

The Effects of Rainfall, Temperature, and Wind on a Community of Montane Birds in Shei-Pa National Park, Taiwan

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Bruno A. Walther, Jane Ren-Jen Chen, Hui-Shan Lin, and Yuan-Hsun Sun (2017) Montane birds are regularly exposed to extreme weather variations. Taiwan's subtropical montane avifauna (which contains many endemic species) is regularly exposed to large weather fluctuations. From 2010 to 2013, we conducted monthly censuses to study the influence of monthly weather variations on species richness and bird density of a montane bird community (> 3000 m a. s. l.) in Shei-Pa National Park. Censuses were conducted along a trail which traverses four distinct habitats with increasing altitude: bush forest ecotone, post-fire grassland, conifer forest, and rocky bushland. The highly variable weather corresponded with large fluctuations in the bird community. We found that lower temperatures had a negative effect on species richness and bird density, and this effect was strongest in the highest elevation habitat, the rocky bushland. Rainfall was positively correlated with bird density, but only explained 15% of the variation, while the effects of wind speed were inconsistent and small. This is the first study to demonstrate such weather effects in Taiwan and probably East Asia. We briefly discuss adaptations to harsh weather conditions in birds which could become a promising future research field for montane birds in Taiwan.

Key words: Weather, Bird density, Species richness, Monitoring, Taiwan.

BACKGROUND

Montane birds are regularly exposed to extreme variations of weather conditions, which can cause reduced survival, reproduction and altitudinal migration (Morton et al. 1972; Rabenold and Rabenold 1985; Hejl et al. 1988; Fjelds  1991; Hendricks and Norment 1992; Elkins 2004; Hahn et al. 2004; Stephenson et al. 2011; Shiao et al. 2015). For example, rainfall, temperature, and wind speed may affect birds directly through heat gain or loss (Root 1988; Bech and Reinertsen 1989; Wolf and Walsberg 1996; Cooper 2000; Petit and V zina 2014) or indirectly through nestling development (Rodr guez and Barba 2016), food availability (Gass and Lertzman 1980; Faaborg et al. 1984; Malizia

2001; Boyle et al. 2010) or predation risk (Reyes-Arriagada et al. 2015).

Taiwan is a mountainous island with a maximum elevation of 3952 m, and its climate ranges from tropical in the south to subtropical in the north and alpine in the high mountains, with a mean annual temperature of 18.0 C and a mean annual precipitation of 2510 mm which is highly seasonal (Yen and Chen 2000; Chen and Chen 2003). Consequently, Taiwan has a subtropical montane avifauna with several endemic species and subspecies (Severinghaus et al. 2010) which is distinct from lower elevation communities found below 2300 m (Shiu and Lee 2003).

This montane avifauna is regularly exposed to large weather fluctuations. For example,

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montane birds regularly move to lower elevations in response to adverse weather conditions (Severinghaus et al. 2010), and many of these montane species breed from late March to September, when the summer monsoon and severe tropical storms may affect them (Shiao et al. 2015).

A series of studies modelled the island-wide distributions and determined hotspots of species richness for all breeding birds of Taiwan, including the montane ones (Walther et al. 2011; Wu et al. 2012; Wu et al. 2013; Wu et al. 2014). Surveys in montane areas demonstrated species richness peaks in March to May, with the peak arriving later as elevation increases (Wang and Sun 1989; Liu et al. 2002; Hsu et al. 2006; Wang 2013). During the non-breeding season, bird density decreased at high elevations (Wu 2008; Ding et al. 2012b) and increased at low elevations (Wang and Sun 1989; Wu 2008), and a large proportion of the montane bird community participated in these altitudinal migrations (Ding et al. 2012b). Finally, the laying dates of the Green-backed Tit *Parus monticolus* and Rufous-faced Warbler *Abroscopus albogularis* were influenced by spring temperature rather than normal rainfall, with both species being negatively affected by heavy seasonal rainfall during the nesting period (Shiao et al. 2015). Except for the last study, none of these studies investigated the influence of weather which must be an important influence on the behaviour of montane birds.

Sheishan is a montane area in northern Taiwan, most of which is protected by Shei-Pa National Park. Sheishan reaches a height of almost 3900 m, so that the highest areas have a distinctive subtropical alpine climate and vegetation. Sheishan's weather has a pronounced seasonality which is characterized not by rainfall but by temperature and, to a lesser extent, wind speed. The temperature regularly falls below 0°C in winter, and rainfall usually peaks during June while wind speeds are higher during the winter months due to the north-eastern monsoons (Wei and Lin 2012).

The Shei-Pa National Park Headquarter launched a long-term monitoring project in 2009 to monitor local ecosystems and to understand how abiotic and biotic factors interact. While resident scientists already knew that the bird abundance varies seasonally because of weather conditions, no previous study had systematically investigated the relationship between weather variables and bird abundances.

Therefore, we studied the bird richness and

density of a montane bird community along an altitudinal gradient within Shei-Pa National Park for four consecutive years (2010-2013) using point count surveys and weather data from four weather stations. We performed this study in order to test our hypothesis that adverse weather conditions affect the species richness and bird density of this montane bird community. We thus report on the influence of three weather variables, namely rainfall, temperature, and wind, on the variation of bird richness and density in order to test for any relationship between the change in weather variables and the two dependent variables, bird richness and density.

MATERIALS AND METHODS

Study site

The study site is located inside Shei-Pa National Park which extends over an area of 768.5 km² and is found in the central part of Taiwan's mountain range. Our study site extended along the Sheidong Trail (Fig. 1). Walking up the trail from east to west, the trail crosses four distinct habitats (Tseng and Tseng 2009):

1.) Bush forest ecotone (3178-3189 m a. s. l.): This habitat consists of a mixture of patches dominated by grasses, predominantly Yushan Cane *Yushania niitakayamensis*, and relatively young trees, mostly Taiwan White Fir *Abies kawakamii* and Yushan Azalea *Rhododendron pseudochrysanthum* in its arbor form.

2.) Post-fire grassland (3146-3265 m a. s. l.): This habitat is also a mixture of patches but dominated by either Yushan Cane or Alpine Silver Grass *Miscanthus transmorrisonensis*. In addition, many annual herb species are growing during the non-winter seasons.

3.) Conifer forest (3301-3545 m a. s. l.): This habitat is a single-species forest composed of older Taiwan White Fir whereby its understory is mainly composed of young trees, and the ground is covered by logs and mosses. The trees' canopies block off much sunlight during all seasons.

