion during courtship (González-García 1994). Thus, dust-bathing behavior can affect individual health, survival, and fitness.

Dust-bathing sites, like other behavior-specific habitat types such as foraging sites, might be consumable because vigorous shaking by dust-bathing birds typically removes and depletes a proportion of fine dust, reducing availability of the fine dust needed to clean plumage (Hein 1970, Olsson and Keeling 2005). Similarly to nest-building, establishing dust-bathing sites might be an energetically costly process, as birds have to clean the ground surface and dig bowl-shaped scrapes with their feet to start their bathing (B. Zhang personal observation). In contrast, dust-bathing sites differ from foraging and nesting sites because of their short use duration and low use frequency. For example, domestic fowl use dust-bathing sites only 3.2–40.0 min every second day (Vestergaard 1982, van Liere et al. 1990, 1991, Lindberg and Nicol 1997), and wild Horned Guans (*Oreophasis derbianus*) use bathing sites 17.5–29.6 min once or twice per day (González-García 1994). Collectively, these characteristics imply that dust-bathing sites represent a distinctive behavior-specific habitat type. However, we have little understanding of site selection, potential interspecific overlap, and partitioning of dust-bathing sites among sympatric species.

In this study, we investigated dust-bathing site selection by 3 sympatric montane ground-dwelling galliform species on the Qinghai-Tibet Plateau in China: the Blood Pheasant (*Ithaginis cruentus*), Szechenyi's Partridge (*Tetraophasis szechenyii*), and White Eared-Pheasant (*Crossoptilon crossoptilon*). First, we compared habitat features and substrate particle size distributions of dust-bathing sites, and then we assessed habitat overlap among species to determine potential interspecific habitat partitioning. We also analyzed the environmental factors that influenced dust-bathing site selection by the 3 species.

METHODS

Study Species and Study Area

All study species belong to the family Phasianidae, order Galliformes. The Blood Pheasant is a widespread species, occurring in coniferous forest, mixed broadleaf–conifer forest, and alpine shrub habitats at altitudes between 2,100 and 4,600 m from central China to western Nepal. The Szechenyi's Partridge is endemic to western China (Tibet, Qinghai, Sichuan, and Yunnan provinces), mainly inhabiting coniferous forests, subalpine shrubs, subalpine and alpine meadows, and rocky ravines at altitudes of 3,350–

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4,600 m. The White Eared-Pheasant is also endemic to western China and has a similar geographic range and habitat preferences to the Szechenyi's Partridge, although it occurs at slightly lower altitudes (3,000–4,600 m; Johnsgard 1999, Zheng 2015). Of the 3 species, the Blood Pheasant is the smallest (length = 39–48 cm; weight = 410–655 g), followed by Szechenyi's Partridge (length = 29–50 cm; weight = 660–1,790 g), and the White Eared-Pheasant is the largest (length = 75–96 cm; weight = 1,450–2,750 g; del Hoyo et al. 1994).

This study was conducted in the western section (29.95°N–30.00°N, 100.85°E–100.95°E) of Gexigou National Nature Reserve, Yajiang County, Sichuan Province, China, where the distributional ranges of the 3 species overlap. The study area covered ~65 km^2, at an altitude of 3,600–4,400 m. The vegetation was mainly comprised of: (1) fir forests, dominated by *Abies squamata* and *Larix potaninii*, accounting for 40% of the study area; (2) oak thickets, dominated by *Quercus aquifolioides*, accounting for 27% of the study area; (3) shrubs, dominated by *Rhododendron nitidulum* and *Salix* spp., accounting for 22% of the study area; and (4) subalpine meadows, dominated by *Kobresia setchwanensis, Polygonum viviparum, Potentilla discolor*, and *Hemiphragma heterophyllum*, accounting for 11% of the study area.

The study area was located on the Qinghai-Tibet Plateau, which experiences a typical semihumid climate, with an annual average temperature of 5.7°C (ranging from –6.5°C to 14.8°C), annual precipitation of 705 mm, and annual average humidity of 53%. More than 90% of annual precipitation is concentrated from May to October (Yajiang Forestry Bureau 2008). Our field survey was conducted during the galliform breeding season (April–August) in 2015, and rainfall was relatively frequent during this period.

Field Surveys

We systematically established 10 transects to survey dust-bathing sites. Transects were 2.0 to 5.5 km long and 50 m wide, and total length and area surveyed were 32 km and 1.6 km^2, respectively. All transects started from a road crossing the study area and were positioned along different orientations. The minimum distance between 2 transects was 500 m, and each transect crossed 2 or 3 types of vegetation. Transects were as straight as possible, but, to bypass rugged terrain, some parts of transects were established along existing paths. Each transect was surveyed once per month and 5 times in total during the study period.

