CORRELATES OF ELEVATIONAL SPECIALISATION IN SOUTHEAST ASIAN TROPICAL BIRDS

Kelvin S.-H. Peh
Conservation Science Group, Department of Zoology, University of Cambridge
Downing Street, Cambridge CB2 3EJ, UK
Email: kelvin.peh@gmail.com (Corresponding author)

Malcolm C. K. Soh
NUS High School of Mathematics and Science, Singapore
Email: malcolmsoh@yahoo.com

Charlotte A.-M. Yap
Email:charlotte_yp@yahoo.com

Cagan H. Sekercioglu
Department of Biology, University of Utah, 257 South 1400 East, Salt Lake City, UT 84112-0840, USA
Email: c.s@utah.edu

ABSTRACT. — The understanding of elevational selectivity in extremely rich tropical biotas is critical to the study of accelerating human-mediated environmental changes (e.g., deforestation and global climate warming). This paper explores the characteristics of Southeast Asian birds that are altitudinal specialists (i.e., lowland specialists and montane specialists) by assessing the relative importance of various species traits (e.g., breeding phenology and clutch size) in determining the altitudinal specialisation of these tropical birds. After controlling for phylogeny, we found that habitat specificity, breeding phenology, and clutch size were significant correlates of lowland specialisation. The most parsimonious model predicting lowland specialisation included the first of these only. Breeding phenology was the significant phylogeny-independent correlate of montane specialisation. Thus, species were confined to altitudinal niches by different constraints. By analysing the altitudinal distribution of Southeast Asian birds, we provide insights on why altitudinal confinement exists in lowland and montane specialists. Understanding such constraints may be important for the conservation of tropical birds.

KEY WORDS. — altitudinal specialisation, breeding phenology, climate change, generalists, habitat specificity, lowland, montane

INTRODUCTION

While some species have been observed to inhabit a wide elevation gradient (Loiselle & Blake, 1991), many species have highly restricted altitudinal ranges. For example, many birds are confined to lowland areas where they are under extreme threat from intensive habitat destruction (Brooks et al., 1999; Peh et al., 2005). Many other species are restricted to montane habitats, i.e., found only in at higher elevations. However, factors explaining birds' altitudinal specialisation are poorly understood. Species that are restricted to certain altitudinal zones may be less likely to cope with human-mediated environmental change, such as deforestation or global climate warming, than those that have a wider niche (Sodhi et al., 2004; Soh et al., 2006; Peh, 2007; Colwell et al., 2008). Thus it is critical to understand the characteristics of altitudinal specialisation in tropical biotas (see Wright et al., 2009). However, little information exists on this topic.

With rapid on-going mass destruction, conversion and deterioration of natural habitats in the tropics, the need to understand these tropical systems is more urgent. Here, we use birds as a study subject as they are relatively easy to study, have a long natural history, and significant trends in tropical ecosystems can be drawn from the wealth of bird studies (e.g., Lack, 1971; Terborgh, 1971; MacArthur, 1972).

We assess the relative importance of various species and ecological traits associated with the altitudinal specialisation of tropical birds in Southeast Asia. These traits were (1) congener density, (2) breeding phenology, (3) clutch size, (4) geographical distribution, (5) sexual dichromatism, (6)

feeding guild, (7) adult body size, and (8) habitat specificity (Gaston & Blackburn, 1995; Sorci et al., 1998; Jones et al., 2001).

We test if habitat specificity and geographical distribution are associated with altitudinal distribution, bearing in mind that common species that have lower habitat specificity do not necessarily occur at both high and low altitudes (e.g., *Garrulax erythrocephalus* [chestnut-crowned laughingthrush; a widespread montane specialist], *Megalaima haemacephala* [coppersmith barbet; a common lowland species]). Likewise, species with wider geographical ranges are not necessarily associated with both low and high altitudes (e.g., *Yuhinia gularis* [whiskered yuhinia; associated with high altitude only], *Psittacula krameri* [rose-ringed parakeet; occurring at low altitude only]).