4.) Rocky bushland (3602-3886 m a. s. l.): This habitat consists predominantly of Single-seed Juniper *Juniperus squamata* and Yushan Azalea in its shrub form, with bare, rocky ground found at much of its highest survey points.

Habitats 1 and 3 have denser and taller vegetation than habitats 2 and 4, whereby habitat 3 has the tallest vegetation because it consists

mostly of older trees (Tseng and Tseng 2009). Habitats 2-4 often experience frost and snow cover during the winter (Tseng and Tseng 2009).

One weather station is located within each habitat along the trail (Fig. 1) in very close proximity to the survey points (see below). Each station collected rainfall (mm), temperature ($^{\circ}\text{C}$), and wind speed (m/s) every hour. We averaged hourly data into monthly means. Using these monthly means, we then calculated the means, standard deviations and ranges of these three weather variables for each habitat over the entire study period (Table 1).

Sampling design and data collection

A project to monitor this bird community on a monthly basis was begun in January 2010 and ended in November 2013. The vast majority of surveys (< 95%) were carried out by the third author, with occasional help from other

experienced ornithological researchers.

For each monthly survey, the researchers walked along an established trail (Fig. 1) for two mornings (one morning walking up, the next morning walking down) at approximately the same date within each month. Surveys began after sunrise and were always completed within a maximum of four hours to minimize detection variation caused by diminishing bird activity over time. This 4-hour limit had been established by Ding (1993). Within each habitat, survey points were established at a minimal interval of 200 m to ensure independence between every two survey points (Fig. 1). There were 4, 6, 7, and 5 survey points in the bush forest ecotone, post-fire grassland, conifer forest, and rocky bushland, respectively.

The variable circular-plot method (Reynolds et al. 1980) was used to assess bird abundance. A single observer stopped at each survey point for 6 min and recorded the following data: species,

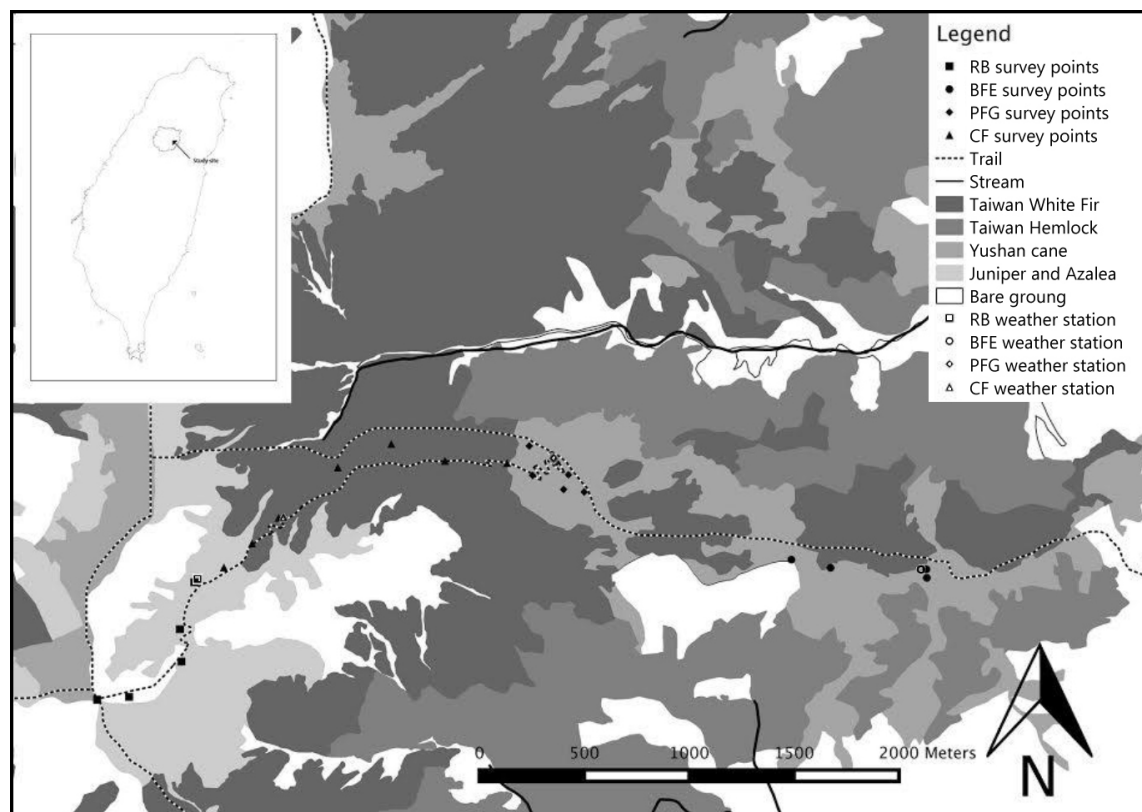


Fig. 1. Map of the study site along the Sheidong Trail, Shei-Pa National Park, Taiwan. The four surveyed habitats and the number of survey points within each were: the bush forest ecotone (4), the post-fire grassland (6), the conifer forest (7), and the rocky bushland (5). The coordinates for the most eastern and western survey points were: 24.3886°N, 121.2707°E (altitude = 3188 m a. s. l.) and 24.3834°N, 121.2317°E (altitude = 3886 m a. s. l.), respectively. The most western survey point is also the highest one, while the lowest one is at 3178 m a. s. l., just west of the most eastern point. The inserted map in the upper left corner shows the location of the study site within Taiwan.

number of individual birds, distance from the observer, and detection method (*i.e.* sight or sound). During a previous study (Ding 1993), the 6-minute sampling period had been determined as sufficient using the species-sampling-time curve. During some months (Feb., May 2010; Nov., Dec. 2011; Jan., Feb., Nov. 2012; Sep., Dec. 2013), surveys were cancelled for one of these reasons: (1) days with persistent rain or snow fall which would have caused significant detection error caused by these weather events; (2) the trail was not visible because the snow cover was too deep.

We *a priori* excluded the following species from further analyses: (1) non-breeding species (except Pale Thrush because it was the most common winter migrant); (2) species detected outside of the basal radius (see definition below). Therefore, 65 species were excluded (Appendix 1), while 23 species remained for analysis of species richness and bird density (Table 2).

