

Spatial interactions between sympatric partridges in the Cardamom Mountains, Southwest Cambodia

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Abstract. How animals use space may vary according to species, presence of conspecifics and heterospecifics, and resource availability. Similar species may be sympatric by sharing resources at different spatial and temporal scales. Thus, identifying causes of variability in habitat use and home range size may increase our understanding of the functional aspects of sympatric species, which is important when planning threatened species conservation. We evaluated the spatial intra- and interspecific interaction between two closely related birds, the chestnut-headed partridge (*Arborophila cambodiana*) and scaly-breasted partridge (*Tropicoperdix chloropus*), which are thought to use similar resources and co-occur in the evergreen forest of the Cardamom Mountains, southwest Cambodia. We quantified and compared microhabitat characteristics believed to influence patterns of habitat use and home range size by comparing the topography and vegetation structure between both occupied and available locations. Binary regression and probabilistic models were used to investigate the habitat requirements of both species. We estimated the home range size of each species based on information provided by four radio-collared *A. cambodiana* and two collared *T. chloropus*. Our habitat-use models indicated that both species appear to select similar habitat by preferring dense coverage of tree seedlings shorter than 0.5 m. *A. cambodiana* has a slightly larger home range size (3.1–5.75 ha) and is restricted to steeper slopes, whilst *T. chloropus* tends to use areas closer to water sources and has a smaller home range (3.2–4.2 ha). Home ranges showed small interspecific overlap and minimal intraspecific overlap, with *A. cambodiana* having a slightly larger intraspecific home range overlap than *T. chloropus*.

Key words. Bokor National Park, scaly-breasted partridge, chestnut-headed partridge, home range, habitat use, intraspecific, interspecific

INTRODUCTION

Organisms use space and resources in varied ways (Virzi et al., 2012). Many birds defend territories and occupy delineated home ranges, which may differ widely in size depending on each species' resource needs and availability (Adams, 2001; Moorcroft et al., 2013). Habitat structure can impact resource use by birds as it relates to foraging and the securing of reproductive success (Cody, 1981; Robinson & Holmes, 1982; Gregory & Gaston, 2000). A quality habitat with rich food availability, safety from predators, and low human disturbance is important in ensuring the survival of

bird populations (Cody, 1981; Frid & Dill, 2002). Whilst numerous studies have assessed the relationship between vegetation structure and species diversity at the landscape scale, studies examining the links between home range size and microhabitat structure are less common (Castaño-Villa et al., 2014). A range of microhabitat features can determine species habitat. Topography, for example, can affect home range use by restricting access to suitable breeding and foraging habitats, food resources, and mates (Powell & Mitchell, 1998). Changes in species distribution may result from habitat alteration (Spiegel et al., 2006), which includes food resource degradation (Kimura et al., 2001; Charmantier et al., 2008) and climate change (Hansen et al., 2006; Round & Gale, 2008; Kannan & James, 2009). Climate change may impact species that are restricted to specific elevation ranges, with species normally restricted to lowland habitats moving to occupy higher elevation habitats. This could lead to detrimental effects on the resident montane species, such as reductions in their population size (Shoo et al., 2005). When moving up an elevation gradient, lowland species must adapt to the different topographies and microhabitats they will encounter (Sekercioglu et al., 2008). Studies examining microhabitat partitioning between species are even less common. Such partitioning has been shown to occur, such as between four Neotropical, terrestrial, insectivorous birds which had different microhabitat preferences in a regenerating Brazilian forest (Stratford & Stouffer, 2015). There, home