We also investigate if the body size and congener density of Southeast Asian tropical birds are associated with their elevational specialisation. Larger species tend to be habitat or dietary generalists (Ziv, 2000; Woodward & Hildrew, 2002). Hence, they may be able to exploit a broader range of resources along the elevation gradient. Species that can be found in both lowland and montane regions may have a larger number of sympatric congeners because they may be more adaptable to different ecological niches and able to exploit different resources and thus may face less interspecific competition (Thiollay, 1997).

Previous studies have shown that nectarivores are less likely to be confined to montane regions. The reason could be that sucrose, the predominant sugar in nectar that is preferred by nectarivores, negatively correlates with elevation (Stiles & Freeman, 1993). The less reliable availability of flowers at higher altitudes may be an important constraint on the montane occurrence of nectarivores in those studies. Hence this study also tests if there is any association of altitudinal specialisation with any feeding guilds.

Sexually monomorphic species, which are more ecologically adaptable, may have a higher tolerance of environmental variability than dimorphic species because monomorphic species do not have to invest energy on the development and maintenance of sexual traits, resulting in a higher fitness of the species during periods of environmental stress (Sorci et al., 1998; McLain et al., 1999). However, results from other studies have found a positive correlation between elevational range and sexual dimorphism. For example, finches that breed over a wider elevational range have a greater distinction in plumage between sexes than finches that breed over a narrow range (Badyaev & Ghalambor, 1998). We also test if there is any association between altitudinal specialisation and the investment of tropical birds in secondary sexual characteristics.

In this study, we assess the traits that are most commonly seen in both lowland and montane specialists. Admittedly, it is not certain if these traits affect elevational specialisation and here we make the broad assumption that they may. Nevertheless, the results enable us to address the plausible existence of causal mechanisms involving ecological traits that may influence or regulate altitudinal specialisation in tropical birds. This provides insights into the extinction susceptibility and management needs of tropical birds that have restricted altitudinal ranges.

METHODS

Much of Southeast Asia occurs within the tropical belt and contains a wide range of habitats (Robson, 2000). The region for this study consists of Cambodia, Laos, Myanmar (Burma), Peninsular Malaysia, Thailand, and Vietnam. Its climate ranges from tropical to seasonal with an annual rainfall between 2000 and 3000 mm. Southeast Asia is an ideal study location for two reasons. First, the region supports a rich avifaunal diversity (>700 resident species) along an elevational range from sea level to above 3000 m, and therefore serves as a good natural laboratory for studying altitudinal specialisation in the tropics. Second, the altitudinal distributions of these bird species are well documented.

The field guide of Southeast Asian birds by Robson (2000) provided the data from which we compiled the checklists of 240 species that are confined only to lowland areas (<1000 m; the elevation cut-off is based on Peh et al., 2011); 181 species that are restricted to higher elevations (>1000 m); and 360 species that have wide altitudinal ranges covering both lowland and montane regions. Publication bias (Møller
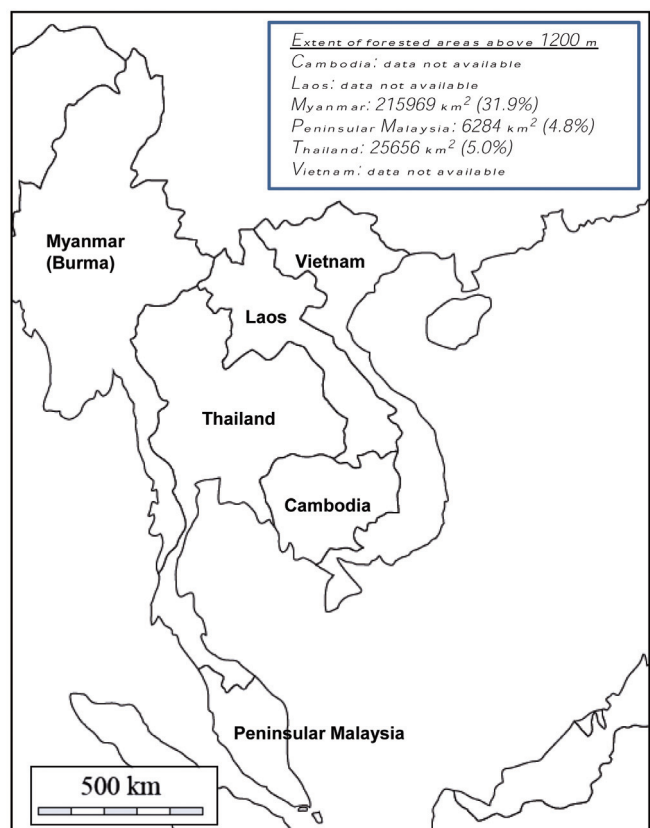