For each of these 23 species, we calculated the mean of body mass measurements in grams published in Severinghaus et al. (2010), except for the Taiwan Bush Warbler for which we combined measurements from Rasmussen et al. (2000) and Severinghaus et al. (2010). If body mass measurements were not available from Severinghaus et al. (2010), we used the data in Dunning (2008). We categorized each species' feeding guild as insectivore, omnivore, or granivore

based on their dietary compositions taken from Di (1977) and Ding (1993). For species not covered by these two studies, we used the general dietary descriptions of Severinghaus et al. (2010). Using Chen's (2013) published categories, species with > 70% of invertebrates in their diet were classified as insectivores; species with > 70% of seeds were classified as granivores; and the remainder were classified as omnivores.

Statistical analyses

Species richness was defined as the total number of bird species detected (Walther and Martin 2001) among the total set of 23 species (Table 2). Since each habitat had a varying number of survey points, we standardized our abundance counts at each survey point into an overall bird density (number of birds/ha) for each habitat. Bird density was calculated using this equation taken from Reynolds et al. (1980)

$$\text{Density} = \frac{N}{\pi r^2 C} \times 10^4$$

where N is the number of individual birds of the 23 species included in our analysis detected within the specific basal radius, r is the specific basal radius (in m) of a species, C is the number of survey points surveyed during a month, and 10⁴ is

Table 1. Mean, standard deviation, and range of the three weather variables used in this study, and bird richness and density, all calculated from monthly means over the entire study period

Habitat (N)	Altitude (m)	Rainfall (mm)	Temperature (°C)
Bush forest ecotone (47)	3184	206.7 ± 143.9 (6.0-556.0)	8.5 ± 3.5 (1.1-13.1)
Post-fire grassland (47)	3206	170.1 ± 155.7 (1.5-706.0)	7.4 ± 3.3 (-0.1-11.5)
Conifer forest (47)	3423	205.4 ± 151.8 (5.0-623.4)	5.4 ± 3.5 (-1.8-9.9)
Rocky bushland (47)	3744	30.4 ± 1.0 (27.0-31.0)	4.7 ± 3.3 (-2.3-9.0)
All (188)	3389	153.2 ± 148.3 (1.50-706.0)	6.5 ± 3.7 (-2.3-13.1)

Habitat (N)	Wind speed (m/s)	Total richness (N)	Mean density (N)
Bush forest ecotone (47)	1.74 ± 0.26 (1.33-2.56)	18 (38)	59.7 ± 40.4 (38)
Post-fire grassland (47)	0.99 ± 0.29 (0.55-1.91)	15 (38)	43.9 ± 22.9 (38)
Conifer forest (47)	0.48 ± 0.31 (0.00-1.17)	17 (34)	119.1 ± 87.9 (34)
Rocky bushland (47)	3.80 ± 0.53 (2.24-4.85)	11 (31)	22.5 ± 20.3 (31)
All (188)	1.75 ± 1.32 (0.00-4.85)	23 (141)	61.6 ± 60.9 (141)

Altitude is the mean of minimum and maximum altitude (see Methods). Total richness is all the species observed of the total of the 23 most common ones (Table 2). Mean density is the average density over the monthly samples. The sample size (N) is 47 months for each of the weather variables, but is lower for richness and density due to bad weather conditions (see Methods).

a constant to avoid very small values. The basal radii of all species were determined in two previous studies (Ding 1993; Liao 2006) and used by us because their study sites shared similar elevation and vegetation composition with our study site.

The non-breeding season (October to February) is the only period during which birds formed flocks. Based on our own observations, these flocks never just flew over the habitat but were always moving within one of the four habitats; thus, their numbers needed to be determined. To determine the number of individual birds within “a flock” detected by either sight or sound, the number of birds within a flock was counted whenever the entire flock was visible. For any flock which was only detected by sight far away or by sound and could therefore not be counted, we used the mean number of birds within all the flocks which had been counted during the entire study period which we called the mean winter flock size. This method was adopted from Sun and Pei (2001).

We then performed two analyses:

- 1.) Determining the influence of weather

variables on species richness and bird density: for each month during which sampling happened, we took the monthly mean rainfall, temperature, and wind speed from the respective habitat as independent variables and correlated them with one dependent variable (either species richness or bird density) determined for that month using multiple linear regression. All variables were Box-Cox transformed prior to the regression analysis (Krebs 1989). We then tested the three independent weather variables for collinearity using the Pearson correlation coefficient. There are many statistical tests to evaluate the degree of multicollinearity among independent variables but no absolute threshold value exists. Most ecological studies have set a threshold value somewhere between 0.6 and 0.9 for the absolute value of the regression coefficient *r*. We used the minimum threshold of 0.6 and still found no multicollinearity between the three independent variables.

For each dependent variable, we then tested the seven candidate models resulting from all the possible combinations of the three independent

Table 2. List of 23 bird species used in this study to calculate bird richness and density

