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Co-occurrence of two sympatric galliform species on a landscape-scale

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Abstract. Similar species may co-occur in sympatry because of the partitioning of habitat use and resources at different spatial and temporal scales. Understanding co-occurrence patterns of species may assist in explaining patterns of habitat selection, which is important when planning conservation actions for threatened species. Little is known about the ecological preferences of Asian hill partridges, especially where multiple species co-occur. We quantitatively tested how topography and forest type affect the presence of two sympatric hill partridge species, the orange-necked partridge (*Arborophila davidi*) and green-legged partridge (*Tropicoperdix chloropus*) in forested habitats in southern Vietnam, and tested the strength of their co-occurrence at the landscape level. We surveyed the occurrence of both species using line transects. We used Poisson regression and probabilistic models to investigate the habitat requirements of both species and co-occurrence patterns. Our habitat-use models indicate that both species use shallow slopes and mosaic forest, while they tend to avoid steep slopes and bamboo forest. The orange-necked partridge seems to be confined to higher elevations while green-legged partridge is distributed over a wider elevational range. This difference in elevational range seems to drive the differences in habitat use between the two species. The orange-necked partridge appears to be strongly associated with mosaic forest, and moderately associated with evergreen forest, but mostly avoided bamboo forest and was never detected in mixed deciduous forest. The green-legged partridge was able to use multiple forest types. The probabilistic models suggest that these two species do not show significant negative or positive co-occurrence when in sympatry. This is the first quantitative data regarding habitat preferences of these sympatric tropical hill partridges at a landscape scale; we presume that their co-occurrence may be maintained by the partitioning of ecological niches or resources at a finer scale. Further research is needed to identify factors controlling their co-occurrence and potential interactions at a micro-scale. An enhanced understanding of habitat preferences of these species will be beneficial for understanding finer scale distribution patterns between species in the genus *Arborophila* and *Tropicoperdix*, especially when multiple species occur in sympatry.

Key words. *Arborophila davidi*, co-occurrence, galliformes, habitat use, sympatric, *Tropicoperdix chloropus*

INTRODUCTION

Habitat segregation has been theoretically considered and empirically found to be the most common form of sympatric-species separation (Schoener, 1974). As such, segregation can help mitigate interspecific competition between ecologically similar species and allow for co-occurrence (Pianka, 1973; Reinert, 1984). Based on the competitive exclusion principle (Hardin, 1960), sympatric congeners can reduce interspecific competition if their specific niche differentiation occurs along at least one of three basic axes of species niche space: (i) spatial differentiation, including differences in habitat (Chiang et al., 2012; Quillfeldt et al., 2013) or micro-habitat selection (Langkilde & Shine, 2004; Li et al., 2010), (ii) temporal differentiation, including daily (Pianka, 1973) or seasonal differences (Schuett et al., 2005), (iii) trophic differentiation, including differences in prey, or resources, type or size (Reynolds & Meslow, 1984; Thomas, 1985; Kaifu et al., 2013).

The galliform genus *Arborophila* is native to Asia, and includes 22 forest-dwelling species (BirdLife International, 2016). Like other galliform species, hill partridges in this genus face various anthropogenic threats, especially hunting and habitat loss (Keane et al., 2005). All are characterised by small, rounded bodies, dark brown cryptic plumage and skulking behavior (Davison, 1982; Madge & McGowan, 2010). Among these hill partridges, there are at least 14 species whose geographical ranges overlap with others in the group and 17 species have narrow distributions (BirdLife International, 2016). Recent phylogenetic analysis indicated that three species, including the widespread green-legged partridge, hereafter GLP (*Tropicoperdix chloropus*), were sufficiently divergent to be assigned to a separate genus *Tropicoperdix*, which is genetically closer to a clade