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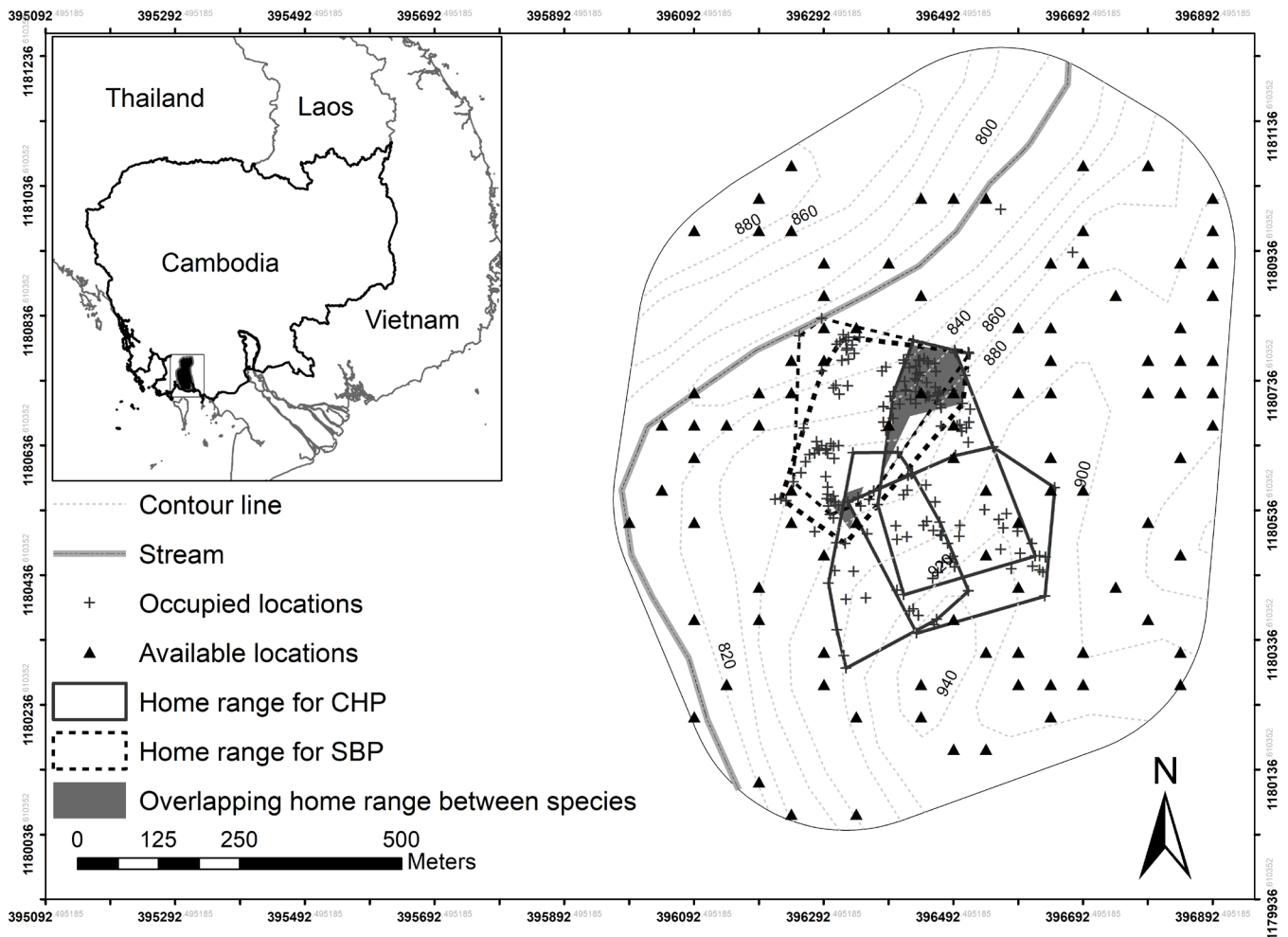


Fig. 1. Occupied and available locations, home range size, and area of overlap of the chestnut-headed partridge (CHP) and scaly-breasted partridge (SBP) in Bokor National Park, southwest Cambodia.

range size and use depended on the spatial arrangement of dense trees, species interactions, and individual physiology and behaviour (Bendel & Gates, 1987).

The galliform group of hill partridges, including the genera *Arborophila* and *Tropicoperdix*, is native to Asia, and includes 22 forest-dwelling species (BirdLife International, 2017). All are characterised by small, rounded bodies; dark brown, cryptic plumage; and skulking behaviour (McGowan et al., 1995). Among these hill partridges, the geographical ranges of at least 14 species overlap, whilst 17 species have narrow ranges (BirdLife International, 2017). Like other Galliformes, hill partridges face various threats, especially hunting and habitat loss (Keane et al., 2005). Ecological studies of tropical hill partridges are few and include studies of the distribution and habitat use of the chestnut-bellied partridge (*Arborophila javanica*) in Indonesia (Nijman, 2003), orange-necked partridge (*Arborophila davidi*) in Vietnam (Vy et al., 2017), and scaly-breasted partridge (*Tropicoperdix chloropus*) in Thailand (Ong-In et al., 2016). The chestnut-headed partridge (*Arborophila cambodiana*; hereafter CHP) of the Cardamom Mountains in southwest Cambodia prefers steep slopes (11–43°) at elevations ≥ 400 m above sea level (Chhin et al., 2018). The CHP co-occurs with the widespread scaly-breasted partridge (*T. chloropus*; hereafter SBP), which, despite having been recently demonstrated to belong

to a different genus (Chen et al., 2015), is similar in shape, morphology, and behaviour, but is slightly larger in size and has a much wider geographical range than the CHP. Given the morphological similarities between the two species it is plausible that they may directly compete for resources and occupy microhabitats similar in vegetation structure, elevation, and topography. However, other Galliformes with overlapping distributions often occupy spatially distinct habitats. In Khao Yai National Park, Thailand, two closely related *Lophura* pheasants (silver pheasant *Lophura nycthemera* and Siamese fireback *Lophura diardi*) occur sympatrically over a wide area, segregated by habitat or elevation (Round & Gale, 2008). Similarly, in southern China, Hume’s pheasant (*Syrnaticus humiae*) and silver pheasant (*Lophura nycthemera*) co-occur in the same habitat, but are spatially separated according to roosting trees (Li et al., 2010). In Cat Tien National Park, Vietnam, SBP were found to be flexible in their preferences for habitat (mixed deciduous to evergreen forests) and elevation, while orange-necked partridges (*Arborophila davidi*) were restricted to a limited elevation range (105–375 m) and had very specific habitat preferences (evergreen forest with complex structure and less bamboo) (Vy et al., 2018).