English name	Latin name	Migratory status	Body mass (g)	Guild	Months	Density
Himalayan Cuckoo	<i>Cuculus saturatus</i>	Summer migrant	81.1 [#]	insectivore	4-5	0.002 ± 0.02 (0-0.16)
Taiwan Barbet	<i>Megalaima nuchalis</i>	Resident	70.1	omnivore	1	0.001 ± 0.012 (0-0.15)
White-backed Woodpecker	<i>Dendrocopos leucotos</i> ²	Resident	117.0 [#]	insectivore	9-10	0.003 ± 0.02 (0-0.18)
Eurasian Nutcracker	<i>Nucifraga caryocatactes</i> ²	Resident	183.0 [#]	granivore	1-3, 6-8, 11	0.01 ± 0.03 (0-0.12)
Large-billed Crow	<i>Corvus macrorhynchos</i>	Resident	633.8	omnivore	4-6, 9, 11-12	0.004 ± 0.02 (0-0.11)
Green-backed Tit	<i>Parus monticolus</i> ²	Resident	8.8	insectivore	3-4, 7, 10	0.01 ± 0.08 (0-0.50)
Coal Tit*	<i>Parus ater</i> ²	Resident	9.2 [#]	insectivore	1-12	0.68 ± 1.19 (0-7.10)
Yellowish-bellied Bush Warbler*	<i>Cettia acanthizoides</i> ²	Resident	6.5	insectivore	2-11	0.97 ± 1.19 (0-4.97)
Taiwan Bush Warbler	<i>Bradypterus alishanensis</i> ¹	Resident	10.6	insectivore	3-10	0.10 ± 0.28 (0-1.62)
White-whiskered Laughing-thrush*	<i>Garrulax morrisonianus</i> ¹	Resident	76.8	omnivore	1-12	0.45 ± 0.55 (0-3.75)
Streak-throated Fulvetta*	<i>Alcippe cinereiceps</i> ¹	Resident	7.4	insectivore	1-12	0.96 ± 1.93 (0-10.32)
Taiwan Yuhina	<i>Yuhina brunneiceps</i> ¹	Resident	12.2	omnivore	3-4, 8	0.03 ± 0.16 (0-1.27)
Golden Parrotbill	<i>Paradoxornis verreauxi</i> ²	Resident	6.0 [#]	omnivore	6-8, 10	0.05 ± 0.27 (0-1.99)
Flamecrest*	<i>Regulus goodfellowi</i> ¹	Resident	5.9	insectivore	1-12	5.34 ± 8.57 (0-38.65)
Winter Wren*	<i>Troglodytes troglodytes</i> ²	Resident	10.5 [#]	insectivore	1-12	0.77 ± 0.84 (0-3.27)
Eurasian Nuthatch	<i>Sitta europaea</i>	Resident	22.6 [#]	insectivore	1, 3, 9, 12	0.03 ± 0.15 (0-1.01)
Pale Thrush	<i>Turdus pallidus</i>	Winter migrant	64.2	insectivore	1-2	0.001 ± 0.012 (0-0.11)
White-browed Shortwing	<i>Brachypteryx montana</i> ²	Resident	14.4	insectivore	8	0.002 ± 0.02 (0-0.22)
White-browed Bush Robin	<i>Luscinia indica</i> ²	Resident	13.6	insectivore	2-10, 12	0.19 ± 0.52 (0-2.53)
Collared Bush Robin*	<i>Luscinia johnstoniae</i> ¹	Resident	13.6	insectivore	2-11	0.57 ± 0.55 (0-2.73)
Alpine Accentor	<i>Prunella collaris</i> ²	Resident	43.5 [#]	insectivore	5-7, 9-11	0.07 ± 0.27 (0-1.41)
Vinaceous Rosefinch*	<i>Carpodacus vinaceus</i> ¹	Resident	22.2 [#]	granivore	1-12	0.80 ± 1.11 (0-5.97)
Grey-headed Bullfinch	<i>Pyrrhula erythaca</i> ²	Resident	19.0 [#]	omnivore	6-10	0.06 ± 0.18 (0-1.27)

Names, migratory status, and taxonomic order were taken from Severinghaus et al. (2010). The eight species marked with an asterisk (*) occurred in every sampled year (2010-2013). Endemic species¹ and subspecies² were taken from Ding et al. (2012a). Body masses were taken from Severinghaus et al. (2010) except those marked with # which were taken from Dunning (2008). See Methods for definition of feeding guilds. The months during which each species was detected are given as numerals corresponding to January (1) through December (12). The mean density is given as mean ± standard deviation (range in brackets).

variables plus the null model which is the model that only includes the intercept. To rank the resulting eight models, we used the information theoretic approach proposed by Burnham and Anderson (2002). For each model, we calculated its AICc value, delta value, and AICc weight. The best model according to this ranking method is the model with the lowest AICc value, a delta value of zero and the highest AICc weight. We accepted only those models if two criteria were met: the model (1) had partial and total P-values of < 0.05 and (2) had a delta value < 2 which indicates 'substantial' support; see recommendations on page 170 in Burnham and Anderson (2002) and also Grabowska-Zhang et al. (2012) and Hong et al. (2016). These inferential statistics in effect mean that we accepted the null hypothesis if none or only one of these criteria were met, and we accepted the alternative hypothesis only if both criteria were met.

2.) Determining the influence of weather variables on individual species: Out of the total of 23 species, eight species had a sufficiently high abundance for individual analyses (Tables 2, 4). However, we refrained from any statistical analyses because these data contained too many zero values which excluded linear regression analysis (Martin et al. 2005). After graphically exploring these data sets, we decided *a priori* that the best way to summarize these data is to summarize observations over five equidistant intervals of rainfall, temperature, and wind speed. We then calculated the mean bird density as shown above for each interval of rainfall, temperature, and wind speed separately.

RESULTS

Description of weather

The mean temperature decreased from 8.5°C in the lowest elevation habitat to 4.7°C in the highest elevation habitat (Table 1). The highest elevation habitat, namely the rocky bushland, was also exposed to the lowest mean rainfall but the highest mean wind speed. In all habitats, rainfall and temperature displayed large monthly and annual variation, respectively, as evidenced by their large standard deviations (Table 1) and graphical fluctuations (Fig. 2), while wind speed varied much less (Table 1, Fig. 2).

Description of bird community

During our surveys, we detected 88 species, of which 23 species (Table 2) qualified for further analyses (see Methods); another 65 species (Appendix 1) were all rarely detected because they occurred at very low densities. Among these 23 species, only three were non-passerine species, and only two were migrants (Table 2). The rocky bushland had the lowest total richness and mean density, and the conifer forest by far the highest mean density (Table 1).

The smallest and largest species had body masses of 5.9 and 633.8 grams, respectively, with the mean body mass being 63.1 grams (Table 2). However, the median body mass was only 14.4 grams because the body mass frequency distribution was right-skewed. The mean body mass of the 10 most abundant species with a mean density ≥ 0.1 was significantly smaller than that of the 13 less abundant species (17.6 versus 98.1 grams; Mann-Whitney test, $U = 28.0$, $P = 0.02$). The mean body masses of the 15 insectivore, 6 omnivore and 2 granivore species were 28.6, 136.3 and 102.6 grams, respectively. By far the most abundant species was the Flamecrest whose density was more than five times higher than the next common species, the Yellowish-bellied Bush Warbler and the Streak-throated Fulvetta. Consequently, the frequency distribution of bird densities was also right-skewed, with 15 species having a density below the mean of 0.48. The only species that were recorded year-round were Coal Tit, White-whiskered Laughing-thrush, Streak-throated Fulvetta, Flamecrest, Winter Wren, and Vinaceous Rosefinch.

Influence of weather variables on species richness and bird density

Bird richness was positively correlated with temperature in each of the four habitats and also in all habitats combined, explaining from 16% to 51% of the variation (Table 3, Fig. 3). Only the model for all habitats included another independent variable, namely wind speed, which was negatively correlated with richness, but wind speed only explained an additional 7% of the variation.