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containing chickens and allies rather than the Arborophilinae clade (Chen et al., 2015). The GLP has a wide geographical distribution that overlaps with the ranges of numerous *Arborophila* species, including the bar-backed partridge (*A. brunneopectus*) in Thailand and Vietnam, chestnut-headed partridge (*A. cambodiana*) in Cambodia, and the orange-necked partridge, hereafter ONP (*A. davidi*), in Vietnam and Cambodia (Madge & McGowan, 2010), with which it might share similar habitats. Some studies have been carried out focusing on the ecology of single species of tropical hill partridges, such as the distribution and habitat use of chestnut-bellied hill-partridge (*Arborophila javanica*) in Indonesia (Nijman, 2003), ONP in Vietnam (Vy et al., 2014), and GLP in Thailand (Ong-in et al., 2016). Overall, however, little is known about the differentiation of habitat use at micro and landscape levels, and co-occurrence patterns for tropical hill partridge genera occurring in sympatry.

Cat Tien National Park (hereafter: Cat Tien NP) contains the only sizeable lowland tropical forest in southern Vietnam (Polet & Ling, 2004), and supports at least seven galliform species, including both ONP and GLP (Atkins & Tentij, 1999; Polet & Ling, 2004). The presence of two sympatric hill partridge genera makes Cat Tien NP an appropriate site to test for co-occurrence patterns in the two species and the habitat components that influence these patterns; the sympatric ONP and GLP represent good examples for understanding habitat use at a landscape scale as well as co-occurrence patterns of tropical hill partridges in South East Asia. Belonging to two different genera, the two hill partridge species show similarities in shape, morphology and behavior, although the size of ONP seems relatively smaller than that of GLP (Madge & McGowan, 2010). Both species have different geographical ranges, being much wider in GLP (about 769,000 km^2) than in ONP (about 4,500 km^2) (BirdLife International, 2015). Such a difference in body size and range variation may render GLP more competitive and adaptable compared to the ONP when both species occur in sympatry (Brown & Sullivan, 2005; Mac Nally & Timewell, 2005; Miller & Spoolman, 2010).

In this study, we quantitatively tested how topography and forest type affect the presence of two sympatric hill partridge species, and tested the strength of their co-occurrence. Although the genus *Arborophila* is now considered distinct from *Tropicoperdix* (Chen et al., 2015), their similarities in morphology, vocalisations, and skulking behaviour (Davison, 1982) could result in similar habitat preferences at a landscape level when both species are sympatric. We tested the co-occurrence patterns of ONP and GLP in Cat Tien NP via three different approaches. We firstly modeled habitat associations using counts of species as a dependent variable and compared the results from the best-ranked habitat models (Hirzel & Le Lay, 2008). If two species coexist via differentiation of habitat use, we predicted that counts of one species would be associated with a different set of environmental variables. Conversely, if ONP and GLP had similar habitat requirements, we expected a large overlap in these habitat variables. Second, we compared models of habitat use of ONP with and without GLP (indexed using count data) as a surrogate for potential interspecific competition. High counts of GLP should be associated with low counts of ONP if there is a competitive advantage of GLP over ONP in interspecific competition. Lastly, we tested for statistically significant pair-wise patterns of species co-occurrence using probabilistic modelling in which we estimated the probability of obtaining the observed presence-absence pattern between the two species. If GLP has a negative impact on counts of ONP, there should be significant negative co-occurrence between the two species.

MATERIAL & METHODS

Study area. Cat Tien NP (720 km^2; 11°20′–11°50′N, 107°09′–107°35′E; ~ 150 km NW of Ho Chi Minh City), includes two separate sectors, named Cat Loc (in the north) and South Cat Tien (in the south). Cat Loc is characterised by small steep hills, ranging from 300–600 m above sea level (asl) intersected by streams draining into the Dong Nai river. South Cat Tien lies at an elevation from 110–300 m with some isolated hills ranging from 200–300 m in elevation (Polet et al., 1999). The vegetation of the park consists of evergreen forest (52%), mixed deciduous forest (11%), bamboo (1%), and a mosaic structurally consisting of small adjacent patches of the three previous forest types (26%), with vegetation types such as wetlands, grasslands, and agricultural land making up the remaining 10%. Cat Tien NP is located in the tropical monsoonal region with an average rainfall of approximately 2,300 mm per year, and an annual mean temperature averaging 35°C (Blanc et al., 2000; Polet, 2003) (Fig. 1).