We aim to identify the microhabitats used by CHP and SBP in sub-montane forest, and estimate the home range

Table 1. Summary of habitat variables measured for the chestnut-headed partridge (CHP; n = 107), scaly-breasted partridge (SBP; n = 90), and randomly selected available locations (n = 100) in Bokor National Park, southwest Cambodia.

Variable	Variable description	Available			CHP			SBP		
		Mean	±	SE	Mean	±	SE	Mean	±	SE
Ele	Elevation (m)	859	±	2.72	873	±	1.76	866	±	1.64
Slo	Slope degree (°)	12	±	0.53	21	±	0.51	13	±	0.35
DV	Distance to stream (m)	257	±	18.08	305	±	10.24	159	±	7.02
FC	Forest cover (%)	77	±	1.73	81	±	0.92	82	±	1.13
TR	Number of trees (DBH > 30 cm)	3	±	0.24	8	±	0.48	8	±	0.49
RF1	Number of trees (Height 0–0.5 m)	133	±	8.52	483	±	23.24	458	±	25.54
RF2	Number of trees (Height 0.5–1 m)	84	±	6.01	295	±	16.81	220	±	19.09
RF3	Number of trees (Height 1–3 m)	55	±	5.48	89	±	3.71	80	±	4.55
RF4	Number of trees (Height 3–5 m)	39	±	3.88	119	±	9.43	84	±	9.12
RF5	Number of trees (Height > 5 m)	39	±	2.65	32	±	1.77	29	±	1.75
LLV	Leaf litter	64	±	2.36	69	±	1.37	71	±	1.80
RO	Presence/absence of boulders	0.11	±	0.03	0.89	±	0.03	0.85	±	0.03
PAL	Presence/absence of palm	0.16	±	0.03	0.68	±	0.04	0.74	±	0.04
RAT	Presence/absence of rattan	0.30	±	0.04	0.52	±	0.04	0.43	±	0.05

size and overlap within and between both species. With this information we test our null hypothesis of no difference in microhabitat preference between these two morphologically and behaviourally similar galliform species.

MATERIAL AND METHODS

Study site. We conducted our study in the 1,400 km² Bokor National Park (10°51'N, 104°02'E; BNP) located in the Elephant Mountains of Southwest Cambodia (Fig. 1). Elevations in BNP range from 30 to 1,079 m (Rundel et al., 2003). The average annual rainfall is more than 5,000 mm per year; it is amongst Indochina's most humid areas (Toyama et al., 2016). The mean temperature throughout the year remains at around 20°C (Rundel et al., 2003). BNP is dominated by a large massif with an extensive plateau at around 1,000 m. The park supports very large and intact areas of semi- to fully evergreen forest, with wet evergreen forests found mostly in the south (sample site area), deciduous and semi-evergreen forests in the north, and dwarf evergreen forests on top of the massif (Fig. 1).

Field methods for determining habitat use. We assessed CHP and SBP microhabitat selection by comparing the topography and vegetation structure of occupied and available

locations (Table 1). We defined occupied locations as those where birds were detected using radio telemetry. To determine available locations, we connected all occupied locations to produce a polygon in GIS, then added a 250 m buffer from the edge of the polygon to generate a 90 ha study area. Using the random point tool in ArcGIS version 10.1 (ESRI 2011), we generated 360 high-resolution 50 m × 50 m grids overlaid on a map of the study area. We then randomly selected 100 available locations as grid centre points.

Previous studies suggest that *Arborophila* species distribution is related to slope, distance to water sources, and forest structure (Madge & McGowan, 2010; Vy et al., 2014; Sukumal et al., 2015; Chhin et al., 2018). We characterised each grid by measuring 14 microhabitat variables (Table 1) within either a 5-m or 10-m radius of the centre of each grid. Within a 10-m radius, we measured elevation (Ele), slope (Slo), and distance to the nearest stream or water source (DV), by extracting data from the ASTER Global Digital Elevation Model (GDEM) (METI & NASA, 2011) at a scale of 30 m × 30 m. We identified forest structure by counting the number of canopy trees with diameter at breast height (DBH) > 0.3 m (TR), and assessed the presence/absence of rattan (RT) and palm species (PAL), of which the fruit is a food source (Simbala & Tallei, 2010; Ruppert et al., 2014). We measured Percentage Canopy Cover (FC) by using an

A4-sized, clear plastic sheet marked with a 100-cell grid, each cell measuring 2 cm × 2 cm, and counting the number of grids shaded by tree canopy. Within a 5-m radius, we assessed the number of tree seedlings of height < 0.5 m (RF1), number of trees of height 0.5–1 m (RF2), number of trees of height 1–3 m (RF3), number of trees of height 3–5 m (RF4), and number of trees of height > 5 m (RF5) (Table 1). On steep slopes, boulders trap leaf litter (Matteucci & Kertész, 2015). Thus, to record ground structure, we assessed the presence/absence of boulders larger than 0.5 m in diameter (RO) and quantified leaf litter (LLV) (into three categories based on cover: < 40%, 41–70%, and 71–100%).

