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Combined effects of habitat and interspecific interaction define co-occurrence patterns of sympatric Galliformes

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Abstract

Background: Disentangling the relative importance of environmental variables and interspecific interaction in modulating co-occurrence patterns of sympatric species is essential for understanding the mechanisms of community assembly and biodiversity. For the two sympatric Galliformes, Silver Pheasants (*Lophura nycthemera*) and White-necklaced Partridges (*Arborophila gingica*), we know little about the role of habitat use and interspecific interactions in modulating their coexistence.

Methods: We adopted a probabilistic approach incorporating habitat preference and interspecific interaction using occupancy model to account for imperfect detection, and used daily activity pattern analysis to investigate the co-occurrence pattern of these two sympatric Galliformes in wet and dry seasons.

Results: We found that the detection probability of Silver Pheasant and White-necklaced Partridge were related to habitat variables and interspecific interaction. The presence of Silver Pheasant increases the detection probability of White-necklaced Partridge in both the wet and dry season. However, the presence of White-necklaced Partridges increases the detection probability of Silver Pheasants in the wet season, but decreases the probability in the dry season. Further, Silver Pheasants were detected frequently in the sites of high values of enhanced vegetable index (EVI) in both the wet and dry season, and in sites away from human residential settlement in the wet season. White-necklaced partridges were mainly detected in low EVI sites. The site use probabilities of two Galliformes were best explained by habitat variables, Silver Pheasants and White-necklaced Partridges preferred steeper areas during the wet and dry season. Both species mainly occurred in low EVI areas during the wet season and occupied sites away from the resident settlement during the dry season. Moreover, the site use probabilities of two species had opposite relationships with forest canopy coverage. Silver Pheasants preferred areas with high forest canopy coverage whereas White-necklaced Partridges preferred low forest canopy coverage in the dry season, and vice versa in the wet season. Species interaction factor (SIF) corroborated weak evidence of the dependence of the site use of one species on that of the other in the either dry or wet season. Temporally, high overlapping of daily activity pattern indicated no significantly temporal niche differentiation between sympatric Galliformes in both wet and dry seasons.

Conclusions: Our results demonstrated that the presence of two species influenced the detection probability interactively and there was no temporal partitioning in activity time between Silver Pheasants and White-necklaced Partridges in the wet and dry seasons. The site use probability of two Galliformes was best explained by habitat variables, especially the forest canopy coverage. Therefore, environmental variables and interspecific interaction are the leading drivers regulating the detection and site use probability and promoting co-occurrence of Silver Pheasants and White-necklaced Partridges.

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Keywords: *Arborophila gingica*, Co-occurrence, Habitat preference, Interspecific interaction, *Lophura nycthemera*, Occupancy model

Background

Understanding terrestrial vertebrates' assemblages and detecting patterns of species co-occurrence are major issues in community ecology (Hutchinson 1957; Hubbell 2001; Webb et al. 2002). Co-occurring species often partition resources along the three main niche dimensions such as habitat, diet, and activity time (Kronfeld-Schor and Dayan 2003; Davies et al. 2007; Yackulic et al. 2014; Kronfeld-Schor et al. 2017). Therefore, the mechanisms of maintaining species co-occurrence are focused on ecological niche partition, including spatial segregation (different habitat preference), different dietary preference and temporal asynchronous (activity pattern) between species, which result in decreasing niche overlap and mitigating interspecific competition (HilleRisLambers et al. 2012).

Environmental variables play key roles in shaping species co-occurrence, in term of resource utilization (Davies et al. 2007). Homogenous habitat may be used by species with similar traits and co-occur through environmental filtering (Kraft et al. 2015; Thakur and Wright 2017). Nevertheless, heterogeneous habitat supports species with different environmental requirements and utilization, allowing for species co-occurrence along resource gradients (Rich et al. 2017; D'Amen et al. 2018). Alternatively, common dispersal barriers could result in species co-occurrence, with distinctive environmental niches between species through interspecific interaction (Di Bitetti et al. 2010).

Interspecific interaction also matters in species co-occurrence (Reif et al. 2018). Negative interspecific interaction such as competition may separate the occupancy of habitat among species, through indirect exploitative competition to differentiate resource use and direct competition to prevent species coexistence (Reif et al. 2018). Several studies show that direct competition mediates the co-occurrence and range partitioning in birds (Jankowski et al. 2010; Haynes et al. 2014). The occupancy probability of Pacific loon (*Gavia pacifica*) has almost a tenfold decrease when yellow-billed loon (*G. adamsii*) presented (Haynes et al. 2014). Positive interspecific interactions such as mutualism could promote species aggregation, with the presence of one species facilitating the presence of the other interacting species (Crowley and Cox 2011). Furthermore, the combined effects of interspecific competition and environmental variables also determine co-occupancy and range partitioning in congeneric species (Bastianelli et al. 2017). Divergent habitat requirements and interspecific competition prompt pipits' co-occurrence (Bastianelli et al. 2017).

Besides the effects of habitat variables and interspecific interaction on coexistence, empirical studies have provided convincing evidence supporting niche displacement at the temporal scale (Kronfeld-Schor and Dayan 2003; Valeix et al. 2007; Di Bitetti et al. 2010). Sympatric species using similar habitats and diets exhibit low overlap in their time activity, as a mechanism to limit behavioral interactions (Tambling et al. 2015). For instance, intra-guild carnivores exhibit temporal partitioning in space use to reduce competition (Dröge et al. 2017). In addition, predator-avoid hypothesis posits that prey species shift their activity time in response to the density of predation risk (Lima and Bednekoff 1999). Hence, interspecific interaction modulates temporal niche partition in co-occurrence species (Di Bitetti et al. 2010).

Seasonal variations in environmental condition, habitat preference, and behaviors promote variations in the co-occurrence pattern. For instance, the seasonal growth of grass has an impact on grassland bird species. Habitat occupancy increased with increasing grass height and decreased with decreasing grass cover (Maphisa et al. 2018). Additionally, seasonal variation in rainfall may have limited the occupancy and detectability of mammals in Udzungwa rainforests (Martin et al. 2017). Habitat preferences of birds demonstrate seasonal shifts in human-modified landscapes during seasonal transitions for 43 forest breeding bird species (Zuckerberg et al. 2016). Although numerous studies focused on the site-occupancy pattern of diverse species, few studies investigate the seasonality of co-occurrence patterns.

Camera trapping and occupancy models provide a solution to disentangle the potential role of interspecific interaction and habitat filtering in regulating species co-occurrence (Burton et al. 2015; D'Amen et al. 2018). Occupancy models permit analyzing species interaction and habitat characteristics simultaneously, while controlling for imperfect detection (Yackulic et al. 2014; Rota et al. 2016). In comparison with other field sampling methods, camera trapping is a cost-effective method for ground-dwelling terrestrial mammals and pheasants (Ahumada et al. 2013). The broad use of camera traps provides a large amount of data to estimate species co-occurrence patterns in spatial (O'Connell et al. 2010; Bailey et al. 2014; Burton et al. 2015; Steenweg et al. 2017) and temporal scales (Rowcliffe et al. 2014; Frey et al.