Bird density was not associated with any of the weather variables within the bush forest ecotone or post-fire grassland (Table 3). However, in the conifer forest, bird density was positively correlated with rainfall and wind speed, explaining 18% of the variation. In the rocky bushland, bird

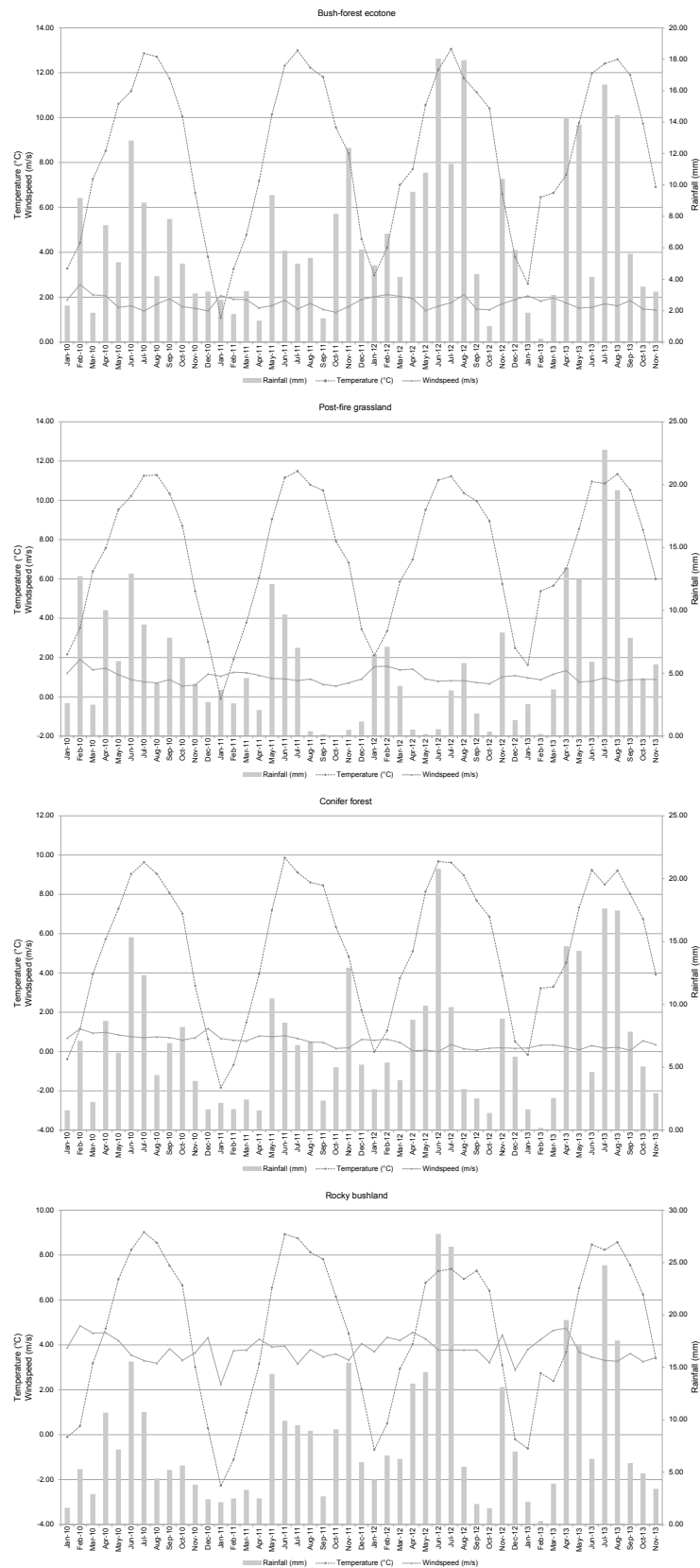


Fig. 2. Temporal variation of the three weather variables, namely temperature, rainfall and wind speed within the four habitats: (A) bush forest ecotone, (B) post-fire grassland, (C) conifer forest, (D) rocky bushland.

density was positively correlated with temperature, explaining 28% of the variation; if an outlying data point was excluded, the explained variation of this correlation increased to 44% (Fig. 4). In the model for all habitats, bird density was positively correlated with rainfall and negatively correlated with wind speed, explaining 15% and 3 % of the variation, respectively; a second alternative model only included rainfall.

Influence of weather variables on individual species

Among the eight species used in this analysis, we observed different responses to changes in the three weather variables (Table 4). While most species observed no clear trend for rainfall, two

species (Yellowish-bellied Bush Warbler, Vinaceous Rosefinch) were most abundant at intermediate rainfall levels. For wind speed, the overall picture was mixed again, although four species had the lowest density at the highest wind speed; however, Winter Wren had the highest density at the highest wind speed. Furthermore, five species had the lowest density at the intermediate wind speed interval, and each interval had at least one of the highest densities, further substantiating the mixed responses by species. The clearest pattern was observed for temperature where six species had the lowest density at the lowest temperature interval, and, among these, three species had the lowest density at the two lowest temperature intervals; the only exceptions were Coal Tit and Flamecrest.