Fig. 1. Map of Southeast Asia with named countries for this study. (Map was modified from downloaded version freely available for use at http://d-maps.com/m/asieorientale/asieorientale06.pdf).

Table 1. Definitions of each bird species trait. All variables are derived from Robson (2000).

Trait	Definition
Congener density	number of congeners occurring in Southeast Asia
Breeding phenology	breeding period: either seasonal or all year round
Clutch size	mid-point of the range of eggs laid per brood
Geographical distribution	breeding/resident range in terms of km^2
Sexual dichromatism	monomorphic: both sexes have identical plumages and size
	dimorphic both sexes have different plumages (regardless of degree) or vary in size
Feeding guild	insectivore: species diet consisting of mainly insects or animal matter
	insectivore-frugivore: species with mixed diet of plants and insects
	insectivore-nectarivore: species with mixed diet of nectar and insects
Adult body size	body length averaged between the sexes
Habitat specificity	high: species restricted to one habitat type
	low: species recorded in more than one habitat type

& Jennions, 2001) for some species may occur when using sources such as field guides but the ecological data from Robson (2000) was the most recent available for the Southeast Asian avifauna. Only resident species were included in this study. As an independent check on the quality of the field guide data, we compared the information on clutch size from Robson (2000) against species accounts in the Handbook of the Birds of the World volumes 1–5 (del Hoyo et al., 1992, 1994, 1996, 1997, 1999) that do not cite Robson (2000). We used paired t-test to determine if the mid-point of the range of eggs laid per brood was substantially different between the Handbook of the Birds of the World and Robson (2000). A subset of 175 bird species was used for comparing the mid-point of the range of eggs laid per brood, and the clutch size for these species given in Robson (2000) was not significantly different from that in Handbook of the Birds of the World ($t = 1.73$, $P > 0.05$).

To assess the effects of species traits that may characterise altitudinal specialisation, we used binary logistic regression between altitudinal specialisation and each trait (i.e., for lowland and montane specialists separately). The response variables were "generalist" (code = 0) and "specialist" (code = 1). We did not code the elevational distribution as a continuous response in terms of the extent of distributional range because this does not adequately represent the elevational characteristics of a species. For example, a lowland specialist could range from 0 to 800 m whereas an elevational generalist could have a narrower altitudinal range from 700 to 1100 m only. Therefore, elevational specialisation does not equate to a narrower altitudinal range. Also, the use of a continuous response using the elevational mid-point of a species is not appropriate because of large overlaps, especially between those of the generalists and the montane specialists (Fig. 2). For example, a generalist ranging from 500 to 3500 m would have the mid-point at 2000 m. Likewise, a montane specialist restricted between the range of 1700 m and 2300 m could also have the mid-point at 2000 m.