2017). Therefore, the investigation of species co-occurrence and interactions with occupancy model have been used for a variety of taxa, including birds (Bailey et al. 2014; Haynes et al. 2014) and mammals, especially carnivores (Bu et al. 2016; Karanth et al. 2017; Davis et al. 2018). To our knowledge, there are few studies about co-occurrence pattern of Galliformes using camera data and occupancy model (Luo et al. 2019).

Silver Pheasants (*Lophura nycthemera*) and endemic White-necklaced Partridges (*Arborophila gingica*) have a moderate overlap in their geographic ranges, especially in Nanling Mountains, where Chebaling National Nature Reserve is located (Zhao 2001; Zheng 2017). Previous studies indicated that Silver Pheasants and White-necklaced Partridges selected similar habitats including primary and secondary forested, and some open habitats (Zhao 2001).

In this study, we aimed to illustrate co-occurrence patterns of the two Galliformes based on the camera trapping data in the Guangdong Chebaling National Nature Reserve. Specifically, we prove the co-occurrence pattern in three aspects, habitat preference in the either wet or dry season, species interaction factor or temporal overlap patterns. In doing so, we want to test the following hypotheses. First, there are niches partition of two species at least on one niche dimension. Secondly, resource utilization is the most important niche dimension promoting co-occurrence, because low direct conflict among two species leads to weak interaction and highly temporal overlap. Thirdly, niche utilization differs greatly in the wet season than that in the dry season, since there are more resource requirements for breeding in the wet season.

Methods

Study site and regions

This study was conducted in Chebaling National Nature Reserve, Shaoguan, Guangdong Province, in southern China, located between 24°40′29″–24°46′21″N, 114°09′04″–114°16′46″E and totaling around 7545 ha. As a transitional zone between tropical and subtropical forest, Chebaling nature reserve is important for protecting typical subtropical evergreen broadleaf forests and rare flora and fauna (Cai and Song 2005). In the reserve, about 1928 plant species and 1558 animal species have been identified and documented (Cai and Song 2005). Vegetation on the study site mainly consisted of *Castanopsis carlesii*, *C. eyrie*, *Lithocarpus glaber*, *Schima superba*, *Liqnidambar formosana* (Shu et al. 2017). Moreover, there are about 259 bird species, mainly including *Hypsipetes leucocephalus*, *Hemixos castanonotus*, *Dendrocitta formosae*, *Lophura nycthemera*, *Arborophila gingica*, *Myophonus caeruleus*, *Turdus hortulorum*, *Garrulax pectoralis*, *Alcippe morrisonia*, *Yuhina castaniceps* (Song and Zou 2017). The climate is typical subtropical monsoon climate, with an average annual temperature of 19.6 °C, ranging from −5.5 °C to 38.4 °C, and an average annual rainfall of 1468 mm, ranging from 1150 to 2126 mm.

Camera trapping survey

We deployed 80 camera stations at Chebaling National Nature Reserve, systematic covering all the reserve area across 80 km^2 from December 2016 to January 2018. This investigation period included dry and wet seasons (the wet season spans from May to July and the dry season spans from October to December). We discretized the reserve into an array of 80 grid cells of 1-km^2 to guide the placement of cameras (Fig. 1). The spacing between camera sites was about 300 m, which is smaller than the diameter of the partridge home range. One assumption of the occupancy model is occupancy status at each site keeps constant during the survey season (closure assumption), which seems likely to be violated (MacKenzie et al. 2017). In order not to circumvent the closure assumption, we used the estimated parameter as local site use probability rather than true occupancy (Latif et al. 2016). We placed camera traps (Ltl Acorn® 6511 MC, Shenzhen, China) in areas based on track and sign knowledge of local guides to increase the capture probability of wildlife (Ahumada et al. 2013). We mounted cameras on trees at a height of 0.5 m from the forest floor, facing away from any dense vegetation that would severely obstruct the camera image or cause false-trigger events. We programmed cameras in photo and video pattern, with three images (image size, 5 MP) and one 10-s video captured per trigger event, and the interval was set at 1 s. We visited cameras at the interval of 3 months to exchange memory cards and batteries during the study session.

Finally, we collected data from 80 camera stations and storage the data in CameraData database (www.cbl.cameradata.ioz.ac.cn). Images were classified to species level and removed those cannot be identified. To address the independence of camera observations, we mandated independent detections of a species as photo events separated by ≥ 30 min between observations of the same species in one camera station unless different individuals could be distinguished. We recorded the maximum number of individuals in independent events as an abundance of this trigger event unless different individuals can be recognized.

Environmental variables

We expected that geographical characteristic (elevation and slope), environmental variables [including forest canopy coverage and vegetation productivity (enhanced

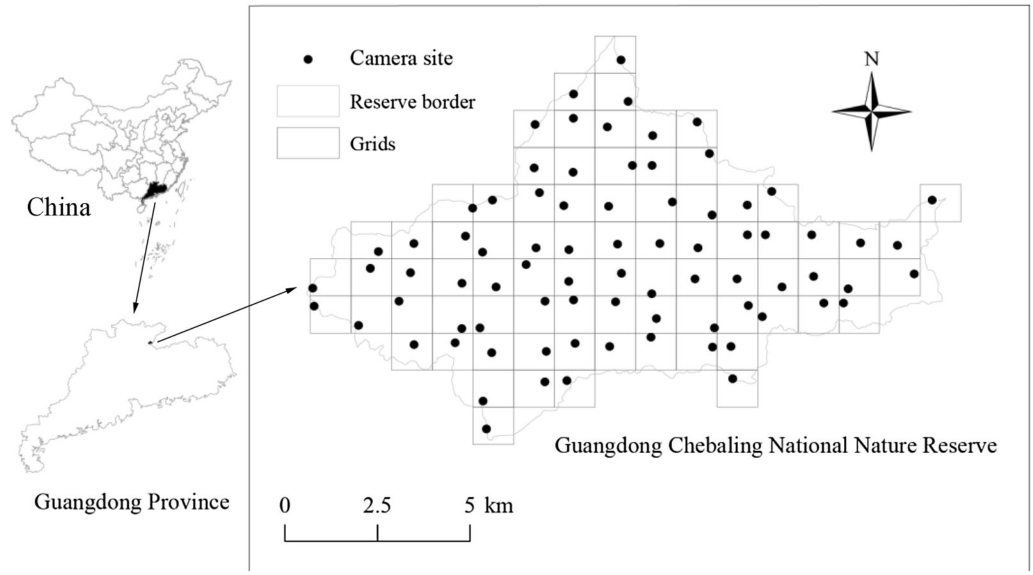

Fig. 1 Study area and camera stations distributed in Chebaling National Nature Reserve, Guangdong Province, China. Black dots denote camera stations, light gray line denotes the reserve border, and gray squares denote grid cells with a size of 1 × 1 km^2

vegetation index, EVI)], human disturbance (the nearest distance to resident settlement, distance for short) and the height of camera placement (height for short) may influence seasonal detection and occupancy patterns of two Galliformes species. Detection probability were influenced by camera placements, camera days, baits or lures and human disturbance (O'Connor et al. 2017). Among those covariates, camera height, EVI and the nearest distance to the resident settlement were used to model detection. The choice of the covariates of occupancy model was mostly governed by knowledge about the ecology and life histories of two Galliformes. As illustrated in Zheng (2015), EVI, forest canopy coverage, elevation, and slope were the main environmental variables determining distribution of two Galliformes, so we used these variables to model occupancy.