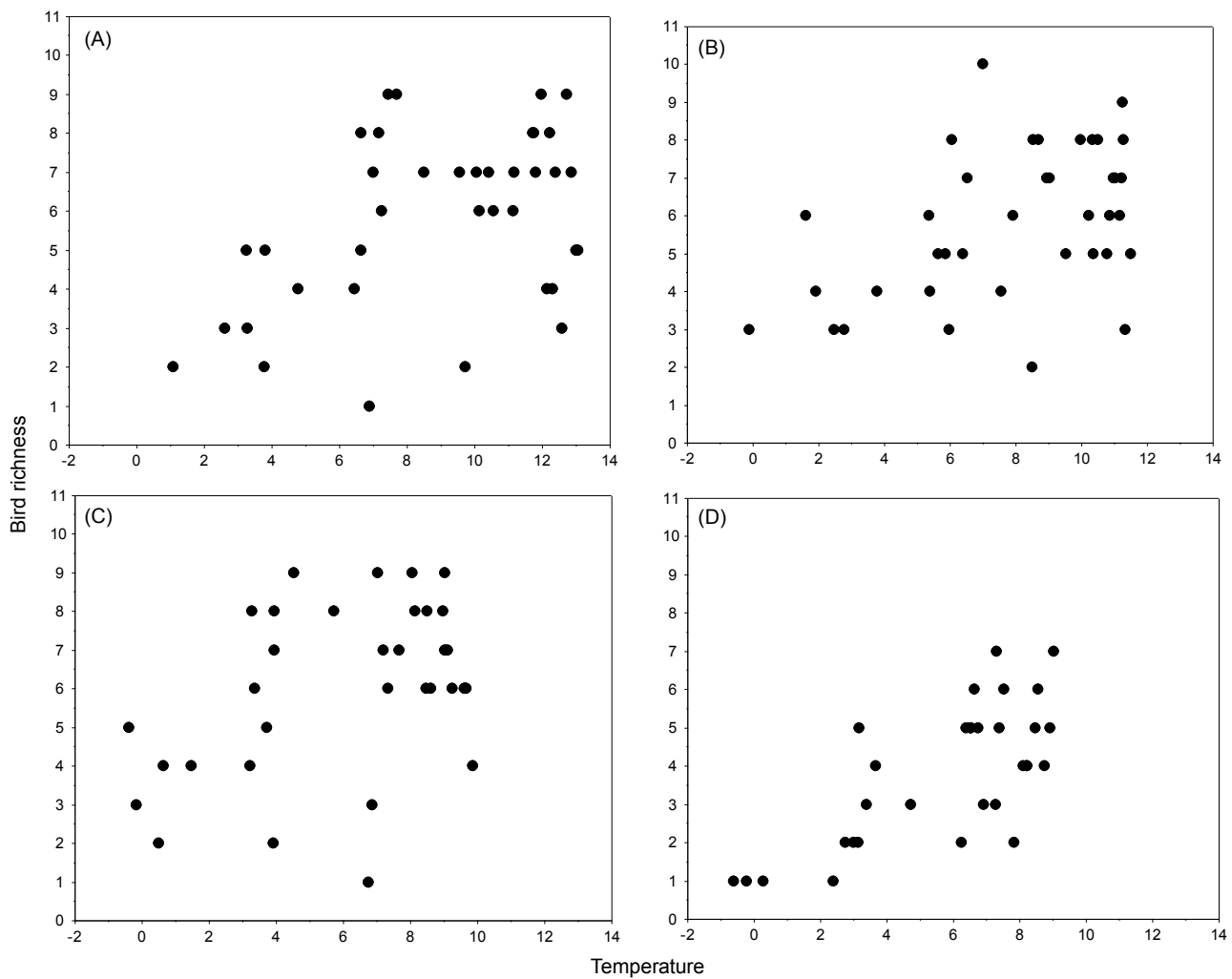


Fig. 3. Temperature (in °C) versus bird richness in four habitats: (A) bush forest ecotone, (B) post-fire grassland, (C) conifer forest, (D) rocky bushland.

DISCUSSION

The relatively low species richness and bird density recorded in this montane bird community is concordant with montane bird communities worldwide (e.g., Colwell et al. 2004; Acharya et al. 2011). The right-skewed body mass frequency distribution is also typical of most bird communities (e.g., Walther and van Niekerk 2014) as is the fact

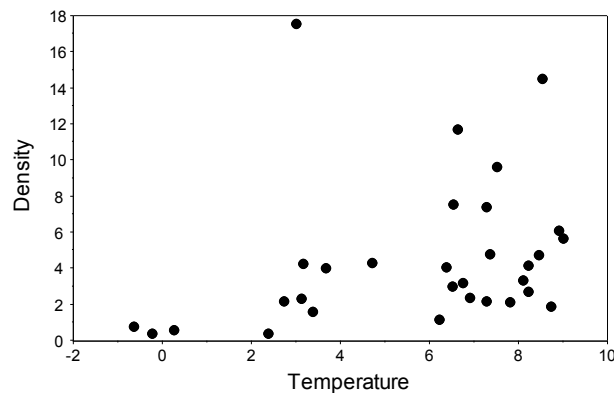


Fig. 4. Temperature (in °C) versus bird density in rocky bushland. The outlying data point (temperature = 3.01°C, density = 17.5) was due to an unusual visit of a flock of Flamecrests to the edge of the rocky bushland in November 2010.

that smaller-bodied species have a higher density (Blackburn and Gaston 1999). Thus, our study community represented a typical montane bird community.

Clearly, the weather at our study site was highly variable, and the bird richness and density of this community were also highly variable. Presumably, these variations observed by us were to some extent influenced by the prevailing weather during different months. While correlations do not prove causation, we below discuss some reasonable causal relationships. It should also be noted that the influence of weather in this study did not result from the momentary effects of these weather variables during our surveys, but were based on correlations with the month-long means of rainfall, temperature, and wind speed. Therefore, it was the prevalent weather during each month which was correlated or not with bird richness and density.

The clearest pattern emerged for the influence of temperature, both for the community-wide and the species-specific analyses. First, richness was positively correlated with temperature in each of the four habitats as well as all habitats combined, and the strongest correlation was observed for the highest-elevation habitat with the lowest mean temperature. During the coldest

Table 3. Linear regression models with ‘substantial’ support (i.e., delta < 2, see Methods) for each habitat and all habitats combined

Indep. vars.	Rainfall				Temperature		Wind speed		Total model			
	N	F	std. coeff.	partial P	std. coeff.	partial P	std. coeff.	partial P	total P	AICc	delta	AICc weight
Richness												
Bush forest ecotone	38	8.10	-	-	0.428 (18%)	0.007	-	-	0.007	29.4	0	0.43
Post-fire grassland	38	9.20	-	-	0.450 (20%)	0.004	-	-	0.004	24.7	0	0.43
Conifer forest	34	6.20	-	-	0.404 (16%)	0.02	-	-	0.02	26.9	0	0.31
Rocky bushland	31	29.9	-	-	0.713 (51%)	<0.0001	-	-	<0.0001	12.7	0	0.60
All habitats	141	31.6	-	-	0.454 (24%)	<0.0001	-0.283 (7%)	0.0001	<0.0001	81.9	0	0.65
Density												
Bush forest ecotone	38	-	-	-	-	-	-	-	-	-	-	-
Post-fire grassland	38	-	-	-	-	-	-	-	-	-	-	-
Conifer forest	34	4.01	0.344 (9%)	0.04	-	-	0.344 (9%)	0.04	0.03	18.8	0.54	0.18
Rocky bushland	31	11.1	-	-	0.526 (28%)	0.002	-	-	0.002	6.8	0	0.53
Rocky bushland*	30	21.7	-	-	0.660 (44%)	<0.0001	-	-	<0.0001	1.9	0	0.29
All habitats	141	15.5	0.305 (15%)	0.0004	-	-	-0.205 (3%)	0.02	<0.0001	41.7	0.00	0.31
All habitats	141	24.1	0.380 (15%)	<0.0001	-	-	-	-	<0.0001	42.2	0.52	0.24