Field methods for home range. We assessed CHP and SBP home range using radio telemetry. During the 2018 breeding season (between January and April), birds were live-trapped using a fishing line leg snare to be fitted with radios. To minimise the risk of injury to the birds, we lightly sprung the snare-loops using bent tree stems driven securely into the ground and checked the snares every 30 minutes. Snares were triggered automatically when a bird disturbed the loose loop. We set three snare lines comprising 100 snares per line. Snares were placed 10–20 m apart and lines were spaced at least 200 m apart. We set snares where calling male partridges were frequently heard. We caught four CHPs and two SBPs (Table 3), and each bird was fitted with a 10 g necklace radio transmitter (type RI-2B, Holohil System Ltd., Canada). These transmitters had an expected battery life of 12 months and weighed less than 5% of the bird's body weight (257–318 g) (Naef-Daenzer, 1993; Johnsgard, 1999). Each bird was then tracked using an ATS R410 Scanning Receiver from dawn to dusk and the locations were recorded using handheld GPS units (Garmin 62SC). We obtained an accuracy of within 3 m by waiting for each bird to move on before we recorded its exact location using GPS. We kept a minimum interval of two hours between two consecutive detections of the same bird, always taking care not to interrupt the bird's natural movements.

Data processing and analysis for habitat use. We used a logistic regression model with logit link function to determine the association between occupied and available bird locations with the “Stats” package in R version 3.6.0 (R Core Team, 2019). Before running the models, we standardised the continuous variables by subtracting each from its mean and dividing by two times its standard deviation: $(x - \text{mean of } x) / (2 \times \text{sd of } x)$ (Gelman, 2008). We tested for multicollinearity between explanatory variables by creating a Pearson's correlation matrix of all environmental variables and generating r values using the “GGally” package in R (Schloerke et al., 2018). We analysed candidate models by running all possible combinations of explanatory variables, with the exclusion of highly correlated variables ($|r| > 0.5$) from the same regression model. We selected models by comparing each model's Akaike Information Criterion (AICc) value adjusted for small sample size (Akaike, 1973): the difference between ΔAICc and AICc weight (AICc_{wi}) as the weight of evidence in favour of a model among all models being compared (Burnham & Anderson, 2002). We created

a model selection table using the package “wiqid” version 0.2.2 (Meredith, 2019), and selected candidate models with cut-off criteria of $\Delta\text{AICc} < 2$ (Burnham & Anderson, 2002). If the difference in AICc values between the top models was less than 2, we averaged the models using the “AICcmodavg” package in R (Mazerolle, 2019). We identified variables that strongly influenced habitat selection based on 85% confidence intervals, as this interval renders model selection and parameter-evaluation criteria more congruent than the narrower interval (95%) widths (Arnold, 2010). We assessed model accuracy using the area under the receiver operating characteristic (AUC) curve (Hosmer et al., 2013) with the “PresenceAbsence” package in R (Freeman & Moisen, 2008). We chose an optimal threshold cut-off value for classification using the minimised difference between the proportions of presences (sensitivity) and absences (specificity) correctly predicted.

Data processing and analysis for home range. We used Characteristic Hull Polygons (Downs & Horner, 2009), a non-probabilistic method of home range estimation, to calculate both species' Home Range (HR) and Core Area (CA). First, we imported all recorded locations into ArcGIS version 10.1 (ESRI, 2011) to create Delaunay triangles of several shape forms and sizes based on their density and spatial distribution. Small triangles represent areas of high ranging activity, and best represent the HR; whilst large triangles represent unused or less frequently visited areas and represent the CA. HR and CA can be calculated according to triangle perimeter length 95% and 60% of the smallest triangles respectively (Downs & Horner, 2009). Alternatively, HR can be calculated using triangles with perimeters less than two standard deviations above the mean, and CA using triangles with perimeters less than the mean (Downs et al., 2012). However, to perform a less arbitrary selection of which triangles form the HR and the CA, we used hot spot analysis in ArcGIS 10.1 (ESRI, 2011). This approach assesses whether long or short triangle perimeters are statistically clustered in space. This analysis provides a z -score with a p -value for each triangle representing its clustering intensity. Therefore, for statistically significant positive z -scores, the larger the score, the more intense the clustering of high values (hot spots of large perimeter triangles). Conversely, for statistically significant negative z -scores, the smaller the score, the more intense the clustering of low values (cold spots of small perimeter triangles). Accordingly, we eliminated long perimeter triangles that were statistically clustered (z -scores > 2), and the remaining triangles formed the HR (z -scores < 2). We used the short perimeter triangles inside the home range, classified as significantly clustered, to define the CA (z -scores < -2).

For comparison, we also calculated home range size using MCP (Minimum Convex Polygons) (Mohr, 1947) with 95% representing HR, and 50% CA. We calculated this in ArcGIS Version 10.1 with the add-in “HRT 2.0 Extension” (Rodgers et al., 2015). We calculated the percentage of overlapping HR and CA both among and between the two species using Intersect Tools in ArcGIS Version 10.1 (ESRI, 2011).