Environmental variables were measured in the field and from existing GIS layers. We determined vegetative cover using the annual forest inventory data of the reserve and then rescale to each camera site grid. We extracted elevation and slope data from ASTER GDEM (https://lpdaac.usgs.gov, ASTER GDEM is a product of NASA and METI) and acquired the average value in each sampling grid. We derived land use and land cover data from digital maps of vegetation and topographic features, which are from high-resolution multispectral satellite data to detect resident settlement and infrastructure (Chinese GF-1 Satellite Imagery, the GF-1 dataset used in our study was available by the satellite environment center of the Ministry of Environmental Protection, http://www.secmep.cn). Then, we measured the Euclidean distances of each camera site to the nearest resident settlement and infrastructure (abbreviated as "distance" in the following context) using ArcGIS 10.2. We derived the EVI from Landsat 8 in the whole year of 2017 with cloud cover less than 80% for a Landsat scene centered over the reserve, calculated the EVI values at each pixel (remove cloud covered pixels), and then acquired the average EVI in wet and dry season (EVI_wet and EVI_dry, for short in following context), rescaled to one km^2 grid cell.

Statistical analysis

Single season, co-occurrence occupancy model

To estimate occupancy for each species and test if the presence or detection of one species influences the presence or detection of the other species, we used two-species occupancy models proposed by (MacKenzie et al. 2004). The two-species occupancy model was used to investigate co-occurrence patterns between species while accounting for imperfect detection and site characteristics (MacKenzie et al. 2004, 2017). The two-species occupancy model relies on a closure assumption as in single species occupancy model, which prohibits changes in occupancy state among repeated sampling sessions (MacKenzie et al. 2002; Kendall and White 2009). However, the closure assumption can be violated when the interval of repeated occasions is long enough to allow species to move among sampling cells. To do not circumvent the closure assumption, researchers define the estimated parameter from "occupancy" to "use" (Latif et al. 2016).

We created two species capture histories, discretized camera data into 10-day intervals, recorded 1 represented when only the dominant species was detected for each trap interval at each camera station, 2 represented when only the subordinate species was detected, 3 represented both species were detected and 0 when neither of two species was detected. The capture histories were organized per species in a matrix with 80 sites (rows) by 9 periods (columns) in the wet season and dry season, respectively.

We used a multi-stage approach to build our single season two species co-occurrence occupancy models (Schuette et al. 2013; Santos et al. 2019). We firstly investigated species effects and interaction on the detection while holding two species occupancy constant, and then estimated covariates' effects (including distance to the nearest residential area, EVI and camera height) on the detection of two species based on models including interaction or no-interaction effects. We constructed all possible models with a single predictor variable or variables combinations. Based on the top detection models, we constructed two models sets to assessed interspecific interaction effects and covariates effects on the occupancy. One model set included species effect and covariates effects, the other set included species effects, covariates effects, and interaction effects. Lastly, we selected the top occupancy models from all models in two sets.

We used information-theoretic approaches to select the most parsimonious model and competing models, models with the lowest value of Akaike information criterion (AIC) or highest Akaike weight (w) were considered the most parsimonious model, and competing model if they had a $\Delta\mathrm{AIC} \leq 2.0$ (Burnham and Anderson 2004). Specifically, we selected the most parsimonious detection model and competing occupancy models to investigate the effect of covariates, and calculated parameter and beta estimates using model-averaged unless the top co-occurrence model was strongly supported (model weight $\geq 80\%$; Burnham and Anderson 2004). Then we draw inference about species' pattern for detection (δ) and occupancy (ψ) according to the species interaction factor (SIF), which was estimated from model-average parameters (Richmond et al. 2010). Values of $\delta < 1$, suggests two species are co-detected less than expected by chance, while $\delta > 1$ suggests two species are co-detected more frequently than expected, and $\delta = 1$ suggests two species are detected independently. Values of $\psi < 1$ would suggest species avoidance (co-occur are less than expected by chance), while $\psi > 1$ would suggest species co-occur more frequently than expected, and $\psi = 1$ would suggest species occur independently (Richmond et al. 2010).

Activity analysis

To estimate the animal activity pattern, we used kernel density estimation on circular data based on the time of independent capture event of each species (Ridout and Linkie 2009). Then, we measured the coefficient of overlap (Δ, range from 0 to 1 no overlap to complete overlap) of the active curve of species pairs and the confidence intervals by bootstrapping 1000 samples from the estimated probability density function of each species. At last, we tested the significance of the difference between the two species' activity curve.

We conducted all analysis and estimated parameters in the statistical software R 3.5.1 (R Core Team 2018). We analyzed data and model averaging in single-season, co-occurrence occupancy model with package RPresence (Version: 2.12.20; MacKenzie and Hines 2018), activity analysis with package overlap (Version: 0.3.2; Meredith and Ridout 2018) and package activity (Version: 1.1; Rowcliffe 2016).

Results

During the investigation of Chebaling National Nature Reserve in 2017, we obtained 246 independent capture events in 10-day intervals for Silver Pheasants and 33 independent capture events for White-necklaced Partridges with survey efforts of 6808 camera-days from 80 camera sites in the wet season. We recorded 280 for Silver Pheasants and 44 for White-necklaced Partridges with survey efforts of 6808 camera-days from 80 camera sites in the dry season. In addition, we recorded 13 and 15 co-occurrence events in the wet and dry season, respectively.

The probability of detection in single-season, co-occurrence occupancy model

For detection model in the wet season, the top-ranked models supported species effect, interaction effect, and variables effects (distance and EVI) (Table 1). The presence of Silver Pheasants increased the detection probability of White-necklaced Partridges ($p_A = 0.211 \pm 0.050$, $r_A = 0.590 \pm 0.053$, $p < 0.01$; Fig. 2a, c; Tables 2, 3), and vice versa ($p_B = 0.017 \pm 0.007$, $r_{BA} = r_{Ba} = 0.086 \pm 0.025$, $p < 0.01$; Fig. 2a, c; Tables 2, 3). Moreover, the top models for detection probability in the wet season included EVI and distance (Table 1). Both EVI and distance have a positive effect on the probability of detection for Silver Pheasants, but a negative on the probability of detection for White-necklaced Partridges in the wet season (Fig. 2a, c).