Data collection. Surveys were carried out in Cat Tien NP during the breeding season (February to May 2014) when partridges were expected to be most vocal (Johnsgard, 1999; Robson, 2011). The surveys were conducted using line transects, following existing ranger patrolling trails. In each forest type, we set up four 2-km transects and one 1.5-km transect, while in evergreen forest we had six 2-km transects and one 1.5-km transect (Fig. 1). The surveys were carried out twice daily, in the morning (0600–0800 hours) and in the afternoon (1600–1800 hours) by one observer per transect for three consecutive days at a speed of 1 km/hour, so that each transect was walked six times in total. Based on the spatial distribution of ecological variables along transects and on the known home range sizes of GLP (6ha) (Ong-in et al., 2016), we divided transects into segments of 500 m length with a total of 84 segment sample blocks. We estimated the maximum distance at which ONP could be heard in the field to be about 120 m for all transects; consequently, buffers with 120 m width on both sides of the segments were generated and these segments contained all detections of both species for analysis.

Birds were detected both aurally and visually. However, we excluded visual detections from our analysis for consistency as there were too few and they included both males and females, in contrast to the calls, which were only from males. To minimise differences in detection skill level between surveyors, prior to data collection, all observers

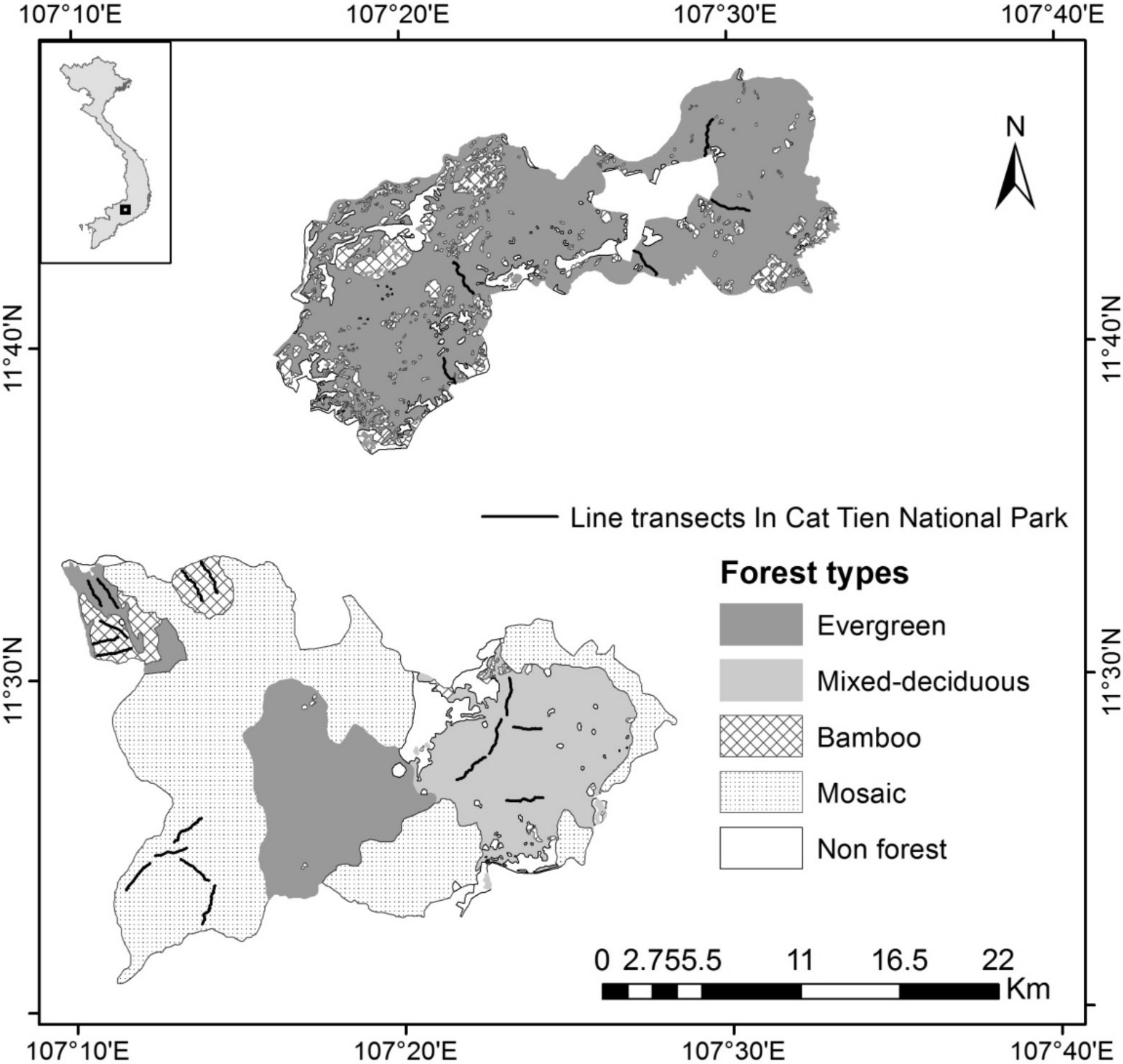

Fig. 1. Map of Cat Tien NP with five survey transects each in bamboo, mixed deciduous, and mosaic forests, and seven transects in evergreen forest.

undertook several surveys together in order to standardise distance estimations (Buckland et al., 2001). Locations with detections were identified on bearings, distances to birds and calling time, and were subsequently mapped using ArcGIS 10.3 (ESRI, Redlands, USA), thereby leading to estimates of the number of detected birds during each survey. Moreover, mapped bird locations on ArcGIS were also used, combined with the time of each detection, to eliminate potential double counts.