For each model, the sample size (N), the F-value, the total P-value of the entire model and its AICc value, delta value, and AICc weight are given. For each independent variable within the respective model, the standard coefficient and partial P-value are given; behind the standard coefficient, the percentage variation explained by the respective variable (i.e., the increase in R² of the entire model due to the inclusion of the respective variable) is given in brackets whereby variables which explained most of the remaining unexplained variation were entered first. The variable inflation factors (VIFs) for each independent variable were all < 10. *This model for rocky bushland excluded one outlying data point (see Fig. 4).

months, only one species was detected, rising up to seven species during the warming months (Fig. 3D). Second, bird density was positively correlated with temperature in the rocky bushland, but not in the other habitats. Third, among the eight most abundant species, six species had their lowest densities at the lowest temperatures. Therefore, temperature clearly influenced the composition of this montane bird community, and this is the first study to demonstrate this effect in Taiwan and, to our best knowledge, in East Asia.

While we also detected some influences of rainfall and wind speed, the emerging patterns were much less clear cut. Rainfall was positively correlated with bird density, but only explained 15% of the variation. Wind speed was both positively and negatively correlated with bird richness and density and explained very little variation. There were no consistent results for these two variables within habitats, or for the species analyses. Therefore, rainfall and wind speed had only small effects on bird community composition.

Previous studies demonstrated relationships between bird richness and bird density and summer temperature (e.g., Enemar et al. 2004; Zhang et al. 2013), winter temperature (e.g., Greenwood and Baillie 1991; Stapanian et al. 1999; Carrascal et al. 2012), altitudinal temperature (e.g., Ferger et al. 2014), rainfall (e.g., Faaborg et al. 1984; Robinson et al. 2014) and wind speed (e.g.,

Stapanian et al. 1999). Therefore, our study adds another example from an East Asian subtropical montane bird community to these general patterns shown in various regions.

Given that only temperature showed strong and consistent effects in our study, we discuss here only possible causal reasons for temperature. The main direct effect of cold temperature is the heat loss and consequent energy expense (see Introduction for references) which then influence a bird's decision to stay or to migrate away. Since the rocky bushland had both the lowest temperatures, highest winds, and the least vegetative cover for shelter (Tseng and Tseng 2009), it seems reasonable that the effect of temperature on bird richness and density should be strongest in this habitat. Since many bird physiological processes show a threshold effect of temperature (e.g., O'Connor 1995; Willis 2007), it is also interesting to note the almost complete or complete absence of several bird species when average temperatures fell below ~4°C and ~1°C (temperature intervals 1 and 2 in Table 4). It is further interesting to note that there was no relationship between the body mass of the eight most abundant species and their propensity to be absent at low temperature or not; e.g., the smallest species, the Flamecrest, was not affected by temperature while another very small species, the Yellowish-bellied Bush Warbler, was strongly affected. Since heat loss is

Table 4. Individual species densities across five equidistant intervals of rainfall, temperature, and wind speed

Variable	Range (N)	CT	YBBW	WWLT	STF	FC	WW	CBR	VR
Rainfall interval 1	1.5-142.4 (88)	0.71 ± 0.95	0.78 ± 1.05	0.47 ± 0.61	0.93 ± 2.07	3.98 ± 7.85	0.77 ± 0.82	0.50 ± 0.54	0.67 ± 0.91
Rainfall interval 2	142.4-283.3 (26)	0.71 ± 0.48	1.18 ± 1.40	0.51 ± 0.57	1.24 ± 2.08	6.69 ± 8.89	0.71 ± 0.77	0.67 ± 0.53	0.90 ± 1.45
Rainfall interval 3	283.3-424.2 (15)	0.77 ± 0.64	1.76 ± 1.42	0.43 ± 0.31	0.81 ± 1.16	7.37 ± 9.78	0.89 ± 0.93	0.78 ± 0.66	1.30 ± 1.61
Rainfall interval 4	424.2-565.1 (9)	0.49 ± 0.57	0.95 ± 1.08	0.27 ± 0.26	0.88 ± 1.53	10.58 ± 9.62	0.89 ± 1.17	0.45 ± 0.39	1.01 ± 0.68
Rainfall interval 5	565.1-706.0 (3)	0.68 ± 0.51	0.88 ± 1.01	0.18 ± 0.16	0.39 ± 0.68	7.58 ± 13.13	0.30 ± 0.53	0.99 ± 0.49	0.77 ± 0.84
Temperature interval 1	-2.28-0.79 (8)	0.85 ± 1.77	0.00 ± 0.00	0.25 ± 0.27	0.43 ± 1.22	7.02 ± 13.27	0.10 ± 0.18	0.00 ± 0.00	0.17 ± 0.47
Temperature interval 2	0.79-3.86 (23)	0.67 ± 1.32	0.09 ± 0.22	0.48 ± 0.68	1.42 ± 3.02	4.82 ± 7.36	0.74 ± 0.70	0.25 ± 0.40	0.24 ± 0.54
Temperature interval 3	3.86-6.92 (27)	0.69 ± 0.53	0.87 ± 1.12	0.50 ± 0.75	0.56 ± 1.21	3.46 ± 6.04	1.12 ± 1.10	0.64 ± 0.59	0.75 ± 1.07
Temperature interval 4	6.92-9.99 (50)	0.74 ± 0.60	0.94 ± 1.07	0.45 ± 0.43	0.45 ± 1.21	6.32 ± 9.08	1.03 ± 0.84	0.72 ± 0.57	0.99 ± 1.18
Temperature interval 5	9.99-13.06 (33)	0.65 ± 0.48	1.95 ± 1.27	0.46 ± 0.51	1.88 ± 2.17	5.33 ± 9.21	0.29 ± 0.35	0.65 ± 0.49	1.11 ± 1.24
Wind speed interval 1	0.00-0.97 (57)	0.98 ± 0.90	0.86 ± 1.05	0.48 ± 0.52	0.60 ± 1.40	6.20 ± 9.08	0.90 ± 0.92	0.73 ± 0.60	1.26 ± 1.38
Wind speed interval 2	0.97-1.94 (45)	0.58 ± 0.82	1.36 ± 1.40	0.32 ± 0.38	2.04 ± 2.62	6.47 ± 9.80	0.54 ± 0.64	0.49 ± 0.47	0.60 ± 0.88
Wind speed interval 3	1.94-2.91 (9)	0.35 ± 0.49	1.55 ± 1.54	0.21 ± 0.21	1.08 ± 1.76	8.39 ± 7.65	0.21 ± 0.28	0.35 ± 0.49	0.17 ± 0.35
Wind speed interval 4	2.91-3.88 (20)	0.42 ± 0.57	0.54 ± 0.73	0.83 ± 0.92	0.00 ± 0.00	1.39 ± 3.59	0.95 ± 0.84	0.42 ± 0.57	0.52 ± 0.56
Wind speed interval 5	3.88-4.85 (10)	0.56 ± 0.51	0.20 ± 0.28	0.34 ± 0.23	0.00 ± 0.00	0.48 ± 1.07	1.25 ± 1.06	0.56 ± 0.51	0.20 ± 0.43