For detection model in the dry season, the top candidate models supported species effect, interaction

Table 1 The top candidate co-occurrence occupancy models (ΔAIC < 2) used to evaluate the effect of environmental variables and interspecific interaction on the probability of detection and occupancy of Silver Pheasants and White-necklaced Patridges in Chebaling National Nature Reserve

Co-occurrence detection models in the dry season		AIC	ΔAIC	Weight	*K*	neg2ll
Model1	*p*(SP + INT_o + SP:INT_o + SP:Distance)	1106.69	0.00	0.1982	8	1090.69
Model2	*p*(SP + INT_o + SP:INT_o + SP:EVI_dry)	1107.08	0.39	0.1629	8	1091.09
Model3	*p*(SP + SP:EVI_dry)	1107.83	1.14	0.1120	6	1095.84
Model4	*p*(SP + INT_o + SP:INT_o)	1108.44	1.75	0.0826	6	1096.44
Model5	*p*(SP + INT_o + SP:INT_o + SP:EVI_dry + SP:Distance)	1108.50	1.81	0.0803	10	1088.50
Co-occurrence detection model in the wet season		**AIC**	**ΔAIC**	**Weight**	***K***	**neg2ll**
Model6	*p*(SP + INT_o + SP:EVI_wet)	946.59	0.00	0.4813	7	932.59
Model7	*p*(SP + INT_o + SP:EVI_wet + SP:Distance)	946.86	0.27	0.4206	9	928.86
Co-occurrence occupancy model in the dry season based on *p*(SP + INT_o + SP:INT_o + SP:Distance)		**AIC**	**ΔAIC**	**Weight**	***K***	**neg2ll**
Model8	*psi*(SP + SP:Coverage + SP:Distance)	1098.74	0.00	0.1606	12	1074.74
Model9	*psi*(SP + SP:Coverage)	1099.54	0.80	0.1075	10	1079.54
Model10	*psi*(SP + SP:Coverage + SP:Slope)	1099.58	0.84	0.1057	12	1075.57
Model11	*psi*(SP + INT + SP:Coverage + SP:Distance)	1100.04	1.30	0.0839	13	1074.03
Co-occurrence occupancy model in the wet season based on *p*(SP + INT_o + SP:EVI_wet)		**AIC**	**ΔAIC**	**Weight**	***K***	**neg2ll**
Model12	*psi*(SP + SP:EVI_wet + SP:Coverage)	940.80	0.00	0.2026	11	918.80
Model13	*psi*(SP + INT + SP:EVI_wet + SP:Coverage)	942.15	1.35	0.1031	12	918.15
Model14	*psi*(SP + SP:Slope + SP:Coverage + SP:EVI_wet)	942.32	1.52	0.0946	13	916.32

K is the number of estimated parameters in the model and ΔAIC is the absolute difference in AIC values relative to the model with the smallest AIC. Weight means AIC weight; neg2ll = the value of twice the negative log-likelihood. SP means species effect on detection or occupancy, INT_o = the occurrence of dominant species changes the detection or occupancy probability of the other subordinate species, INT_d = the detection of dominant species changes the detection or occupancy probability of the subordinate species in the same survey, SP:INT_o means occurrence of two species change the detection probability interactively. The term "EVI_dry" in parentheses denotes that the detection probability of species was estimated for enhanced vegetation index in the dry season, "EVI_wet" means enhanced vegetation index in the wet season, "Distance" means the nearest distance to the resident settlement, "Coverage" means forest canopy coverage, "Elevation" means the mean elevation of each grid cell, and "Slope" means the mean slope of each grid cell

effect, distance and EVI effects (Table 1). On the basis of model weight, interaction effect has the larger effect (cumulative weight = 0.65) than distance (cumulative weight = 0.41) and EVI (cumulative weight = 0.47) on detection. Model average results show the presence of White-necklaced Partridges has a negative effect on detection probability of Silver Pheasants in the dry season ($p_A = 0.438 \pm 0.043$, $r_A = 0.388 \pm 0.049$, $p < 0.01$; Fig. 2b, d; Tables 2, 3). The presence of Silver Pheasants increases the detection probability of White-necklaced Partridges ($p_B = 0.089 \pm 0.101$, $r_{BA} = r_{Ba} = 0.194 \pm 0.080$, $p < 0.01$), while the effect of detection of Silver Pheasants on the detection probability of White-necklaced Partridges was not included in top-ranked models (Table 1). The detection of two Galliformes both decreased along distance to the resident settlement (Fig. 2c). However, there is a contrast effect of EVI on the detection probability of two Galliformes, the detection of Silver Pheasant increased with EVI and the detection of White-necklaced Partridge decreased with EVI (Fig. 2d).

The probability of occupancy in single-season, co-occurrence occupancy model

Based on the most parsimonious model for detection probability, we build the co-occurrence occupancy model for site use probability of Silver Pheasants and White-necklaced Partridges in the wet and dry season, respectively. For occupancy models in the wet season, the top-ranked models included species effect, coverage, slope and EVI effect and interaction effect (Table 1). The EVI has a stronger effect (cumulative weight = 0.956) than coverage (cumulative weight = 0.750), slope (cumulative weight = 0.565) and interaction effect (cumulative weight = 0.545). The site use probability of Silver Pheasants decreases with the coverage and EVI, and increases with slope (Fig. 3a, c, e), the site use probability of White-necklaced Partridges increases with slope and coverage and decreases with the EVI (Fig. 3a, c, e). Therefore, the coverage has an opposite effect on the site use probability of two Galliformes (Table 2; Fig. 3c). The model averaging results show that the presence of Silver Pheasants