Table 2. Logistic regression models predicting the presence/absence of the chestnut-headed partridge (CHP) and scaly-breasted partridge (SBP) in Bokor National Park, southwest Cambodia. *K*, number of model parameters; $\Delta AICc$, difference in relation to the best model within the AICc; *AICc*, model score; *AICc_{wi}*, a measure of relative support for each model; AUC, area under the receiver operating characteristic curve.

Model	Variable	K	AICc	$\Delta AICc$	AICc _{wi}	AUC
Chestnut-headed partridge (20 models tested)						
1	Slope + trees (height 0–0.5 m)	3	62.88	0.00	0.69	0.99
2	Slope + trees (height 0–0.5 m) + leaf litter	4	64.50	1.54	0.31	0.99
Scaly-breasted partridge (19 models tested)						
1	Distance to stream + slope + trees (height 0–0.5 m)	4	143.34	0	0.37	0.91
2	Slope + trees (height 0–0.5 m)	3	144.31	0.97	0.23	0.90
3	Distance to stream + trees (height 0–0.5 m)	3	145.03	1.69	0.16	0.90

Table 3. Model averaging of all logistic regression models with delta AICc < 2 for both the chestnut-headed partridge and scaly-breasted partridge in Bokor National Park, southwest Cambodia. Overlap of confidence intervals with zero indicates weak or no effect. *Variables resulting from standardised data.

Variables* estimated	Coefficient	Unconditional SE	Lower 85%	Upper 85%
Chestnut-headed partridge				
Slope	6.79	1.44	4.71	8.87
Number of trees (height 0–0.5 m)	11.03	2.22	7.84	14.22
Leaf litter	– 0.46	0.69	– 1.46	0.54
Scaly-breasted partridge				
Slope	0.77	0.41	1.8	1.37
Number of trees (height 0–0.5 m)	6.05	0.98	4.63	7.46
Distance to stream	– 0.85	0.52	– 1.60	– 0.10

RESULTS

Microhabitat selection. There was a high level of correlation between several covariates, e.g., large tree density (TR), the presence of boulders (RO), and all four levels of the number of tree seedlings (RF1–4) (Fig. 2). Thus, we excluded these variables from the same model. For CHP, we evaluated microhabitat selection by testing 20 logistic regression models (Table 2). The two best models had a $\Delta AICc < 2$, with the top model having an *AICc_{wi}* double that of the second-best model. As the difference in *AICc* values between these two models was < 2, we averaged them (Table 3). This showed CHP presence to be positively correlated with steeper slope ($\beta = 6.79$) and an increasing number of small tree seedlings of height < 0.5 m ($\beta = 11.03$). However, in the averaged model, leaf litter (LLV) explained little as the 85% confidence intervals did not overlap (Table 3). Thus, CHP’s preferred habitat was nearly twice as steep as randomly selected locations (21.4 vs. 11.8), whilst the number of tree seedlings < 0.5 m in height was over 3.5 times as many as sampled at randomly selected locations (133 vs. 483) (Table 1).

For SBP, we tested 19 models of which three best explained SBP microhabitat selection, each having a difference in $\Delta AICc < 2$ (Table 2). The variables highlighted by the three models were slope, number of tree seedlings < 0.5 m high,

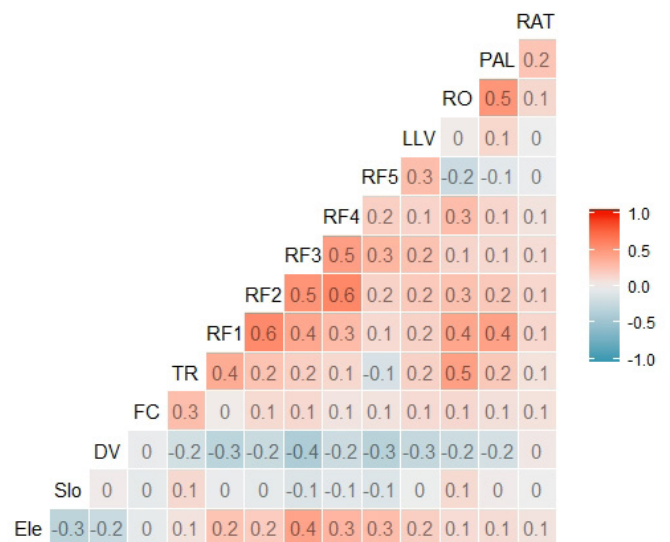


Fig. 2. Pearson’s correlation matrix of environmental covariates showing r values. Descriptions of covariate abbreviations can be found in Table 1.

and the distance to the nearest stream. As the difference in $\Delta AICc$ between the three best models was < 2, we averaged the beta coefficient. The presence of SBP was most associated with number of tree seedlings of 0–0.5 m height ($\beta = 6.05$), followed by slope ($\beta = 0.77$) and distance