All 3 species are able to create new scrapes themselves through dust-bathing behavior. When dust-bathing, they generally squat down on the ground, continuously shake their bodies, and rub their legs and wings in the dust, leaving obvious bowl-shaped scrapes on the ground (B. Zhang personal observation). We identified the species responsible for each scrape mainly by the feathers left in the scrapes, with droppings as adminicle. This excluded scrapes where only down feathers or broken droppings remained, which could not be accurately identified and attributed to a species. Adult feathers are easily distinguishable between the 3 species as there are obvious differences in plumage coloration. Blood Pheasant males have dark ash-colored feathers on the back, while feathers on the breast, belly, sides, and tail have green tips with crimson margins. Blood Pheasant females have mostly uniformly dull brown feathers over much of the body. One distinctive characteristic of both genders is a pale white belt close to the rachis throughout the vane of each contour feather. Male and female Szechenyi's Partridges have gray–brown contour feathers with white bars on the tips of flight and tail feathers, small black spots on the breast, and yellow to brown spots on the belly. The feathers of male and female White Eared-Pheasants are much larger and are mostly white, gray, and black, with a black rachis and a blue metallic luster. The 3 species' droppings are also distinguishable: Blood Pheasant droppings are prasinous or straw yellow, and resemble a curved cylinder with almost identical diameter (6–9 mm) throughout their length (3–4 cm); Szechenyi's Partridge droppings are between 4 and 6 cm long and covered with white uric acid, beginning with thicker spherical parts ($>$13 mm in diameter) and tapering to a slender tail, and are usually contorted; and White Eared-Pheasant droppings are similar to those of the Szechenyi's Partridge in shape, but their spherical parts are much thicker in diameter (20–35 mm).

We removed all feathers and droppings after each survey to determine whether a scrape was used repeatedly. For those scrapes that were reused, we only recorded habitat variables upon first detection. We recorded habitat variables for the dust-bathing scrapes and sites. Once a dust-bathing scrape was detected, we measured its long diameter (cm; extreme rim distance), short diameter (cm; perpendicular to the long diameter), and depth of the center (cm). We then established a 1×1 m small quadrat with the dust-bathing scrape at the center to record fine-scale habitat variables. If there were multiple scrapes close to each other, only the central (or closest to center) scrape was selected for positioning of the small quadrat. For each small quadrat, we measured the percentage cover of trees (SQTC; we defined a woody plant $>$5 m tall as a tree), shrubs (SQSC), and grasses (SQGC), and the mean height of shrubs (m; SQSH) and grasses (m; SQGH). We measured the distance from each small quadrat to the nearest tree (m; DNT) and the nearest path (m; DNP). Paths were defined as small footpaths or trails that were established by local villagers for occasional activities such as herb gathering, livestock grazing, and logging.

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The visibility of a scrape was also measured to represent the degree of safety that it provided to a dust-bathing individual. We used a piece of cardboard (30 × 30 cm) equally divided into 100 squares and alternately colored (in a checkerboard pattern) to measure visibilities of dust-bathing scrapes. The cardboard was positioned within the scrape perpendicular to the ground, with the checkered grid facing the observer. We viewed the cardboard grid from 4 directions, 2 in alignment with the slope and 2 perpendicular to the slope: (1) above and (2) below the scrape along the slope line, and (3 and 4) to either side of the scrape at right angles to the slope. Visibility was measured from 3 distances (10 m, 15 m, and 20 m) in each of the 4 directions. Percentage visibility was calculated from the number of squares of the grid that were visible from each direction. Mean percent visibility at each distance (10 m: VIS10; 15 m: VIS15; 20 m: VIS20) was calculated using the percentages from the 4 directions. A higher visibility percentage indicated a higher probability of a dust-bathing individual being detected.

Dust-bathing site habitat characteristics were measured using a 10 × 10 m quadrat, with the 1 × 1 m small quadrat at its center. We measured topographical attributes of this larger quadrat, including aspect (°; ASP), slope (°; SLO), and altitude (m; ALT). The aspect in degrees (e.g., $0^\circ =$ north, $180^\circ =$ south) was adjusted by subtracting 180° to represent how close the slope was to the adret (Stohlgren 2007). The vegetation type of each quadrat was classified based on the dominant species in the dominant stratum; a stratum was considered dominant if it had higher priority order (tree stratum > shrub stratum > herb stratum) and >20% cover. The species with the highest cover in this stratum was considered the dominant plant species (Li 2012). For example, a quadrat with >20% tree cover and with firs as the dominant tree in the canopy was recorded as a fir forest site. Within each quadrat, trees (height >5 m) were counted (count; QTN), and measured for mean height (m; QTH), mean diameter at breast height (m; QTDBH), and percent cover (QTC). Shrubs (height <5 m) were measured for mean height (m; QSH) and percent cover (QSC). For grasses, we placed four 1 × 1 m subquadrats at the 4 quarter points of the 2 diagonals of the quadrat and calculated mean height (m; QGH) and percent cover (QGC) by averaging the values measured at the 4 subquadrats. Plant cover was estimated visually by the same researcher (B. Zhang) throughout the study period for consistency.

Control sites were evenly sampled at a fixed altitude interval of 100 m along each transect (for example, if the altitude of a transect ranged from 3,650 m to 4,100 m, we sampled control sites at ~3,650, 3,750, 3,850, 3,950, and 4,050 m) to represent habitats available for use as dust-bathing sites. The center of each control site was considered as a representative control scrape. We sampled 64 control sites in total, and recorded the same sets of habitat variables that we measured at dust-bathing site quadrats and scrape small quadrats.