Species trait data were taken from MacKinnon & Phillipps (1997) and Robson (2000) (see Table 1 for the definitions of each species trait). Congener density, clutch size, geographical distribution, and adult body size were continuous predictor variables. These dataset enabled us to also compare between the lowland specialists and montane specialists. The congener density ranged from 1 (e.g., *Hypogramma hypogrammicum*) to 36 (e.g., *Garrulax canorus*).Where a range of clutch sizes was reported, the mid-point of the range was calculated. The average body size was calculated if the adult body length between the genders was different. The geographical distribution was the estimated breeding range derived from the BirdLife Data Zone (http://www/birdlife.org/datazone/). Breeding phenology (seasonal or all year round), sexual dichromatism (monomorphic or dimorphic), feeding guild (insectivore, insectivore-frugivore, or insectivore-nectarivore) and habitat specificity (high or low) were categorical predictors. We followed the habitat classification scheme used by Robson (2000). Admittedly, habitat specificity—instead of being a binary variable—could be calculated as continuous indices for all species. However, this method may not be appropriate because we do not have evidence that the species with higher indices are truly able to sustain their populations in all the habitats they occur.

To control for phylogenetic bias, the analysis was repeated including family as a covariate. This is an alternative method to control for the effects of phylogenetic autocorrelations
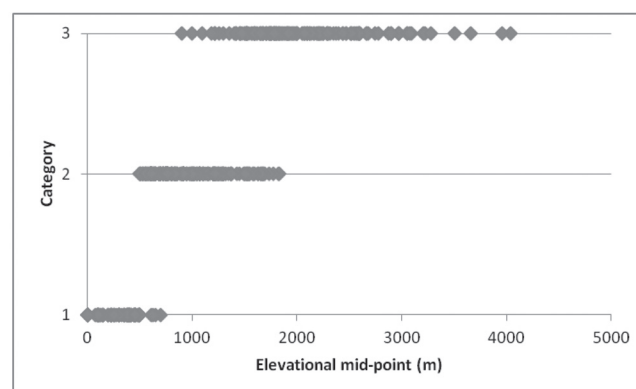

Fig. 2. Elevational mid-point versus elevational category (1 = lowland specialist; 2 = elevational generalist; 3 = montane specialist).

Table 2. Summary data of congener density, clutch size, and body length of the lowland specialists, montane specialists, and the elevational generalists.

Group	Congener density (number of congeners)		Clutch size (number of eggs)		Geographical distribution (million km²)		Body length (cm)	
	mean	± 95% C	mean	± 95% CI	mean	± 95% CI	mean	± 95% CI
Lowland	5.89	0.71	2.99	0.21	3.26	1.37	30.72	2.80
Montane	8.65	1.50	3.61	0.23	4.21	2.47	20.29	1.67
Generalist	6.45	0.81	3.28	0.14	7.37	2.37	27.04	1.99

as the inclusion of categorical variables (e.g., breeding phenology, habitat specificity) precluded the use of both nested analysis of variance and independent contrast analysis (see Koh et al., 2003).

We used principal components analysis (PCA) to check for collinearity among significant variables (Chatterjee et al., 2000). A measure of the overall collinearity of the variable was obtained by calculating the condition number (κ) which is defined by $\kappa = \sqrt{\lambda_1 / \lambda_p}$, where λ_1 is the maximum eigenvalue of the correlation matrix and λ_p is the minimum eigenvalue of the correlation matrix. Collinearity is deemed to be a problem among the variables if $\kappa > 15$ (Chatterjee et al., 2000).

To determine the most parsimonious model predicting altitudinal specialisations, we used the information-theoretical approach (Akaike's Information Criterion; AIC; see Burnham & Anderson, 1998). Since the over dispersion factor for our dataset was >1, we used AIC for over dispersed data (QAIC) to evaluate the relative strength of support for each of the candidate models. To estimate the relative importance of each predictor variable in the best model, we used QAIC on another set of models that consisted of all possible combinations of the predictor variables in the best model and calculated the sum of Akaike weights over the subset of models that included the particular variable. This method of quantifying the evidence for the importance of each variable is more appropriate than the more common use of stepwise analysis, because the latter fails to take the model selection uncertainty into consideration (Burnham & Anderson, 1998). Due to the potential issue of circularity between habitat specificity and altitudinal specialisation, we repeated the selection of the most parsimonious model without the influence of habitat specificity.