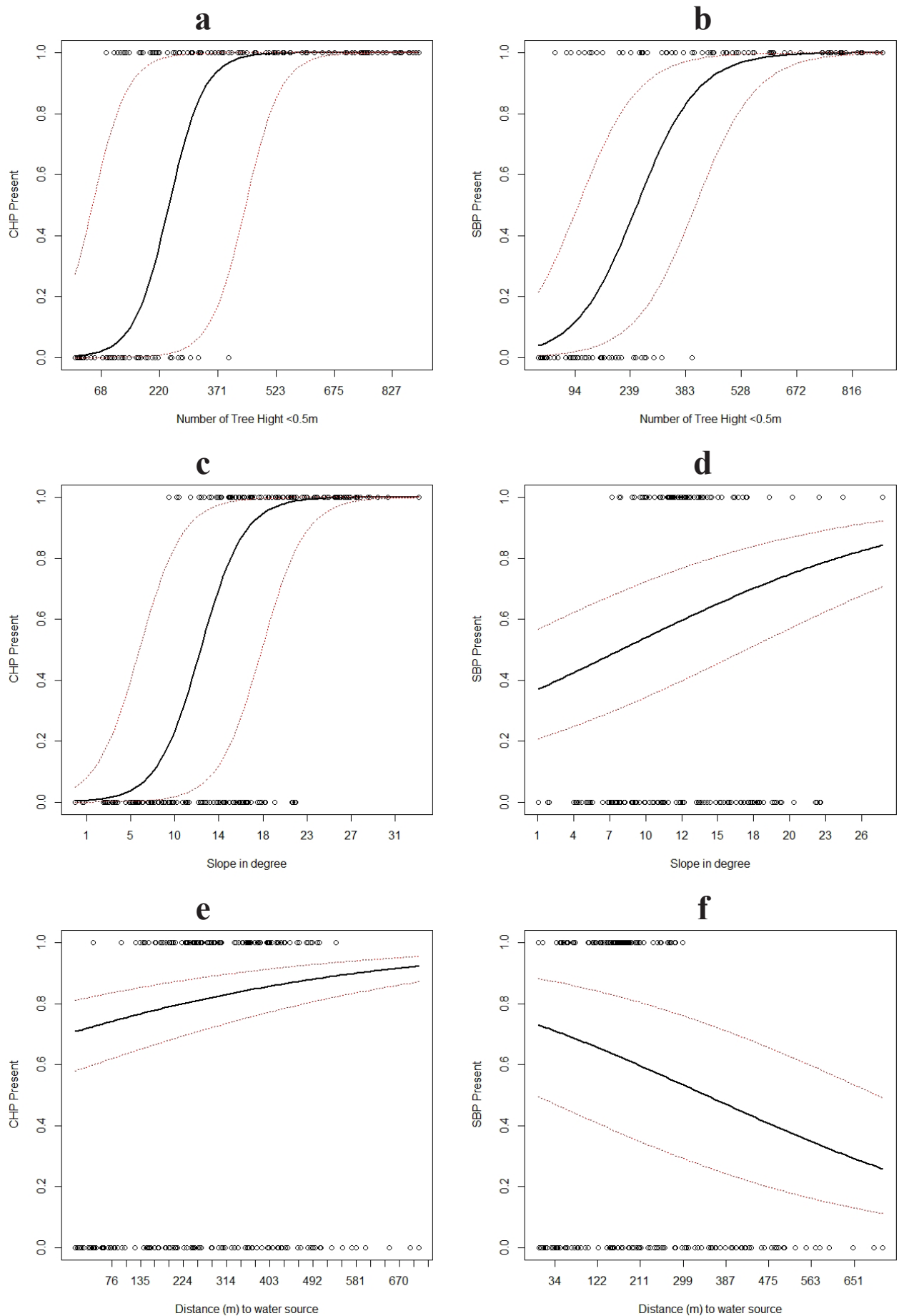


Fig. 3. Modelled probability of chestnut-headed partridge (CHP) and scaly-breasted partridge (SBP) presence as a function of three microhabitat variables (black line) with 85% confidence intervals (red lines) in Bokor National Park, southwest Cambodia. a, c, e, CHP; b, d, f, SBP.

Table 4. Home range (HR) and core area (CA) estimates in hectares for individually tracked chestnut-headed partridges (CHP) and scaly-breasted partridges (SBP) in Bokor National Park, southwest Cambodia. Estimates were made using the characteristic Hull Polygons Hot Spot Method and Minimum Convex Polygons (MCP). *CHP4, with only 11 detected locations, was excluded from the analysis.

Radio-tracked bird	Number of points	Hot spot		MCP	
		HR	CA	95%	50%
CHP1	43	5.8	1.8	5.9	1.6
CHP2	24	4.6	0.9	6.1	0.4
CHP3	29	3.1	0.2	4.6	1.5
CHP4*	11	-	-	-	-
SBP1	50	4.2	0.3	5.1	1.6
SBP2	40	3.2	1.3	4.7	1.4

to the nearest stream ($\beta = -0.85$) (Table 3). Like the CHP, SBP preferred habitats with almost 3.5 times as many small trees (height < 0.5 m) than were sampled from randomly selected locations (458 vs. 133) (Table 1). There was little difference in the slope preferred by SBP when compared to the available locations (12.8 vs. 11.8). SBP were also more likely to be found closer to streams (159 m) when compared to the random locations (257 m).