To determine potential differences in dust-bathing substrate among the 3 species' scrape sites, we sampled ~100 g of soil from the center of each dust-bathing scrape (excluding old scrapes) and control scrape with a small shovel, after removing litter and rocks from the surface. Soil samples were dried at 70°C in a thermostatic drying oven for 12 hr. Samples were then sieved using a set of 4 sieves with mesh openings of 2.0, 0.9, 0.45, and 0.2 mm, progressively sieving from the largest to smallest mesh size. Soil particles remaining in each sieve were weighed and soil particle size distribution (%) was calculated according to 5 size gradients (i.e. >2.0, 2.0–0.9, 0.9–0.45, 0.45–0.2, and <0.2 mm in diameter).

Data Analysis

We used a multivariate analysis of variance (MANOVA) to examine potential differences in dimensions and substrate particle size distribution among the 3 species' dust-bathing scrapes. If there were no significant differences in particle size distribution among species' scrapes, we pooled data from all species and used MANOVA with Bonferroni adjustment to determine differences between dust-bathing and control scrapes (Manly et al. 2002; due to 5 particle size gradients, $P < 0.01$ (0.05/5) was considered to be significant for tests of each individual variable, with consideration if any of the tests had a P-value above this cutoff but below 0.05). We also used MANOVA to compare the particle size distribution of control scrapes in different vegetation types to examine potential differences in substrate structure among vegetation types.

We used Fisher's exact tests to determine differences in vegetation type among the dust-bathing sites used by different species. If there were no significant differences, we pooled data from all 3 species to examine vegetation type selection, and calculated Jacobs' index (Jacobs 1974) for each vegetation type as:

$$D_i = \frac{r_i - p_i}{r_i + p_i - 2r_ip_i}, \qquad (1)$$

where D_i is the Jacobs' index, r_i is the use proportion of vegetation type i, and p_i is the available proportion of vegetation type i in the study area (which was estimated by counting the number of control sites intersecting each type). Jacobs' index ranges from -1 (total avoidance of a vegetation type) to $+1$ (maximum selection of a vegetation type), and values close to 0 indicate the use of a vegetation type proportional to its availability. Chi-square tests with Bonferroni adjustment were used to examine differences between the use of each vegetation type and its relative availability estimated by systematically sampled control sites (Manly et al. 2002; $P < 0.013$ (0.05/4) was considered

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to be significant due to 4 vegetation types, with consideration if any of the tests had a P-value above this cutoff but below 0.05).

To summarize patterns of covariance among all habitat variables, including features measured within small (1×1 m) and site quadrats (10×10 m), and distance and visibility variables, and to overcome the multicollinearity problem, we first conducted a correlation-based principal component analysis (PCA). We selected PCA components that explained most of the variability in the data using the broken-stick criterion (Jackson 1993). Variables with loading values higher than 0.5 were retained for interpretation, and scores of the PCA components that were extracted were used in the subsequent analyses. We computed habitat overlap indices for dust-bathing sites between each species pair along each PCA component using:

$$\hat{a} = \left(\frac{2s_1s_2}{s_1^2 + s_2^2}\right)^{\frac{1}{2}} \exp\left[\frac{-d^2}{2(s_1^2 + s_2^2)}\right], \qquad (2)$$

where $\hat{a}$ was the overlap index, s_1 and s_2 were the standard deviations of the PCA scores for each species, and d was the distance between the species means of PCA scores (Maurer 1982). Total overlap indices were then calculated as products of the overlap values for all retained components (Maurer 1982, Finch 1989, Laughlin et al. 2013). The overlap index ranges from 0 (completely segregated habitats) to 1 (completely overlapping habitats).

We used MANOVA to examine habitat differences among the 3 species' scrapes by including the principal components yielded from the PCA. If there were no significant differences, we pooled data from the 3 species to determine the general structure of the dust-bathing sites used by these species. Pooled data were analyzed using logistic regression, where explanatory variables were the PCA components and the response variable was used dust-bathing sites vs. control sites. We used Akaike's information criterion corrected for small sample size (AIC_c) to assess a candidate set of models of all of the possible combinations of variables (no interactions). The model with the lowest AIC_c value was considered the best-fitting model, given that there was only one model with $\Delta AIC_c < 2$ (Burnham and Anderson 2002). We used a Hosmer-Lemeshow goodness-of-fit test to evaluate the global model, and we assumed that fit was adequate when $P > 0.05$ (Hosmer and Lemeshow 2000).

All analyses were performed in R 3.3.2 (R Core Team 2016), with the XNomial package (Engels 2014), the psych package (Revelle 2018), the glmulti package (Calcagno 2013), the MuMIn package (Bartoń 2015), and the ResourceSelection package (Lele et al. 2016). We present results as means ± SE.