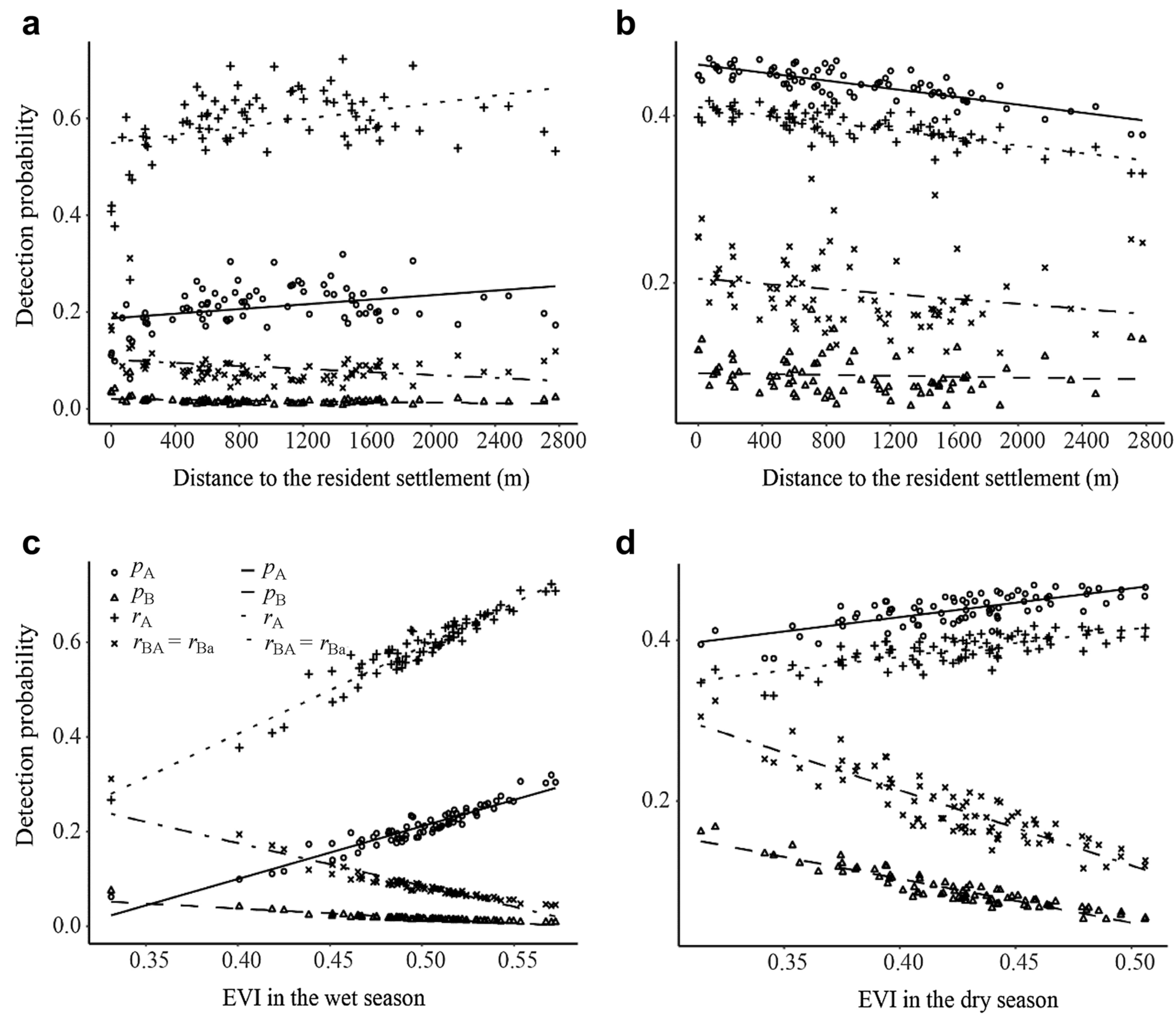

Fig. 2 Estimated detection probability for Silver Pheasants and White-necklaced Partridges conditioned on the presence or absence of Silver Pheasants in the co-occurrence occupancy model in the wet season (**a**, **c**) and dry season (**b**, **d**) in 2017. Results were model averaged across all the models (Additional file 1: Table S1). Specifically, the effect of distance on detection of Silver Pheasants and White-necklaced Partridges in the wet season (**a**) and the dry season (**b**), the effect of EVI on detection of Silver Pheasants and White-necklaced Partridges in the wet season (**c**) and the dry season (**d**). p_A denotes the probability of detecting the dominant species, given the absence of the subordinate. p_B denotes the probability of detecting the subordinate, given the absence of the dominant. r_A denotes the probability of detecting the dominant, given both are present. r_{BA} denotes the probability of detecting the subordinate, given both are present and the dominant is detected. r_{Ba} denotes the probability of detecting the subordinate species, given both are present and the dominant is not detected

increases the site use of White-necklaced Partridges ($psi_{BA} = 0.518 \pm 0.116$, $psi_{Ba} = 0.384 \pm 0.252$, $p = 0.209$; Table 3). Further, SIF for site use was 1.032, verifying the limited effect of interaction on site use probability.

For occupancy models in the dry season, the top-ranked models supported the species effect, coverage, slope, distance and interaction effect (Table 1) . On the basis of models weight, the coverage has the strongest effect (cumulative weight = 0.989), among distance (cumulative weight = 0.748), slope (cumulative weight = 0.607) and interaction effect (cumulative weight = 0.562). Further, the coverage also had the largest model weights and an opposite effect on the site use probability of two Galliformes (Table 2; Fig. 3d). However, the site use probability of Silver Pheasants and White-necklaced Partridges increases with the slope and distance (Fig. 3b, f). The model averaging results show no evidence that the presence of Silver Pheasants influences the site use probability of White-necklaced Partridges in the dry season ($psi_{BA} = 0.479 \pm 0.212$,

Table 2 The beta parameters estimated through model averaging of all co-occurrence occupancy models (ΔAIC < 2) used to evaluate the effect of environmental variables and interspecific interaction on the probability of detection and occupancy of Silver Pheasants and White-necklaced Patridges in Chebaling National Nature Reserve

Detection model	p_A	p_B	r_A	r_{BA}	$p_{A:EVI}$	$p_{B:EVI}$	$p_{A:Distance}$	$p_{B:Distance}$
Model1	− 0.198 ± 0.13	− 3.696 ± 1.328	− 0.345 ± 0.234	2.594 ± 1.333			− 0.133 ± 0.098	− 0.429 ± 0.233
Model2	− 0.223 ± 0.114	− 3.292 ± 1.375	− 0.298 ± 0.213	2.499 ± 1.4	0.121 ± 0.086	− 0.53 ± 0.263		
Model3	− 0.328 ± 0.087	− 0.987 ± 0.233			0.09 ± 0.083	− 0.613 ± 0.257		
Model4	− 0.225 ± 0.122	− 3.464 ± 1.278	− 0.284 ± 0.23	2.48 ± 1.298				
Model5	− 0.203 ± 0.127	− 3.4 ± 1.364	− 0.351 ± 0.232	2.481 ± 1.304	0.118 ± 0.086	− 0.306 ± 0.593	− 0.14 ± 0.099	− 0.245 ± 0.511
Model6	− 1.335 ± 0.246	− 2.81 ± 0.249	1.715 ± 0.255		0.289 ± 0.125	− 0.37 ± 0.146		
Model7	− 1.367 ± 0.257	− 2.771 ± 0.25	1.724 ± 0.261		0.296 ± 0.13	− 0.325 ± 0.153	0.197 ± 0.118	− 0.142 ± 0.212