Home range size and overlap. A total of 107 locations were collected from four collared CHP and 90 from two SBP (Table 3). 11 locations used by CHP (ID CHP4) were excluded from the home range estimation due to too few detections (Mohr, 1947). From the three collared CHP with 96 detections, we estimated a home range size of between 3.1 to 5.7 ha and core area of between 0.2 to 1.7 ha. From the 90 locations detected from the two SBPs, we estimated the home range size to be between 3.1 and 4.2 ha and the core area to be between 0.3 and 1.2 ha. Different range estimators produced discrepant estimates of range sizes measured for both species. In general, hot spots produced smaller ranges than MCP (Table 3).

CHP home ranges overlapped by up to 20%. The two SBP home ranges overlapped by 34%, whilst overlap between the two species was up to 10%. There was no overlap in core area between any of the four collared CHP, compared to 17% overlap in core area between the two SBP. There was 10 to 25% core area overlap between CHP and SBP in the study area (Table 4).

DISCUSSION

Chestnut-headed partridges prefer dense understory vegetation (Fig. 3a, b) and steep slopes (Fig. 3c, d), while scaly-breasted partridges prefer similarly dense understory (Fig. 3b) but gentle slopes (Fig. 3d), and are more likely to be found closer to streams (Fig. 3f). Different slope preferences suggest that the wide-ranging SBP could possibly force the restricted-range CHP to move to more steeply sloping but lower quality habitat (e.g., Forman, 1995; Vy et al., 2018).

This may explain the CHP's larger home range than SBP. SBP's proximity to streams could be due to streams being associated with flatter terrain at the study site. As topography was the main parameter differentiating the two species' habitat selection, ignoring it may lead to misunderstanding the ecology and behaviour of montane animals (Powell & Mitchell, 1998).

CHP and SBP use similar ecological variables. Our regression model showed that CHP and SBP both prefer areas of dense low vegetation. Preference for dense vegetation may provide birds with greater protection from terrestrial predators and raptors (Ferrari, 2009; Ribeiro-Troian et al., 2009). Avoidance of open habitat has also been observed for the common hill partridge *Arborophila torqueola* (Liao et al., 2007), Sichuan hill partridge *Arborophila rufipectus* (Liao et al., 2008; Bo et al., 2009), orange-necked partridge *Arborophila davidi*, and scaly-breasted partridge *Tropicoperdix chloropus* (Vy et al., 2017). The same has been recorded for pheasants, such as Siamese fireback *Lopura diardi* (Sukumal et al., 2010; Suwanrat et al., 2014) and Hume's pheasant *Syrmaticus humiae* (Iamsiri & Gale, 2008). Those species prefer wet and closed habitats with less bamboo, like our study area, which consists of montane wet evergreen forest and lacks bamboo. Whilst the diet of CHP and SBP is poorly understood, we can assume that they, like other tropical partridges, are omnivorous, mainly consuming seeds, fruits, and invertebrates (including a relatively high proportion of insects), especially while rearing chicks (McGowan, 1994; Johnsgard, 1999; Madge & McGowan, 2010). Food availability could explain the preference of both species for habitat with dense tree seedlings, where wetter soil covered with leaf litter provides abundant seeds and diverse arthropods, small reptiles, and amphibians, which are essential foods for partridges (Lieberman & Dock, 1982; Lieberman, 1986; Fauth et al., 1989; Vy et al., 2018).

Slope was the main difference in habitat preference between the two species. CHP preferred steeper slopes whilst SBP used gentler slopes. Steeper slopes can reduce both predation risk (Lima, 1993; Hanners & Patton, 1998; Sukumal & Savini, 2009) and competition from other species (Murray et

Table 5. Percentage of home range and core area overlap among and between individual chestnut-headed partridges (CHP) and scaly-breasted partridges (SBP), Bokor National Park, southwest Cambodia. Home range (HR) variables on the bottom left and core area (CA) variables on the top right are separated by a diagonal line of blank spaces.

HR \ CA (%)	CHP1	CHP2	CHP3	SBP1	SBP2
CHP1		0.0	0.0	11.5	25.3
CHP2	21.0		0.0	0.0	0.0
CHP3	14.4	7.1		0.0	0.0
SBP1	8.5	1.5	1.8		16.8
SBP2	10.7	1.6	0.5	33.8	

al., 2008). Their preference for steeper slopes could explain why CHP do not extend through much of the Cardamom Mountains National Park south of the Gulf of Thailand, where the topography is mostly flat (Chhin et al., 2018). Several other Galliformes also show a preference for steeper slopes, including the common hill partridge *A. torquella* (Liao et al., 2007) and Sichuan hill partridge (Bo et al., 1998; Liao et al., 2007) in China, orange-necked partridge (Vy et al., 2018) in southern Vietnam, and silver pheasant (Sukumal et al., 2010) and Siamese fireback (Suwanrat et al., 2014) in eastern Thailand.