RESULTS

In total, 121 dust-bathing scrapes were detected, and we found feathers or droppings left by galliform species in 94% of them ($n = 114$). Of these, 105 dust-bathing scrapes were attributed to species, and 58 dust-bathing site quadrats were established. We found that some scrapes were used by >1 species, as indicated by feathers and/or droppings from different species in a single scrape (Figure 1). We found that 35% (37/105) of dust-bathing scrapes and 21% (12/58) of dust-bathing sites were used by multiple species (Table 1). In addition, 20% of scrapes were repeatedly used by a single species ($n = 12$) or >1 species ($n = 9$). The typical dust-bathing substrate of the majority of scrapes was loose, fine, dry soil dust ranging in color from light to dark brown, mixed with gravel and small pieces of dry litter from coniferous trees (Figure 1). There was no significant difference in long diameter, short diameter, or depth among the scrapes used by the different species (MANOVA, Wilks' $\lambda = 1.0$, $P = 0.38$; Table 2).

We collected soil samples from relatively new dust-bathing scrapes ($n = 87$) and control scrapes ($n = 64$). The particle size distribution of dust-bathing substrates did not differ significantly among the 3 species (MANOVA, Wilks' $\lambda = 0.8$, $P = 0.62$). The pooled data from the 3 species showed that the particle size distribution varied significantly between dust-bathing and control scrapes (MANOVA, Wilks' $\lambda = 0.7$, $P < 0.001$). Compared with control scrapes, the soil substrate of used dust-bathing scrapes had a significantly lower proportion of coarse particles (>2.0 mm in diameter) and a significantly higher proportion of fine particles (<0.45 mm in diameter; Figure 2). The particle size distribution of control scrapes did not vary significantly among the 4 vegetation types (MANOVA, Wilks' $\lambda = 0.8$, $P = 0.41$).

For all 3 species, $>70\%$ of dust-bathing sites were in fir forests, followed by oak thickets and shrubs, and we did not find any dust-bathing scrapes in subalpine meadows (Figure 3). The percentages of vegetation types used as dust-bathing sites did not vary significantly among the 3 species (Fisher's exact test, $P = 0.88$). The pooled data showed significant selection of vegetation types for dust-bathing sites: All species had a strong preference for fir forests, and avoided using shrubs and subalpine meadows (Figure 4).

The PCA of habitat variables yielded 3 components that explained most of the variability in the data (Table 3). PC1 described lower tree cover, number, mean height, and mean diameter at breast height within dust-bathing site quadrats, lower tree cover but higher grass cover in dust-bathing scrape small quadrats, longer distances to the nearest tree, and higher visibilities from the 3 distances. PC2 described low shrub height and cover in both site and

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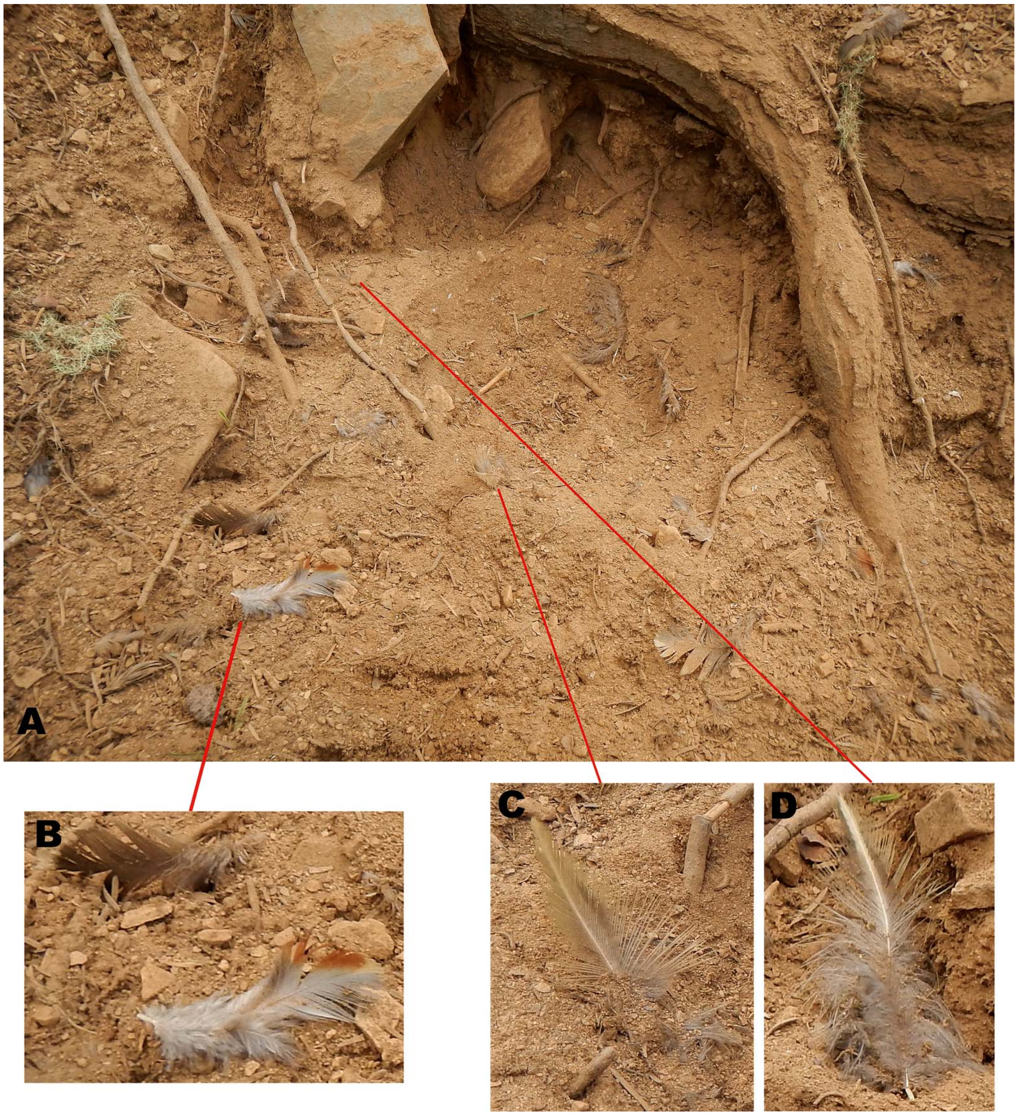