Environmental variables. Four environmental variables at the landscape-scale were quantified for our study: elevation, slope, forest type and distance to water sources, to examine their impacts on habitats used by the two species. These variables were used because prior studies have suggested that the ONP's distribution was associated with elevation (Madge & McGowan, 2010; Vy et al., 2014), slope (like other *Arborophila* species (Liao et al., 2007; BirdLife International, 2016) and distance to water sources (similar to other Galliformes [Liao et al., 2007; Sukumal et al., 2015]). In addition, the ONP was reported to prefer dense non-thorny bamboo forest (6–10 m high) with sparse undergrowth (Madge & McGowan, 2010) although a quantitative analysis of the species occurrence suggested that detection rates were low in bamboo forest (Vy et al., 2014). These variables were derived using ArcGIS10.3 from the following sources: (1) elevation and (2) slope extracted from the ASTER GDEM (Global Digital Elevation Model) downloaded from the Earth Remote Sensing Data Analysis Center (http://www.ersdac.or.jp), (3) river and stream system maps from the Ministry of Science and Technology, (4) forest types defined as evergreen, bamboo, mixed deciduous (Corlett, 2009) and a mosaic of those three types classified from LANDSAT 8 (2015) using supervised classification, ground-truthed by

Table 1. The two most supported models derived from a set of regression models to examine habitat use of the orange-necked partridge, ONP (*Arborophila davidi*) and green-legged partridge, GLP (*Tropicoperdix chloropus*). Counts of green-legged partridge, the presumed dominant species, were added into these models as a surrogate for potential interspecific competition in order to examine co-occurrence patterns between these species.