Occupancy model	psi_A	psi_{BA}	psi_{Ba}	$psi_{A:Coverage}$	$psi_{BA:Coverage}$	$psi_{A: Distance}$	$psi_{BA:Distance}$	$psi_{A:Slope}$	$psi_{BA:Slope}$
Model8	1.99 ± 0.389	− 1.154 ± 0.872		0.762 ± 0.332	− 2.506 ± 1.184	− 0.106 ± 0.341	2.475 ± 1.223		
Model9	1.987 ± 0.388	− 2.403 ± 0.549		0.736 ± 0.32	− 0.888 ± 0.457				
Model10	1.988 ± 0.388	− 2.358 ± 0.556		0.734 ± 0.328	− 1.186 ± 0.474			0.006 ± 0.347	0.867 ± 0.465
Model11	1.988 ± 0.388	− 1.009 ± 0.867	− 0.238 ± 2.367	0.763 ± 0.332	− 2.724 ± 1.167			− 0.104 ± 0.341	2.617 ± 1.197
Model12	4.657 ± 2.211	− 4.575 ± 2.267		− 2.036 ± 1.243	0.866 ± 0.391	$psi_{A:EVI\_summer}$	$psi_{BA:EVI\_summer}$		
Model13	4.386 ± 2.395	− 4.289 ± 2.467	− 23.101 ± 87,326	− 1.923 ± 1.31	0.882 ± 0.394	− 2.706 ± 1.760	− 0.587 ± 0.391		
Model14	7.063 ± 2.688	− 7.003 ± 2.707		− 2.381 ± 1.306	0.78 ± 0.403	− 4.251 ± 1.902	− 0.536 ± 0.389	1.636 ± 1.132	0.144 ± 0.319

The model names are the same as in Table 1. The beta parameter of psi_A denotes occupancy probability of the dominant species (Silver Pheasants). psi_{BA} denotes occupancy probability of the subordinate species (White-necklaced Partridges) when the dominant is present. psi_{Ba} denotes occupancy probability of the subordinate species in the absence of the dominant species. p_A denotes the probability of detecting the dominant species, given the absence of the subordinate. p_B denotes the probability of detecting the subordinate, given the absence of the dominant. r_A denotes the probability of detecting the dominant, given both are present. r_{BA} denotes the probability of detecting the subordinate, given both are present and the dominant is detected. r_{Ba} denotes the probability of detecting the subordinate species, given both are present and the dominant is not detected. The combination of beta parameters with variables means the variable effect on detection and occupancy probability

$psi_{Ba} = 0.432 \pm 0.302$, $p = 0.209$; Table 3). The SIF for occupancy was 1.013 in the dry season, supporting weak evidence of the dependence of the site use probability of one species on that of the other.

Animal activity pattern

The activity event of Silver Pheasants and White-necklaced Partridges were 576 and 43, respectively, in the wet season, the overlap coefficient of the active pattern of two species is $\Delta = 0.789 \pm 0.136$, $p = 0.014$. Besides, the activity event of Silver Pheasants and White-necklaced Partridges were 320 and 34, respectively, the overlap coefficient of the active pattern of two species in the dry season is $\Delta = 0.946 \pm 0.025$, $p = 0.998$. We found evidence that the activity pattern of Silver Pheasants and White-necklaced Partridges in the dry season had a higher temporal overlap than that in the dry season (Fig. 4).

Discussion

We found Silver Pheasants and White-necklaced Partridges had different habitat preference on environmental variables, with an opposite preference on forest canopy coverage in both the wet and dry season, which may enhance species co-occurrence. Further, the presence of two Galliformes affected the detection probability interactively. However, interspecific interaction effects on site use were insignificant and there is no temporal partition in the aspect of daily activity pattern.

For site use probability, Silver Pheasants and White-necklaced Partridges exhibited different habitat preference in our research. The site use probability of Silver Pheasants was similar in spite of declining trend along the gradient of forest canopy coverage, while, White-necklaced Partridges used sites with low forest canopy coverage in the wet season. Two Galliformes shifted their preference in the dry season. The opposite selection on canopy coverage had been recorded in other sympatric Galliformes Kalij Pheasants (*Lophura leucomelanos*) was mostly found in low canopy cover and Red Jungle Fowl (*Gallus gallus*) was associated with moderate coverage (Sukumal and Savini 2009). Silver Pheasants and White-necklaced Partridge preferred high forest canopy coverage in the wet season, may be related to resource energy requirement, supplied by the dense and impenetrable vegetation (Sukumal and Savini 2009). Silver Pheasants occupied high canopy coverage in the dry season, may explain by avoiding predation risk when rearing young chicks (Zheng 2015). In addition, Silver Pheasants and

Table 3 Co-occurrence model average estimates of occupancy (*psi*) and detection parameters (*p* and *r*) of two sympatric Galliformes, Silver Pheasants and White-necklaced Partridges in the dry and wet season in Chebaling national nature reserve

Parameters	Estimate	S.E.	Lower	Upper
Co-occurrence model average in the dry season				
psi_{A}	0.859	0.072	0.665	0.953
psi_{BA}	0.479	0.212	0.115	0.816
psi_{Ba}	0.432	0.302	0.039	0.906
p_{A}	0.438	0.043	0.356	0.523
p_{B}	0.089	0.101	0.009	0.507
r_{A}	0.388	0.049	0.297	0.488
r_{Ba}	0.194	0.080	0.086	0.388
r_{BA}	0.190	0.080	0.082	0.387
Co-occurrence model average in the wet season				
psi_{A}	0.896	0.067	0.382	0.981
psi_{BA}	0.518	0.116	0.300	0.734
psi_{Ba}	0.384	0.252	0.064	0.818
p_{A}	0.211	0.050	0.130	0.325
p_{B}	0.017	0.007	0.007	0.039
r_{A}	0.590	0.053	0.484	0.690
r_{Ba}	0.086	0.025	0.048	0.150
r_{BA}	0.086	0.025	0.048	0.150

S.E. denotes standard error. psi_{A} denotes occupancy probability of the dominant species (Silver Pheasants). psi_{BA} denotes occupancy probability of the subordinate species (White-necklaced Partridges) when the dominant is present. psi_{Ba} denotes occupancy probability of the subordinate species in the absence of the dominant species. p_{A} denotes the probability of detecting the dominant species, given the absence of the subordinate. p_{B} denotes the probability of detecting the subordinate, given the absence of the dominant. r_{A} denotes the probability of detecting the dominant, given both are present. r_{BA} denotes the probability of detecting the subordinate, given both are present and the dominant is detected. r_{Ba} denotes the probability of detecting the subordinate species, given both are present and the dominant is not detected

White-necklaced Partridges were more restricted in a high forest canopy coverage where human disturbance is less. As illustrated in the present study, two Galliformes preferred site away from resident settlement (Fig. 3f). Silver Pheasants and White-necklaced Partridges preferred on steeper site in the wet and dry season, which was reported in another research (Sukumal and Savini 2009). Steep slopes may facilitate Galliformes "escape-flushing" down-slope in response to approaching predators (Lima and Bednekoff 1999). For the effect of EVI on site use, two Galliformes mainly occurred on high EVI areas in the wet season in spite of downward trend, and high EVI areas offer more seeds and fruits for pheasants for reproduction in the season (Bastianelli et al. 2017). Therefore, the differentiation of habitat choice, especially in canopy coverage, between Silver Pheasants and White-necklaced Partridges may be the main mechanism driving their coexistence.