FIGURE 1. Photograph of a typical dust-bathing scrape used by Blood Pheasants and Szechenyi's Partridges, showing (**A**) the dust-bathing substrate, and (**B**) feathers that were left by a Szechenyi's Partridge, and (**C**, **D**) feathers left by a Blood Pheasant.

scrape quadrats. PC3 represented lush grasses, being positively related to grass cover and height in site quadrats, and grass height in small quadrats.

Using the formula proposed by Maurer (1982), the total habitat overlap indices were quantified as 0.869 between Blood Pheasant and Szechenyi's Partridge, 0.951 between Blood Pheasant and White Eared-Pheasant, and 0.839 between Szechenyi's Partridge and White Eared-Pheasant, suggesting a high level of overlap of dust-bathing sites between each species pair. MANOVA of the 3 components yielded by the PCA showed that there were no significant differences in habitat features among the 3 species' sites (Wilks' $\lambda = 0.9$, $P = 0.49$). We used logistic regression to determine the habitat structure of the 3 species' dust-

TABLE 1. Counts and proportions of dust-bathing scrapes and sites used by different individual and multiple galliform species.

	Bathing scrape		Bathing site	
Species [a]	Percentage	*n*	Percentage	*n*
Individual species				
BP	36	38	41	24
SP	10	11	17	10
WEP	18	19	21	12
Multiple species				
BP & SP	9	9	7	4
BP & WEP	18	19	9	5
SP & WEP	3	3	2	1
BP & SP & WEP	6	6	3	2

[a] BP = Blood Pheasant; SP = Szechenyi's Partridge; WEP = White Eared-Pheasant.

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TABLE 2. Dimensions (mean ± SE) of dust-bathing scrapes used by different galliform species. BP = Blood Pheasant; SP = Szechenyi's Partridge; and WEP = White Eared-Pheasant.

Species	BP (n = 72)	SP (n = 29)	WEP (n = 47)
Long diameter (cm)	27.03 ± 0.55	26.90 ± 1.04	29.08 ± 0.71
Short diameter (cm)	24.30 ± 0.56	24.26 ± 0.79	25.57 ± 0.61
Depth (cm)	6.07 ± 0.18	6.10 ± 0.25	6.29 ± 0.21

bathing sites. In total, 8 (2^3) candidate models were constructed with the 3 principal components. The model including PC1 and PC2 had the lowest AIC_c value and was the best-fitting logistic regression model for determining dust-bathing site selection by the 3 species (Table 4). The Hosmer-Lemeshow goodness-of-fit test ($P = 0.193$) indicated that the predictive capability of the model was acceptable. A site with lower PC1 and PC2 was more likely to be used by all 3 galliform species for dust-bathing (Table 5). Based on the coefficients of factor loadings for habitat variables summarized in each of these components (Table 3), the 3 species were more likely to select a dust-bathing site with higher tree cover, number, mean height, and mean diameter at breast height, higher shrub cover and height, and lower visibility. Similarly, dust-bathing scrapes with higher tree cover, shrub cover and height, and shorter distances to the nearest tree were selected.

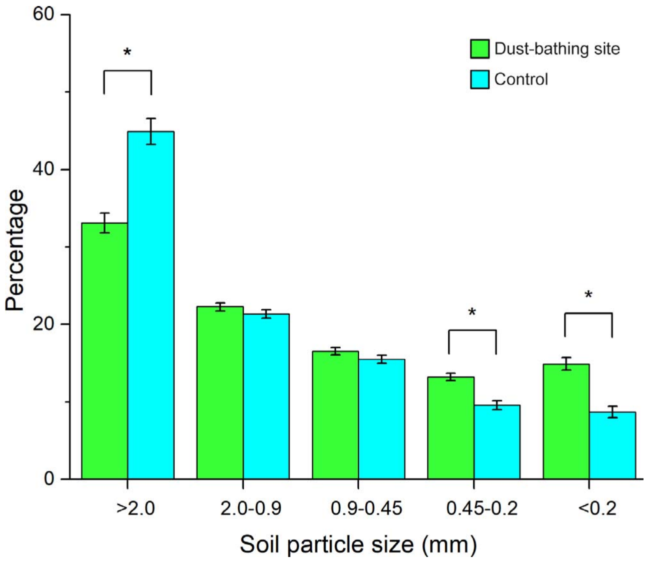

FIGURE 2. Comparison of soil particle size distribution (mean ± SE) of dust-bathing scrapes used by Blood Pheasants, Szechenyi's Partridges, and White Eared-Pheasants (green bars) and control scrapes (blue bars). Asterisks (*) indicate statistically significant differences (significance set at $P < 0.01$; MANOVA with Bonferroni adjustment).