Species	Models and variables	K	AICc	ΔAICc	wi
ONP	(13 models tested including a null model)				
	Elevation + Slope + Forest + (1 transect)	7	359.39	0.00	0.50
	Slope + Forest + (1 transect)	6	360.35	0.96	0.31
	1 + (1 transect)	2	380.81	21.41	0.00
ONP vs GLP	Elevation + Slope + Forest + GLP + (1 transect)	8	356.95	0.00	0.43
	Slope + Forest + GLP + (1 transect)	7	357.56	0.61	0.32
GLP	(13 models tested including a null model)				
	Slope + Forest + (1 transect)	6	578.06	0.00	0.72
	Elevation + Slope + Forest + (1 transect)	7	580.11	2.05	0.26
	1 + (1 transect)	2	606.92	28.86	0.00

K is the number of parameters in the model; ΔAIC*c* is the difference in AIC*c* (model score) value, model with ΔAIC*c* value 0 has most support, values between 0 and 2 has substantial support, and values greater than 2 has less support; *wi* = Akaike model weights. Forest includes four types, bamboo, evergreen, mixed deciduous, and mosaic.

Table 2. Estimates of coefficients of environmental variables derived from model averaging (averaged across all models that contain such variables), unconditional SEs and 85% confidence intervals for habitat use of ONP with and without counts of GLP. Estimates of coefficients of environmental variables for habitat use of GLP were derived from the most supported model (72% AICc weight).

Species	Variables estimated	Coefficient	Uncond.S.E	Lower 85%	Upper 85%
ONP	Elevation	3.26	1.53	1.06	5.46
	Slope	-2.30	0.65	-3.23	-1.36
	Bamboo forest (Intercept)	-4.46	2.92	-8.68	-0.25
	Evergreen forest	2.53	1.89	-0.20	5.25
	Mixed deciduous forest	-27.59	4.94E+06	-7.12E+06	7.12E+06
	Mosaic forest	4.10	1.72	1.63	6.58
ONP vs GLP	GLP	0.29	0.13	0.11	0.48
	Elevation	3.03	1.48	0.90	5.17
	Slope	-2.04	0.65	-2.98	-1.09
	Bamboo forest (Intercept)	-4.35	2.77	-8.35	-0.36
	Evergreen forest	2.45	1.78	-0.12	5.02
	Mixed deciduous forest	-21.25	1.47E+05	-2.11E+05	2.11E+05
	Mosaic forest	3.68	1.63	1.33	6.03
GLP	Slope	-1.51	0.48	-2.23	-0.84
	Bamboo forest (Intercept)	-2.41	0.99	-3.98	-1.06
	Evergreen forest	1.54	0.97	0.18	3.06
	Mixed deciduous forest	3.42	0.88	2.26	4.86
	Mosaic forest	3.93	0.87	2.78	5.36

Values in italics correspond to unreasonably high SEs as a result of no ONP observations.

the first author (VNT), using ArcGIS 10.3. All data were re-projected to the WGS84 datum before analysis.

Data analysis. Habitat models for both species were developed using 504 surveys from 84 sample blocks. As we conducted repeated surveys on the same transect, we used multilevel Poisson regression (Gelman & Hill, 2007) to examine the association between ecological variables and the call counts of ONP and GLP. Explanatory variables (fixed effects) included elevation, slope, forest type, and distance to water sources; we treated transect ID as a random (intercept) effect. Prior to running the models, the continuous variables including elevation, slope, and distance to water sources were standardised by dividing values by twice their standard deviation (Gelman, 2008). We did not include highly correlated (r > 0.5) variables in the same regression model. To identify the appropriate error term for the response variables, we examined the distribution of our observed data by calculating the variance to mean ratio. The results of the overdispersion tests indicated a Poisson distribution was suitable for both species (ONP = 0.65 and GLP = 1.09) (Züur et al., 2009). Model selection was based on comparison of Akaike Information Criterion (AICc) values adjusted for small samples (Akaike, 1973). Akaike model weights (*wi*) were calculated as the weight of evidence in favor of model *i* among the models being compared. Model averaging was used to estimate the coefficients of models where ΔAIC*c* <2. We used 85% confidence intervals to identify variables with significant influence on species calling counts; this interval renders model selection and parameter-evaluation criteria more congruent than 95% widths (Arnold, 2010).