The ranges for each equidistant interval are given in the same units as in Table 1 (plus sample size N). For each species, its density is given as mean ± standard deviation. Species abbreviations are: Coal Tit (CT), Yellowish-bellied Bush Warbler (YBBW), White-whiskered Laughingthrush (WWLT), Streak-throated Fulvetta (STF), Flamecrest (FC), Winter Wren (WW), Collared Bush Robin (CBR), Vinaceous Rosefinch (VR).

negatively related to body mass (Kendeigh 1970; Walsberg 1983), and smaller species have larger mass-specific metabolic requirements (i.e., use more energy per gram of body mass) (Blackburn and Gaston 1999), one would expect the smallest species to be most affected by low temperatures. Because we did not see such a relationship, we therefore conclude that it was probably not only the direct effects of temperature which affected our study species, but also the indirect effects, such as changes in food availability. Future studies should thus attempt to determine what foods sustain the few species that remain at high altitudes even at the most adverse weather conditions, especially during the long winter.

We did not present data on food availability or predation risk in this study, but Chen et al. (unpublished data) showed that temperature at our study site was positively and significantly correlated with insect abundance and with the number of fruit-bearing plant species. Likewise, the peak of the fruiting season in Sheishan was in July and August (Tseng et al. 2012), matching the peak in temperature, and the same pattern was observed for insect abundance (Yeh and Li 2012) and grass seed abundance (Lai 2012). These studies thus concur with the general trend that food availability declines with decreasing temperatures, especially in montane habitats (e.g., Carrascal et al. 2012; Ferger et al. 2014). Therefore, the abundance of food during warm months and the lack of food during cold months is another reasonable explanation for the observed decreasing bird richness and density. Future studies should attempt to include measurements of food availability and predation risk.

Except for the long-distance migrant species, it is reasonable to assume that monthly decreases in bird richness and density were due to mostly local or regional movements of birds within Taiwan. As these birds occupy the highest available habitats, these movements invariably involve altitudinal migrations to lower-elevation habitats. Since no individual birds were marked in this study, we cannot know where they migrated to. However, it is generally known that Taiwanese birds usually move to lower elevations in response to adverse weather conditions (Severinghaus et al. 2010), and altitudinal movements of species present in Sheishan have been reported for other localities in Taiwan (Wang and Sun 1991; Wang 1992; Shiu 2003; Ding et al. 2012b). However, some species remained in abundant numbers even during the harshest winter months, e.g., Coal Tit, White-

whiskered Laughing-thrush, Streak-throated Fulvetta, Flamecrest, and Winter Wren (Tables 2 and 4), although insect abundance was then at its lowest point (Yeh and Li 2012).

Our results thus also throw up the question what kind of adaptations those of our study species which remained during adverse weather may have evolved to deal with its physiological and ecological consequences. The most common adaptation, as discussed above, is of course escape by moving to more amenable altitudes (Hejl et al. 1988; Fjeldså 1991; Hendricks and Norment 1992; Elkins 2004; Hahn et al. 2004). However, if a species remains in adverse weather conditions, then two common physiological adaptations to adapt to cold and windy conditions are: (1) lowering heat loss through increasing the body's insulation or the body's size, and (2) increasing heat production through raising the body's metabolism (Scholander et al. 1950a; 1950b; Kendeigh and Blem 1974; a less common mechanism is the lowering of the metabolism through hypothermia or torpor, see Steen 1958; Reinertsen and Haftorn 1986; Cooper and Swanson 1994). The first one can be achieved through the growth of additional feathers and accumulation of insulating body fat (Wetmore 1936; Hutt and Ball 1938; Kendeigh 1970; Dawson et al. 1983; O'Connor 1995), body posture (Scholander et al. 1950a; Steen 1958), resting in nests and/or with conspecifics (du Plessis et al. 1994), or increasing body size (often referred to as Bergmann's rule, e.g., Kendeigh 1969). Just like the first one, the second one can have both a genetic and a physiological component; in other words, species and races can evolve a higher metabolism over many generations, but individuals living in adverse conditions can also increase their metabolic rates through habituation over relatively short time periods (Kendeigh and Blem 1974; Lustick and Adams 1977; Dawson et al. 1983; Reinertsen and Haftorn 1986; Cooper and Swanson 1994; O'Connor 1995; Petit and Vézina 2014). In very cold climates, heat production can also be increased instantaneously through behavioural changes, e.g., shivering (Brooks 1968). Increasing heat production involves of course a corresponding higher energy uptake (Brooks 1968). Therefore, birds must be able to increase their energy uptake during weather conditions when usually food resources are at their lowest (see also Discussion above), e.g., by feeding on high-calorie foods such as seeds, or by increasing their digestive efficiency (Brooks 1968). In our present study, we did not study such

adaptations to harsh weather conditions in birds, but investigating such questions could become a promising future research field for montane birds in Taiwan.

CONCLUSIONS

Our hypothesis that adverse weather conditions affect the species richness and bird density of this montane bird community was supported mostly for the negative effects of colder temperatures on species richness in all habitats. Meanwhile, bird density decreased with colder temperatures only in the highest-elevation habitat which is the habitat which is most affected by cold temperatures and strong winds. The positive effect of rainfall on bird density was much weaker, and wind had almost no effect. Given the uniqueness of Taiwan's montane bird communities, further ecological and conservation studies are called for which will investigate the long-term effects of weather, climate and other ecological factors on these montane avifaunae and their ecosystems.

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Appendix 1. List of 65 bird species detected outside the basal radius during the surveys (and therefore not included in Table 2). Names and taxonomic order were taken from Severinghaus et al. (2010) and endemic species¹ and subspecies² from Ding et al. (2012a). The months during which each species was detected are given as numerals corresponding to January (1) through December (12) (download)