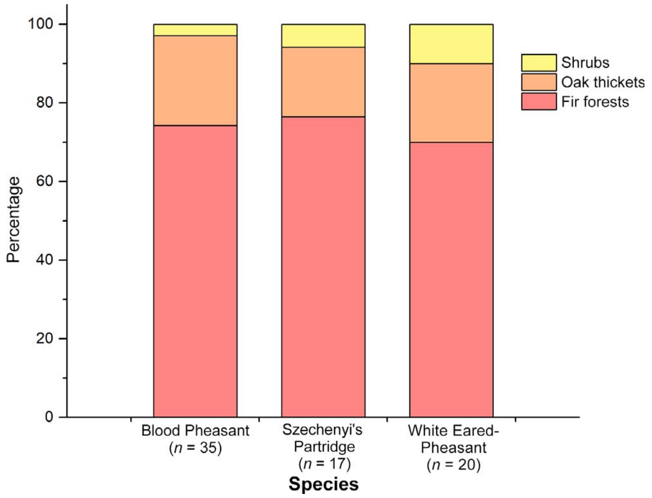

FIGURE 3. Percentage of vegetation types in which dust-bathing sites were used by Blood Pheasants, Szechenyi's Partridges, and White Eared-Pheasants. We did not find any dust-bathing sites in subalpine meadows.

DISCUSSION

Overlap in Dust-bathing Sites among Species

Interspecific competition and habitat partitioning are presumed to arise when the habitats being shared by 2 species are limiting (i.e. supply < demand) in the environment (Pianka 1974, Alley 1982). Dust-bathing sites, like other general behavior-specific habitat types such as foraging sites (Lara et al. 2015) and nesting sites (Ingold 1989), might be a limiting resource in the natural

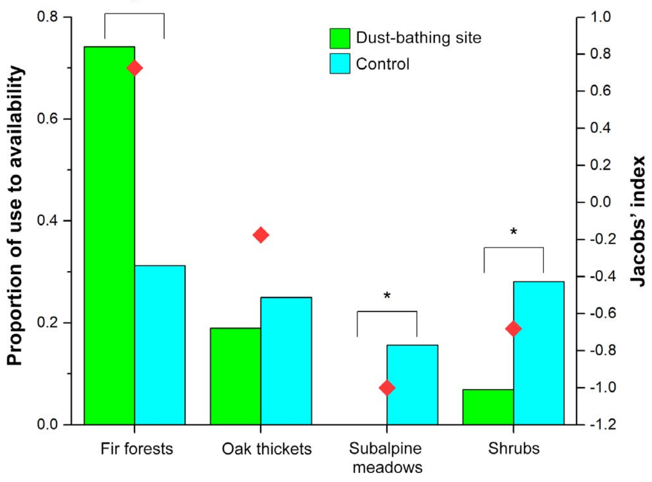

FIGURE 4. Proportion of vegetation types that had dust-bathing sites used by the 3 galliform study species (green bars) compared with control sites (blue bars). Jacobs' index values (diamonds) indicate preference (>0) or avoidance (<0). Asterisks (*) indicate statistically significant differences (significance set at $P < 0.013$; chi-square tests with Bonferroni adjustment).

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TABLE 3. Factor loadings (absolute values >0.5 highlighted in bold font), and total and cumulative percentage of variance explained by the principal component analysis of noncategorical habitat variables measured at dust-bathing sites used by different galliform species and control sites.

	Principal component		
Habitat variable	PC1	PC2	PC3
Variables measured at site quadrat [a]			
QTC	**−0.763**	0.279	−0.008
QTN	**−0.665**	0.194	0.066
QTH	**−0.789**	0.276	−0.010
QTDBH	**−0.663**	0.266	0.006
QSC	0.035	**−0.701**	0.094
QSH	0.089	**−0.654**	−0.038
QGC	0.422	0.446	**0.500**
QGH	0.170	0.255	**0.741**
ALT	−0.208	−0.051	−0.221
ASP	0.139	−0.159	−0.138
SLO	−0.298	−0.100	0.491
Variables measured at scrape small quadrat [b]			
SQTC	**−0.660**	0.109	−0.065
SQSC	0.294	**−0.661**	0.161
SQSH	0.183	**−0.648**	0.059
SQGC	**0.640**	0.414	0.492
SQGH	0.257	0.158	**0.758**
Distance variables [c]			
DNT	**0.797**	−0.137	0.057
DNP	−0.239	0.226	−0.111
Visibility variables [d]			
VIS10	**0.681**	0.423	−0.390
VIS15	**0.688**	0.397	−0.454
VIS20	**0.672**	0.373	−0.427
Percentage of variance explained	27	15	12
Cumulative percentage explained	27	42	54

[a] Site quadrat = 10 × 10 m quadrat to record dust-bathing site habitat characteristics. QTC = quadrat tree cover; QTN = quadrat tree number; QTH = quadrat tree mean height; QTDBH = quadrat tree mean diameter at breast height; QSC = quadrat shrub cover; QSH = quadrat shrub mean height; QGC = quadrat grass cover; QGH = quadrat grass mean height; ALT = altitude; ASP = aspect of slope; SLO = degree of slope.