RESULTS

Generally in Southeast Asia, there is a large number of species that are seasonal breeders, monomorphic, insectivorous, and have low habitat specificity (Fig. 3). Both lowland and montane specialists are not significantly different from the elevational generalists in terms of congener density, clutch size, and body length (Table 2). However, the lowland specialists have significantly lower congener density, smaller clutch size, and larger body size than the montane specialists (Table 2).

Lowland specialisation. — Habitat specificity, body size,
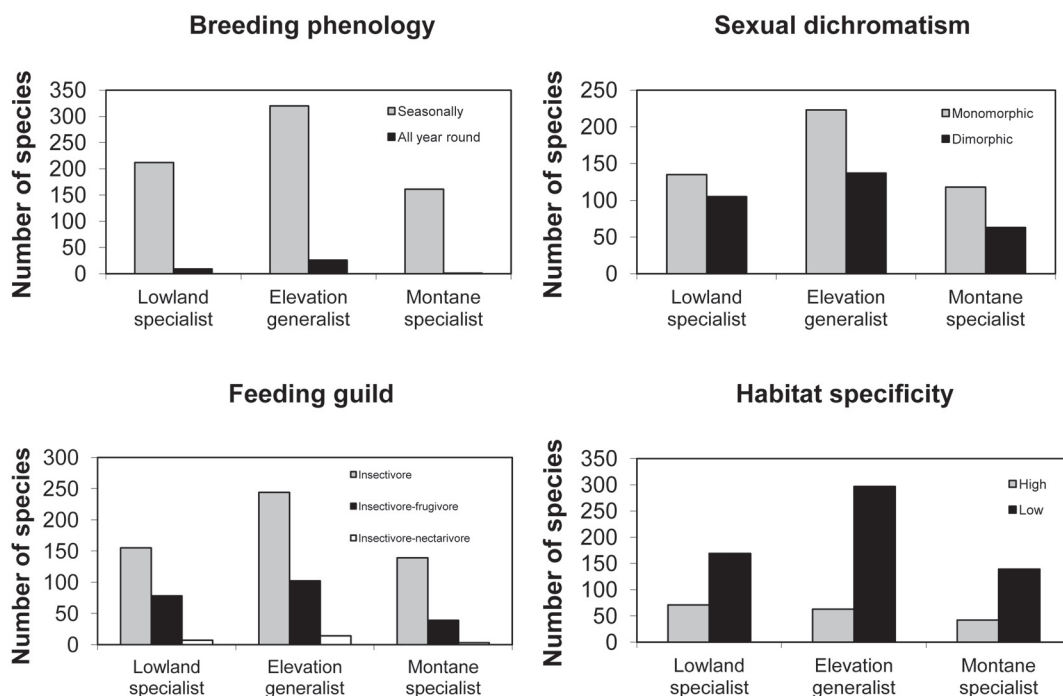

Fig. 3. Number of lowland specialists, elevation generalists, montane specialists for each trait.

Table 3. Relationship between traits of tropical bird species and altitudinal specialisation. The response variables were "non-specialisation" (code = 0) and "specialisation" (code = 1; binary logistic regression was performed for lowland specialisation and montane specialisation separately). Variables in bold are significant correlates of altitudinal specialisation after accounting for taxonomy.