We have no evidence supported interspecific interaction have an effect on the site use of two Galliformes in the present study. Two Galliformes' site use probability was independent of the presence and detection of the other species in the dry and wet season. It was similar to the co-occurrence pattern of mesocarnivores in the Temperate Forests of Southwest China (Bu et al. 2016) and sympatric tinamous in southeast Brazil (Estevo et al. 2017). Another study supported interspecific competition is not the main cause for the pattern of 51 species of Galliformes species co-occurring in China (Chen and Luiselli 2009). Territorial defense behavior of Silver Pheasants and White-necklaced Partridges may be responsible for weak interspecific interaction because both species have moderate territorial defense behavior among intraspecific individuals and no recording of obviously defense behavior among interspecific individuals in breeding and non-breeding seasons (Zheng 2015). Occasionally, Silver Pheasants foraged together with other species, such as *Polyplectron katsumatae* and *Arborophila ardens* (Zheng 2015). In addition, co-occurrence patterns of Galliformes were in part scale-dependent. Spatial scale of variables based on resolution of remote sensing data determined the species-habitat associations, inappropriate spatial scales may fail to detect species habitat associations (Niedballa et al. 2015). The 1-km^2 grid sampled was smaller than Galliformes' home range thus, the effects of interspecific competition in local scales may be masked by environmental variables (Chen and Luiselli 2009).

For Silver Pheasants and White-necklaced Partridges, the detection probabilities were explained by interspecific interaction and habitat variables. The presence of Silver Pheasants and White-necklaced Partridges influenced the detection probability interactively. The interspecific effect on the detection could be related to competitive exclusion or similar resources utilization (Haynes et al. 2014; Petersen et al. 2019). The SIF for detection and site use probability supported little effect of interspecific interaction in the present study, so the detection probably resulted from resource selection or utilization. The presence of Silver Pheasants increased the detection of White-necklaced Partridges in the wet and dry seasons, probably related to similar resource selection, such as slope and EVI shown by our occupancy models. Additionally, EVI had an opposite effect on the detection of Silver Pheasants and White-necklaced Partridges, indicating that species and habitat variables interactively influenced the detection. As illustrated above, incorporating detection probability increased our ability to

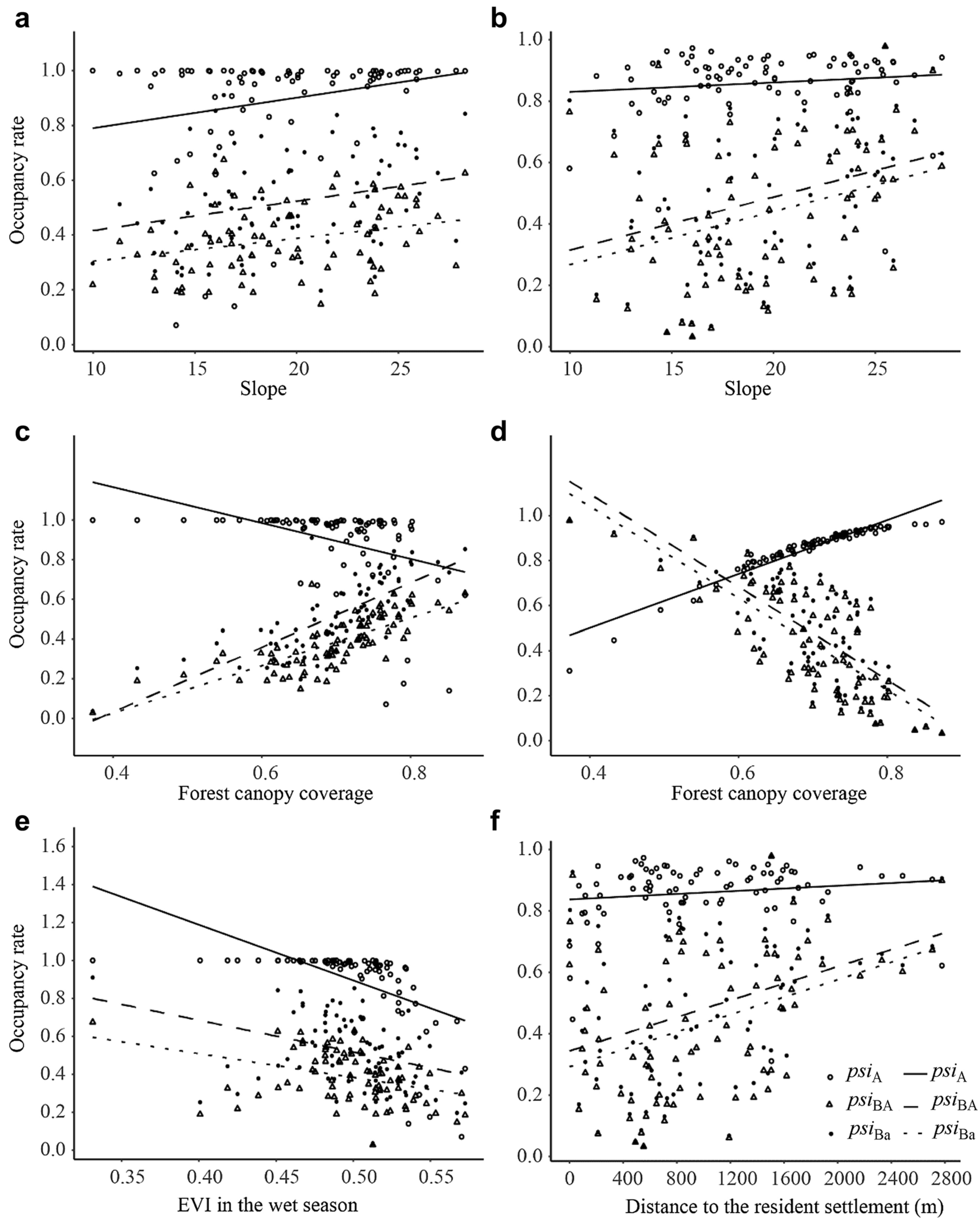

Fig. 3 Estimated occupancy probability for Silver Pheasants and White-necklaced Partridges conditioned on the presence or absence of silver pheasant in the co-occurrence occupancy model in the wet season (**a**, **c**, **e**) and dry season (**b**, **d**, **f**) in 2017. Results were model averaged across all the models (Additional file 1: Table S2). Specifically, the effect of slope on occupancy of Silver Pheasants and White-necklaced Partridges in wet season (**a**) and the dry season (**b**), the effect of forest canopy coverage on occupancy of Silver Pheasants and White-necklaced Partridges in wet season (**c**) and the dry season (**d**); the effect of EVI on occupancy of Silver Pheasants and White-necklaced Partridges in the wet season (**e**) and the effect of distance to the nearest resident settlement on occupancy of Silver Pheasants and White-necklaced Partridges in in dry season (**f**). psi_A means the probability of occupancy of Silver Pheasants, psi_{BA} and psi_{Ba} mean the occupancy probability of White-necklaced Partridges in the presence or absence of Silver Pheasants