[b] Scrape small quadrat = 1 × 1 m quadrat with the dust-bathing scrape at the center to record fine-scale habitat variables. SQTC = small quadrat tree cover; SQSC = small quadrat shrub cover; SQSH = small quadrat shrub mean height; SQGC = small quadrat grass cover; SQGH = small quadrat grass mean height.

[c] DNT = distance to the nearest tree; DNP = distance to the nearest path.

[d] VIS10, VIS15, and VIS20 = scrape mean visibility from 10 m, 15 m, and 20 m, respectively.

TABLE 4. Candidate set of logistic regression models for determining dust-bathing site selection of 3 galliform species.

Model [a]	K [b]	logLik [c]	ΔAIC_c [d]	w_i [e]
PC1 + PC2	3	−48.269	0.00	0.67
PC1 + PC2 + PC3	4	−48.257	2.11	0.23
PC1	2	−51.618	4.60	0.07
PC1 + PC3	3	−51.605	6.67	0.02
Null	1	−84.421	68.12	0.00
PC2	2	−83.822	69.00	0.00
PC3	2	−84.258	69.88	0.00
PC2 + PC3	3	−83.659	70.78	0.00

[a] Principal components. See Table 3.

[b] Number of model parameters.

[c] Model log-likelihood value.

[d] Difference in Akaike's information criterion corrected for small sample sizes (AIC_c) relative to the minimum AIC_c. The minimum AIC_c value = 102.74.

[e] Akaike weight.

environment because of fine dust availability or energetically costly establishment (Hein 1970, Olsson and Keeling 2005, B. Zhang personal observation). Our findings suggest that dust-bathing sites in our study area may be limited because the 3 sympatric montane galliform species repeatedly used sites and some sites were used by more than one species. Furthermore, all 3 species clearly preferred fir forests when choosing locations for dust-bathing sites and scrapes. We did not find any evidence of habitat partitioning of dust-bathing sites among the 3 species. There was no statistical difference in particle size distribution of dust-bathing substrates among the 3 species' scrapes, nor did we detect significant habitat feature differences among selected dust-bathing sites: All the pairwise overlap indices were above the ecologically significant threshold of 0.6 (Zaret and Rand 1971). Collectively, these results suggest that the 3 species allowed for high overlap in their selection of dust-bathing sites as they have similar habitat requirements.

A high habitat overlap value has been proposed to limit the mutual coexistence of a species pair (Gorman 1988, Bosakowski et al. 1992, Krüger 2002a, 2002b). Dust-bathing sites differ from many other behavior-specific habitats in their temporal usage, particularly their short use duration and low use frequency (van Liere et al. 1990, 1991, González-García 1994). Short duration and low frequency of use imply that a species or individual does not need to occupy a dust-bathing scrape exclusively for a long period of time, offering chances for site sharing (Hendricks and Hendricks 1995, Coppedge and Shaw 2000). For the 3 galliform species that we studied, it might be that individuals (conspecifics or heterospecifics) used the same dust-bathing scrapes but at different times (temporal

TABLE 5. Parameter estimates, standard errors, and 95% confidence limits (CL) of the top-ranked logistic regression model (Table 4) for estimating the dust-bathing site selection of 3 galliform species.

Habitat feature	Estimate	SE	Lower 95% CL	Upper 95% CL
Intercept	−0.433	0.287	−0.996	0.130
PC1	−2.565	0.471	−3.488	−1.641
PC2	−0.752	0.311	−1.362	−0.142

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partitioning), minimizing potential interspecific competition while satisfying an individual's own dust-bathing requirements (Hendricks and Hendricks 1995). Temporal partitioning would allow the 3 species to share sites despite high habitat overlap.

Although all 3 species could have bathed in a suitable substrate while creating new scrapes themselves, using an existing scrape is likely to be less energetically expensive. The dimensions of dust-bathing scrapes would not limit joint use by different species, as they are highly plastic and vary with continual use (González-García 1994). A small individual could bathe in a scrape larger than it needs, whereas a large individual could easily make a small scrape larger. In addition, the shared use of dust-bathing scrapes might be a form of mutualism for sympatric galliform species, because continual use of the same scrapes would keep the soil dust dry and loose, which is an ideal dust-bathing substrate for Galliformes (Hein 1970, González-García 1994).