We tested the potential co-occurrence pattern between two species with three different approaches: Firstly, multilevel Poisson regression models were used to access the association between counts of each species and ecological variables separately and evaluate the differences in habitat use between the two species in the study sites (section above). Second, prior studies have suggested that large and medium-sized species appeared to outcompete smaller species for space and resources (Grey et al., 1997; Brown & Sullivan, 2005; Mac Nally & Timewell, 2005). For this analysis, we assumed that GLP was the dominant species when the two co-occur. Therefore, counts of GLP were used as a covariate, and added into the most supported habitat use model of ONP to test the influence of counts of GLP on the counts of ONP. Lastly, we used probabilistic models to test for statistically significant pairwise patterns of species co-occurrence (Veech, 2013), via the R cooccur package (Griffith et al., 2016). This model allows one to calculate the probability (P) that two species co-occur at a frequency either less than (P_{lt}) or greater than (P_{gt}) the observed frequency of co-occurrence. The model is based on calculating Pj, the probability that two species co-occur at exactly j sites (sample blocks). Thus, if $P_{-lt} < 0.05$, two species have a negative co-occurrence and if $P_{-gt} < 0.05$ then there is positive co-occurrence between the two species. All analyses were performed using program R version 3.2.1 (R Development Core Team, 2015) with multi-level Poisson regression analyses performed using the lme4 package (Bates et al., 2015) and model averaging using the AICcmodavg package (Mazerolle, 2015).

RESULTS

Habitat association models. A set of 13 multilevel Poisson regression models including the null (intercept) model were fitted to evaluate the association between counts of ONP and the selected ecological variables, and similarly for GLP. For the ONP, the two models with the strongest support, based on ΔAICc and AICc weights, comprised three variables: elevation, slope, and forest type (Table 1). Model averaging was used to estimate the coefficients of those variables in the confidence set (ΔAIC*c* < 2, Table 2). The counts of ONP were positively associated with elevation, where a one standard deviation increase in elevation (128 m) was associated with an average increase of 26 call detections, but ONP was negatively related to slope (fewer detections in steeper areas). The counts of ONP exhibited a stronger association with mosaic rather than evergreen forests, and was less likely to occur in bamboo forest compared to all other forest types except mixed deciduous. The species was not detected in mixed deciduous forest, which produced a model estimate with very large coefficients and standard errors (Table 2). The best fit model for GLP included slope + forest type, with 72% AICc weight (Table 1). Counts of GLP were negatively associated with slope ($\beta = -1.51$). There were also more counts of GLP in mosaic, mixed deciduous, and evergreen forests relative to bamboo forests. From both ONP and GLP results, the mosaic forest tended to support higher counts than other forest types, with the second-lowest counts observed for ONP and lowest counts for GLP in bamboo forest. Distance to water source did not influence the counts of either species (Table 2).

Models that assumed no negative effects of GLP on the counts of ONP received the strongest support, based on ΔAICc and AICc weights, and comprised three variables: elevation, slope, and forest type (Table 1 & 2). Coefficients of those variables in the models with the greatest support were obtained by model averaging (Table 2). Contrary to our expectations, the results showed that the counts of ONP were slightly positively associated with the counts of GLP in study sites where both species were in sympatry (Table 2).

Interspecific relationship between ONP and GLP. Total detections of ONP and GLP in 84 sample blocks were 15 (18%) and 38 (45%) respectively, including 7 sample blocks and 30 sample blocks where only ONPs and GLPs were detected respectively. The number of sample blocks where both species co-occurred was 8, which was not statistically different from the number of blocks they were expected to co-occur by chance (6.8, $p = 0.08$). The results of the probabilistic model revealed that these two species did not exhibit significant negative or positive co-occurrence patterns at the study site ($P_{-lt} = 0.84$, $P_{-gt} = 0.34$).