Variable	n	Not controlling for taxonomy			Controlling for taxonomy		
		p	odds ratio (95% CI)	coefficient	p	odds ratio (95% CI)	coefficient
Lowland specialisation							
Congener density	600	0.34	0.99 (0.97–1.01)	-0.01	0.24	0.98 (0.95–1.01)	-0.02
Breeding phenology							
all year round	567	0.10	0.52 (0.24–1.14)	-0.65	**0.01**	**0.25 (0.09–0.75)**	**-1.37**
Clutch size	**529**	**0.02**	**0.85 (0.74–0.97)**	**-0.17**	**<0.01**	**0.53 (0.41–0.68)**	**-0.63**
Geographical distribution	154	0.02	1.00 (1.00–1.00)	0.00	0.14	1.00 (1.00–1.00)	0.00
Sexual dichromatism							
dimorphic	600	0.16	1.27 (0.91–1.76)	0.24	0.24	1.36 (0.81–2.27)	0.31
Feeding guild							
insectivore-frugivore	600	0.31	1.20 (0.84–1.72)	0.19	0.87	0.85 (0.12–6.04)	-0.16
insectivore-nectarivore	600	0.61	0.79 (0.31–1.99)	-0.24	0.92	1.13 (0.09–14.29)	0.12
Adult body size	600	0.03	1.01 (1.00–1.02)	0.01	0.75	1.00 (0.99–1.02)	0.00
Habitat specificity							
habitat specialist	**600**	**<0.01**	**1.98 (1.34–2.92)**	**0.68**	**<0.01**	**2.03 (1.27–3.23)**	**0.71**
Montane specialisation							
Congener density	541	0.01	1.03 (1.01–1.05)	0.03	0.28	0.99 (0.96–1.01)	-0.01
Breeding phenology							
all year round	**508**	**0.01**	**0.08 (0.01–0.57)**	**-2.57**	**0.03**	**0.08 (0.01–0.79)**	**-2.52**
Clutch size	463	0.02	1.20 (1.04–1.40)	0.18	0.85	1.02 (0.80–1.32)	0.03
Geographical distribution	120	0.16	1.00 (1.00–1.00)	0.00	0.73	1.00 (1.00–1.00)	0.00
Sexual dichromatism							
dimorphic	541	0.46	0.87 (0.60–1.26)	-0.14	0.15	1.59 (0.84–3.03)	0.47
Feeding guild							
insectivore-frugivore	541	0.07	0.67 (0.44–1.03)	-0.40	0.18	6.91 (0.41–117.01)	1.93
insectivore-nectarivore	541	0.13	0.38 (0.11–1.33)	-0.98	0.19	11.84 (0.29–491.59)	2.47
Adult body size	541	<0.01	0.97 (0.95–0.98)	-0.03	0.77	1.00 (0.98–1.03)	0.00
Habitat specificity							
habitat specialist	541	0.11	1.42 (0.92–2.21)	0.35	0.19	1.44 (0.83–2.49)	0.37

n denotes the number of species; CI stands for confidence interval. Complete information is not available for all species.

Table 4. Binary logistic regression models for predicting low altitudinal specialisation of Southeast Asian birds with corresponding log-likelihood, number of parameters (K), Akaike's information Criterion for overdispersed data (QAIC) score, and Akaike parameter weight (wp). ΔQAIC indicates the difference between each model and the best model (lowest ΔQAIC; rank 1). Models are ranked by ΔQAIC and wp. The best model with ΔQAIC < 2 is in bold.

Rank	Model	Log-likelihood	K	QAIC	ΔQAIC	wp
Lowland specialisation						
1	**Family + Habitat specificity**	**−335.71**	**64**	**−543.42**	**0.00**	**1.00**
2	Family + Breeding phenology	−312.11	64	−496.21	47.21	<0.01
3	Family + Breeding phenology + Habitat specificity	307.81	65	−485.63	57.79	<0.01
4	Family + Clutch size	−280.00	64	−432.00	111.42	<0.01
5	Family + Clutch size + Habitat specificity	−278.14	65	−426.28	117.14	<0.01
6	Family + Breeding phenology + Clutch size	−269.10	65	−408.20	135.22	<0.01
7	Family + Breeding phenology + Clutch size + Habitat specificity	−267.43	66	−402.86	140.56	<0.01
Lowland specialisation (excluding Habitat specificity)						
1	**Family + Breeding phenology**	**−312.11**	**64**	**−496.21**	**0.00**	**1.00**
2	Family + Clutch size	−280.00	64	−432.00	64.21	<0.01
3	Family + Breeding phenology + Clutch size	−269.10	65	−408.20	88.01	<0.01

clutch size, and geographical distribution were significant correlates of lowland specialisation ($p < 0.05$; Table 3). After controlling for taxonomy, only breeding phenology, clutch size and habitat specificity were included for the selection of the most parsimonious model predicting lowland specialisation (Table 4). Multicollinearity was not detected between these variables ($\kappa = 1.55$).