Nevertheless, ~65% of scrapes and ~80% of sites were not shared by different species. We suspect that destruction of dust-bathing scrapes was responsible for this high occurrence of single species use (González-García 1994). During field surveys, we found that some dust-bathing scrapes in open areas were destroyed by rain, but new scrapes were created in adjacent areas. Given frequent rainfall during the galliform species' breeding season, destruction of dust-bathing scrapes might have resulted in a reduced estimate of the proportion of jointly used dust-bathing scrapes and sites. In addition, population density of the 3 species could affect the proportion of shared dust-bathing scrapes and sites. The demand for dust-bathing sites would likely increase with population growth, limiting supply and thus increasing the frequency of use of shared sites.

General Pattern of Dust-bathing Site Selection

Previous studies have suggested that suitable dust-bathing substrates and adequate safety are the 2 most important factors influencing dust-bathing site selection (Hein 1970). The 3 studied species all selected soil with fine particles for dust-bathing (Figure 2). This is consistent with previous studies of both wild Galliformes (Hein 1970, González-García 1994) and captive fowl (Van Liere et al. 1990, Olsson and Keeling 2005), as fine and loose materials easily pass through the feathers and effectively remove stale lipids and ectoparasites.

Generally, habitat selection by birds for increased safety is a tradeoff between concealment and view of the surroundings (Götmark and Blomqvist 1995). Depending on the species and situation, Galliformes may select sites with better concealment from predation (Li et al. 2010, 2012), or may prefer sites with open lines of sight that enable them to detect and escape predators early (Hein 1970, Li et al. 2011). Based on our results, it appears that the 3 study species were more likely to adopt concealment as their primary antipredator strategy, because they showed an overwhelming preference for dust-bathing sites in fir forests with well-developed tree and shrub strata and low visibility. A dense tree canopy could provide better cover from aerial predators (including Bearded Vultures [*Gypaetus barbatus*], Himalayan Griffons [*Gyps himalayensis*], and Golden Eagles [*Aquila chrysaetos*]; Yang 2012), and thick shrubs could provide shelter from ground-based predators (such as wild boars [*Sus scrofa*], leopard cats [*Prionailurus bengalensis*], yellow-throated martens [*Martes flavigula*], Siberian weasels [*Mustela sibirica*], gray wolves [*Canis lupus*], and Tibetan foxes [*Vulpes ferrilata*]; Yang 2012). Furthermore, the proximity of large trees could possibly help individuals to escape from predators, as they could climb a tree and then glide away (B. Wang personal observation). It is also possible that selection of areas close to trees and with dense tree and shrub cover for dust-bathing scrapes could partly shelter the scrapes from precipitation (rain, hail, and snow) and maintain the dryness of the dust, given that damp substrates are not favored by Galliformes (Hein 1970, González-García 1994). Unsurprisingly, dense tree and shrub cover also limits the growth and dispersal of grasses, but selection of dust-bathing sites with sparse grass cover might instead indicate a preference for soil with finer particles as a dust-bathing substrate.

In addition to vegetation structure, habitat selection for dust-bathing sites might be related to the physical properties of the plant community's soil, such as particle size, hardness, water content, and pH (Hein 1970, González-García 1994). It is possible that the 3 galliform species preferred fir forests rather than oak thickets partly due to fir forests having more acidic and clay soils (Wu 1980). However, we found that the soil particle size distribution along 5 size gradients (i.e. $>$2.0, 2.0–0.9, 0.9–0.45, 0.45–0.2, and $<$0.2 mm in diameter) did not significantly differ among the vegetation types. Therefore, further studies are needed to examine the relationship between the distribution of dust-bathing scrapes and soil particle size, especially along particle size gradients $<$0.2 mm, as well as other physical properties of soil such as hardness, water content, and pH.

In conclusion, the 3 sympatric galliform species allowed overlap in their selection of dust-bathing sites as they had similar habitat requirements. The 3 species chose and shared dust-bathing sites in fir forests with dense tree and shrub strata, which provided good concealment from predators and protection from precipitation, and suitable substrates containing fine-particle dust. Temporal partitioning of the shared dust-bathing sites and scrapes is a possible mechanism for minimizing potential interspecific competition between the 3 species while satisfying an

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individual's own dust-bathing requirements. We recommend further monitoring of temporal use of dust-bathing sites in the field by building a transparent roof above detected dust-bathing scrapes and utilizing infrared-triggered cameras to better estimate the proportion of jointly used dust-bathing scrapes and sites by several species and to test this potential temporal partitioning mechanism of avoiding competition. Furthermore, we suggest that additional studies should measure more physical soil properties to better understand habitat differences and dust-bathing site selection by galliform species.

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Ethics statement: The study was approved by Yajiang County Forestry Bureau. Our study protocol only involved field searches, observations, and measuring. No birds were sacrificed or harmed due to our study. All the fieldwork was also approved by the Ethics Committee of Sichuan University, and conducted under the Law of the People's Republic of China on the Protection of Wildlife.

Author contributions: J.R. and T.Z. conceived the idea, design, and experiment; B.W., B.Z., and X.H. performed the experiments; B.W., Y.X., and Y.W. wrote the paper; and B.W., Y.X., and Y.W. analyzed the data.

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