DISCUSSION

The habitat use models from this study suggest that ONP and GLP have similarities as well as differences in habitat preference. Both species tended to avoid steep slopes and bamboo forests, but appeared to be more abundant in mosaic forest, the complex structure of which might provide suitable micro-habitat for both species as well as higher food availability. GLP appears to be flexible in relation to elevation, while ONP appeared to be restricted to higher elevations, making this topographical variable the main difference in habitat requirements between the two species. ONP appeared not to use mixed deciduous forest while GLP instead exhibited a strong affinity for this habitat type. Similarly, evergreen forest was also used mainly by GLP. As a result of these similarities and differences in habitat requirements on a landscape scale, the findings from this study suggest that ONP and GLP co-occur in sympatry, sharing habitat preferences with no detectable interactions occurring between them (following Veech, 2013) at our study site.

GLP and ONP share several similarities in ecological requirements. Our analysis showed that both GLPs and ONPs significantly avoided slopes and bamboo forest.

The bamboo forest has an open canopy (Corlett, 2009) which could increase the risk of mortality due to exposure to predators. Avoiding open habitat has been observed in other hill partridge species such as common hill partridge (*Arborophila torqueola*) (Liao et al., 2007) and Sichuan hill partridge (*Arborophila rufipectus*) (Liao et al., 2008; Bo et al., 2009), both of which prefer closed canopy habitats with a low density of bamboo. This result partially contradicts that reported by Robson et al. (1993) whose results, however, were not quantitative. Though the diet of GLPs and ONPs in the wild is poorly understood, we can assume that they are like other tropical partridge species, omnivorous, mainly consuming seeds, fruits, invertebrates (including a relatively high proportion of insects), especially while rearing chicks (McGowan, 1994; Johnsgard, 1999; Madge & McGowan, 2010). Food availability could explain high counts of both species in flat areas which are considered the wettest places, while hillslopes are drier (Forman, 1995) because most water runs off from upper slopes and enters the soil on lower, flatter lands (Smith & Smith, 2012), causing higher erosion on upper slopes and increasing accumulation of eroded material including leaf litter (Smith & Smith, 2012). Deeper leaf litter layers generally sustain more diverse arthropod, reptile and amphibian populations (Lieberman & Dock, 1982; Lieberman, 1986; Fauth et al., 1989), which could be essential foods for these partridges.

Both GLP and ONP used evergreen forest but at different levels of preference. Evergreen forest was used mainly by GLP while this habitat did not appear to be important to ONP. Evergreen forest, a main component of mosaic forest in the study area, provides structural complexity with multiple layers and greater canopy cover (Park, 2003; Corlett, 2009). Preference for this structurally complex habitat type can be observed in other pheasant species in the region such as Siamese fireback (*Lopura diardi*) (Sukumal et al., 2010; Suwanrat et al., 2014) and Hume's pheasant (*Syrmaticus humiae*) (Iamsiri & Gale, 2008). Other partridges, such as common hill partridge (*Arborophila torqueola*) (Liao et al., 2007) and Sichuan hill partridge (*Arborophila rufipectus*) (Liao et al., 2008; Bo et al., 2009), also prefer closed canopies in dense broadleaf forest including primary as well as older secondary forests. This can be interpreted as a strategy to reduce vulnerability to predators. Our results suggested that both species were relatively numerous in mosaic habitat, especially ONP (Table 2). This selection could be due to the advantage of its closed canopy as mosaic forest at our study site has a major component of evergreen forest, which as mentioned above appears to provide suitable shelter for the species, while at the same time it creates a complex structural environment which could provide higher resource availability for both species, thereby reducing competition. In addition, the topography is represented by gently rolling hills with elevations ranging from 150–375 m (Blanc et al., 2000) which is suitable for the ONP (Madge & McGowan, 2010; Vy et al., 2014; BirdLife International, 2015).