The QAIC applied to the models considered ranked the two-term model, incorporating family and habitat specificity as the highest, accounting for almost all information-theoretical weight. Thus, habitat specificity was identified as the most important ecological correlate of lowland specialisation (Table 4). Among species that were classified as lowland specialists, the odds ratio for high habitat specificity to that for low habitat specificity was 2.0 (Table 3). The logistic regression model using habitat specificity with family as a covariate for predicting lowland specialisation had the concordance, discordance and ties of 71.4%, 25.0%, and 3.7%, respectively.

Without the influence of habitat specificity, a two-term model incorporating family and breeding phenology was ranked the highest accounting for almost all the information-theoretical weight. The ratio of the odds for seasonal breeders to the odds for all-year breeders in lowland specialisation is 1.9. Using breeding phenology with family as covariate in the logistic regression model for predicting lowland specialisation had the concordance of 71.0%, discordance of 24.1%, and ties of 4.9%.

Montane specialisation. — The significant correlates of montane specialisation were congener density, breeding phenology, clutch size, and body length ($p < 0.05$). However, after controlling for taxonomy, only breeding phenology was significantly associated with montane specialisation (Table 3). In our dataset, the odds of year-round breeders being classified as montane specialists were 0.04. For seasonal breeders, the odds of being classified as montane specialists were 0.50. Among species that were classified as montane specialists, the odds ratio for being a seasonal breeder versus a year-round breeder was 13. The logistic regression models using breeding phenology with family as a covariate for predicting montane specialisation had the concordance of 80.9%, discordance of 9.5%, and ties of 9.6%.

DISCUSSION

We demonstrated that habitat specificity is the most important correlate of lowland altitudinal specialisation across all families of resident birds in Southeast Asia. Species found in the lowlands with high habitat specificity were two times more likely to be restricted to low elevations only. Conversely, those that could tolerate habitat variability tended to occur across the altitudinal gradient. Habitat specificity of some lowland specialists might be influenced by their food choice (e.g., in snails; Negovetic & Jokela, 2000). Lowland specialists might outperform generalists in their niche area but may be unable to maintain high performance (e.g., growth) over a

broader scale (i.e., across the elevational gradient) (Caley & Munday, 2003). In contrast to the findings for lowland specialists, this study did not support a restriction of montane specialists to one habitat type.

There was concern about the potential interdependence in our analyses between elevational specialisation and habitat specificity. However, we argue that there is not necessarily circularity because there are species that occur in both pristine forest and degraded areas (such as open countryside and urban areas), but are still restricted to a specific elevational zone. Some examples of lowland specialist-habitat generalists are *Picus miniaceus* (banded woodpecker) and *Psittacula longicauda* (long-tailed parakeet; Peh et al., 2006); and examples of their montane counterparts are *Alcippe castaneceps* (mountain fulvetta), *Garrulax lugubris* (chestnut-capped laughingthrush) and *Orthotomus cuculatus* (mountain tailorbird; Soh et al., 2006). Indeed, there was no evidence showing that the strictly montane group was less ecologically flexible than species with wider elevational ranges. Nevertheless, we reexamined the influence of ignoring habitat specificity in our model-building strategy and found that the model ranking according to ΔQAIC favoured the least complex model with the addition of the terms family and breeding phenology.