Home range. CHP has a wider home range (hot spot range: 3.1–5.75 ha) than SBP (range: 3.2–4.2 ha). Home range showed minimal intraspecific overlap for either species, with CHP having a slightly larger intraspecific overlap in home range than SBP. Home range overlap between CHP and SBP was also minimal (Table 4). However, given the small sample size, these differences may not be significant. Core use areas (50% kernels) were similar in size within and between species, with very little interspecific overlap (11–25%), suggesting that each species uses a similarly sized territorial core during the breeding season, despite potentially using different amounts of peripheral space around that principal area. The home range for both species resembles that of the lowland grey partridge *Perdix perdix* (1–7 ha) in Boora (O’Gorman et al., 1999), whilst the Sichuan hill partridge, an inhabitant of higher altitudes and steep slopes, has a larger home range (9.5 ha) in China (Bo et al., 2009).

Patterns of small home range overlap suggest strong territorial defence within and between species (Warning & Benedict, 2015). This result is similar to that of a study of two closely related wren species (*Thryomanes bewickii* and *Thryophilus rufalbus*), which exclude each other from interspecifically defended territories (Farwell & Marzluff, 2013; Battiston et al., 2015). However, it differs from two ecologically similar wrens (*Catherpes mexicanus* and *Salpinctes obsoletus*) in America (Warning & Benedict, 2015), whose home ranges overlapped by up to 68%. This study also suggested that heterospecific territory defence between both wren species was low and that these species have adopted different methods for using shared resources.

The generally larger home ranges recorded for CHP could be related to lower quality, drier, steeper slopes (Forman, 1995; Vy et al., 2018). Steeper slopes are often drier (Forman, 1995) as most water runs off upper slopes and enters the soil on lower and flatter land (Smith & Smith, 2012), causing higher erosion on steeper slopes and increasing accumulation of eroded materials, including leaf litter, which could provide essential foraging habitat. Thus, CHP may need wider home ranges in order to obtain enough resources for survival. On the contrary, SBP, inhabiting better quality flatter areas, are able to acquire enough resources in smaller home ranges (McGowan et al., 1995; Goes, 2013; Vy et al., 2018). The use of better quality habitat could be a consequence of SBP (body length: 27–32 cm) being slightly larger than CHP (28–29 cm) (Robson, 2008; McGowan et al., 2019), suggesting that SBP may be dominant over CHP where they co-occur within the same habitat (Brown & Maurer, 1986; Robinson-Wolrath & Owens, 2003; Mac Nally & Timewell, 2005; Vy et al., 2018). The two species’ microhabitat partitioning may be related to a difference in body size and range variation. SBP may be more competitive and adaptable compared to CHP when both species occur in sympatry. This would mirror the findings of Vy et al. (2017), who found that the orange-necked partridge, which is also smaller than the SBP, occupies a limited geographical range in South Vietnam.

Our study was limited as it was conducted at only one location during the dry and breeding season (January to April), and at a suitable elevation (mean 873 m) for CHP. Also, the number of birds caught and radio-tracked was sub-optimal. Thus, research across a wider range of overlapping habitat is needed to confirm our findings. Our finding that the widespread and larger-bodied SBP occupies a smaller home range habitat than the smaller-sized, restricted-range CHP suggests a despotic model of habitat occupancy (Calsbeek & Sinervo, 2002). If this is the case, we would expect to find similar relationships between SBP and other small-bodied *Arborophila*, such as the orange-necked partridge in South Vietnam (27–28 cm), red-breasted partridge (*Arborophila hyperythra*) in Borneo (25–27 cm), and collared partridge (*Arborophila gingica*) and Sichuan hill partridge in southeastern China (25–30 cm and 28–30 cm respectively) (McGowan et al., 2019), where they occur sympatrically.

CONCLUSION

Our study is one of few that have examined tropical forest hill partridge habitat use by means of radio-tracking. However, it was limited to only one location across the two species' shared distribution, and was conducted during the dry and breeding season, at a suitable elevation for CHP. In addition, we could unfortunately only capture and radio-track six birds. Nevertheless, our analysis provides an important starting point in understanding the similarities and differences in habitat use and home range size of these two species. As observed in other Galliformes, our finding confirmed that, when found sympatrically, the two species tend to separate following topographical patterns, with CHP selecting steeper habitat and seemingly occupying larger home ranges than SBP. This suggests that CHP may have less habitat flexibility, akin to the Sichuan hill partridge in China (Liao et al., 2008). SBP occupy flatter land closer to water sources and require a slightly smaller home range than CHP, which could explain why they have a wider distribution across Southeast Asia (BirdLife International, 2017). The restricted habitat of CHP found in this study, coupled with the recommendation that it be listed as near threatened (Chhin et al., 2018), suggest the need for active conservation. That CHP occupies steeper slopes likely provides some protection from logging, which is more prevalent on flatter land. However, hunting presents the greatest threat (Samnang et al., 2009), and the snares and land clearance we observed in Bokor National Park deserve attention.

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