Pattern of co-occurrence between GLP and ONP. Our results suggest that counts of GLP did not have a negative effect on the counts of ONP, and these two species did not show significant negative or positive co-occurrences. This suggests that there were unlikely to be strong interactions between them on a landscape scale. The positive coefficient (0.29) of GLP in the ONP model suggests that the presence of GLP has a relatively weak positive association with the counts of ONP. In addition, the positive association between counts of GLP and ONP across the range where both species occur in sympatry also suggests large overlapping habitat preferences in such areas, where their co-occurrence may be maintained by micro-habitat or other resource partitioning (Chesson, 2000). This pattern may be unsurprising given that the two species are not closely related within galliforms (Chen et al., 2015) and exhibit morphological similarities that may largely be due to convergence.

The co-occurrence of similar species in the same habitat through microhabitat partitioning to avoid competition was observed in recent studies, including a study in China in which two sympatric pheasant species, Hume's pheasant (*Syrmaticus humiae*) and silver pheasant (*Lophura nycthemera*), co-occurred in the same habitat via spatial separation of roosting trees (Li et al., 2010). Research on other avian taxa also revealed that pygmy (*Sitta pygmaea*) and white-breasted (*Sitta carolinensis*) nuthatches used different areas on trees when foraging to maintain their co-occurrence (Cloyed, 2014; Lara et al., 2015). However, our study was only conducted on a landscape scale; therefore, further research is needed to determine micro-habitat use of both species before further generalised conclusions are made regarding their co-occurrence patterns on a micro-habitat scale.

Differences in habitat preferences between GLP and ONP and their effect on the distribution of the species. For every one standard deviation increase in elevation (128 m) there was an average increase of 26 ONP detections whereas elevation did not influence the counts of GLP. This difference in elevation use between the two species may have led to the observed differences in their habitat selection, such that ONP does not occur in mixed deciduous forests in the eastern part of Cat Tien NP, as reported previously (Robson et al., 1993; Atkins & Tentij, 1999; Vy et al., 2014), as this forest type is found only in low-lying and relatively flat terrain with altitudes not exceeding 150 m (Blanc et al., 2000). It was however detected in the low hills ranging from 120–600 m (Madge & McGowan, 2010; Vy et al., 2014; BirdLife International, 2015). In contrast to the absence of ONP in this area, the habitat use models suggest that mixed-deciduous forest supported high counts of GLP (Table 2) as reported by Robson et al. (1993).

Our findings suggest that GLP is relatively flexible in both habitat and elevation use while ONP appear to be more restricted in habitat use probably mostly linked to its use of a limited range of elevations. The ability to exploit a wider range of habitats and topography in GLP could explain its wider geographical range while the limitation in habitat use for ONP could explain its restriction to a much smaller geographical range (Madge & McGowan, 2010; BirdLife International, 2015). Moreover, from our results some level of competition between the two species would seem likely. Based on the relatively large body size and its higher flexibility in habitat use, GLP could be considered dominant over ONP when in sympatry (Brown & Sullivan, 2005; Mac Nally & Timewell, 2005; Miller & Spoolman, 2010). Unfortunately, as this is the first published habitat use and co-occurrence study of two sympatric tropical partridges in South East Asia at a landscape scale, it is not possible to compare our results to other studies. Furthermore, we can assume that their co-occurrence may be maintained by partitioning their ecological niches or resources at a finer scale; thus, further studies are needed to determine factors controlling their co-occurrence and potential interactions at a micro-scale.

In conclusion, the data obtained in this study are essential not merely for developing a greater understanding of these partridges' differentiation in ecology, but also a better assessment of habitat conservation measures needed for species in the genera *Arborophila* and *Tropicoperdix*. The findings of this work also suggest that the distribution of the ONP is confined by elevation, perhaps making its geographical range narrow (BirdLife International, 2015). In addition, the remaining suitable habitats of this species face a number of threats, especially habitat loss and hunting, even in protected areas (Polet et al., 1999; Polet & Ling, 2004; Brook et al., 2011), making it increasingly vulnerable in the long term, unless relevant conservation activities are implemented.

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