Overall, we found that reproductive traits are important correlates of elevational specialisation in Southeast Asian tropical birds. We demonstrated that breeding phenology was a significant correlate of both lowland and montane specialisation. Lowland and montane specialists were more likely than elevational generalists to be seasonal breeders. Such variation in life-history strategies as compared to those that occur across the elevational gradient could be caused by environmental factors. Interestingly, breeding phenology is the only significant correlate of montane specialisation. The elevational specialists, may not have the opportunity to exploit more abundant resources that may occur across a wider altitudinal range. Studies have shown that avian breeding phenology is influenced by food resource availability (e.g., Yap et al., 2007) and that strong seasonality in food resources occurs in tropical montane forests (Kimura et al., 2001). This may imply that the breeding seasons of montane specialists are strongly synchronised with the timing of food resource availability because of their inability to forage at lower elevations.

Our study has demonstrated that lowland specialists were more likely to have small clutch sizes. Although we failed to find evidence for the importance of clutch size as a correlates of montane specialisation, birds confined to the lowlands tended to have smaller clutch sizes than montane specialists, suggesting that clutch size correlates positively with elevation. This is consistent with the latitudinal gradient in clutch size that may be the result of adaptation to the greater abundance of food resources available in the breeding season relative to the non-breeding season (Griebeler & Böhning-Gaese, 2004; Jetz et al., 2008). The restricted breeding periods of high-elevation birds may be compensated by their larger

clutch size, but such compensation is not observed in low-elevation birds with shorter breeding periods. This study also failed to identify body size, congener density, sexual dichromatism, and feeding guild as important ecological correlates of altitudinal specialisation in tropical bird species. Nevertheless, our study demonstrated that caution is needed when generalising the role of body size and clutch size in the altitudinal distributions of birds. After taxonomy was controlled for, adult body size and clutch size became non-significant factors in influencing altitudinal specialisation.

Conservation implications. — The current analyses identified the characteristics of tropical birds associated with different altitudinal zones. Species may be confined to an altitudinal niche due to different constraints and understanding such constraints is important for the conservation of the tropical birds. Our findings suggest that the strictly-lowland group could be highly vulnerable to the alterations of their habitats from climate change (Sekercioglu et al., 2008; Laurance et al., 2011), land-use change (Peh et al., 2005), and invasions of introduced species (Peh, 2010). Despite the looming threats, these species would be confined to their shrinking area of occupancy due to their rigid habitat requirement (Manne et al., 1999), and be unable to move uphill (in the case of warming temperatures) or to other suitable habitats (Williams et al., 2007). Indeed, previous work has ascertained that ecological specialists are more susceptible to environmental changes as compared to ecological generalists (Fisher et al., 2003; Munday, 2004; Sekercioglu et al. 2004); and habitat specialists face a greater population declines than the generalists (Jiguet et al., 2007, 2010). However, we caution against concluding that lowland species deserve more conservation attention than montane species as habitat specificity may not necessarily be indicative of sensitivity to habitat degradation or loss. For instance, montane bird communities in Peninsular Malaysia were predicted to be more vulnerable to habitat loss than lowland communities (Soh et al., 2006).

Furthermore, the global climate, hence the phenology of the birds' breeding environment, is going to become increasingly variable during the next century (Pachauri & Reisinger, 2007). Both lowland and montane specialists—also considered thermal specialists—may not able to tolerate extreme climatic events (Jiguet et al., 2006; Loarie et al., 2009). Such phenological change could have major effects on species assemblages. Thus, some tropical elevational specialists, particularly those that are restricted to (1) a single natural habitat type only; and/or (2) a geographical area of potential climate change, should be considered potentially vulnerable to extinction and assessed regularly. In the light of our results, it is questionable whether our current knowledge alone is sufficient to prepare for the effects of climate change on tropical bird populations. We believe that conservation programmes based on basic ecological data collection, long-term monitoring, and adaptive management (i.e., periodically re-evaluating and improving current conservation practices) are the approaches for ensuring the survival of these species in our changing world.

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