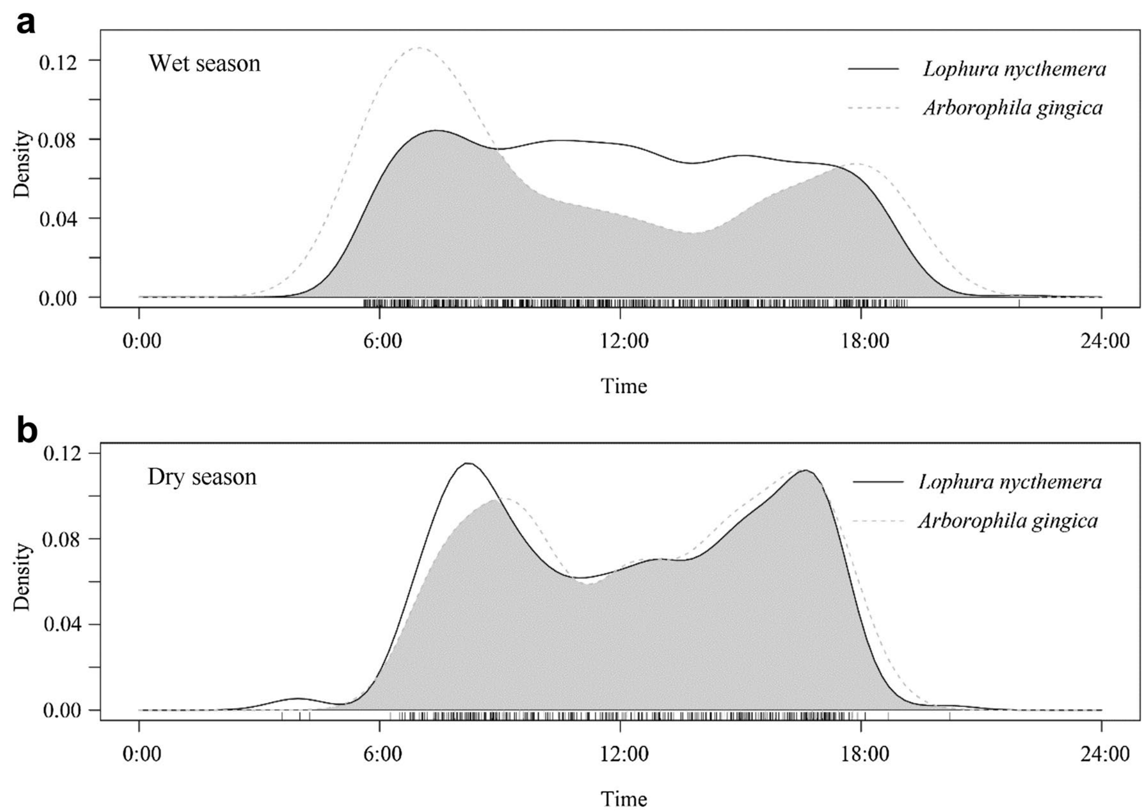

Fig. 4 The active pattern of Silver Pheasants and White-necklaced Partridges in wet (**a**) and dry season (**b**) in Chebaling National Nature Reserve. The coefficient of overlapping equals the area in grey below both curves, the black line is for Silver Pheasants and the blue dash line is for White-necklaced Partridges the event records are shown at the bottom of the figure as rugs

speculate potential competition effect on species co-occurrence (Petersen et al. 2019).

Plenty of studies have highlighted the prevalence and importance of temporal niche partitioning for enabling coexistence of sympatric species within diverse taxa, including mammals and bird (Kronfeld-Schor and Dayan 2003; Kronfeld-Schor et al. 2017). Sympatric cormorants, *Phalacrocorax niger* and *P. fuscicollis*, effectively used time as a resource to exploit the food resources and successful coexistence (Mahendiran 2016). However, we found no evidence for time partitioning between the two Galliformes birds. Instead, the two species highly overlapped in their activity time. High overlap in daily activity also was found in other sympatric ground-dwelling birds, the Brown Tinamou (*Crypturellus obsoletus*) and the Tataupa Tinamou (*C. tataupa*) (Estevo et al. 2017). There are three possible explanation for highly overlapped trends in the daily activity of two Galliformes. Firstly, the strength of direct interference competition between sympatric Galliformes was weak, insufficient to drive temporal niche separation (Zhao 2001). Secondly, coexisting species consumed other environmental variables independently, such as forest canopy coverage in the present research, resulting in high tolerance in activity time overlap. Lastly, the two species may share similar predation risk, activity in a similar time to avoid common predators' activity (Kronfeld-Schor et al. 2017).

Conclusion

Our results demonstrated that interspecific interaction and habitat variables change the detection probability of Silver Pheasants and White-necklaced Partridges in the wet and dry season. The results of site use probability indicate that habitat characteristics can play a bigger role than direct interspecific interactions in regulating the site use of Silver Pheasants and White-necklaced Partridges. There is no temporal partitioning in activity time between Silver Pheasants and White-necklaced Partridges. Therefore, environmental variables and interspecific interaction are the leading drivers regulating the detection and site use probability, promoting co-occurrence of Silver Pheasants and White-necklaced Partridges. By exploring habitat preference and interspecific interactions with occupancy models simultaneously, we were able to illustrate the relative role of habitat and interspecific relationships more accurately in the investigation of co-occurrence patterns.

Additional file

Additional file 1: Table S1. All co-occurrence occupancy models used to evaluate the effect of detection and the presence of Silver Pheasant on the detection of White-necklaced Partridge in Chebaling National Nature Reserve. **Table S2.** All co-occurrence occupancy models used to evaluate the effect of detection and the presence of Silver Pheasant on the occupancy of White-necklaced Partridge in Chebaling National Nature Reserve.

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Authors' contributions
LC conceived the ideas, designed research; LC, ZS, WY, YM and XH collected and identified the data; LC analyzed the data and write the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials
The datasets used in the present study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate
Not applicable.

Consent for publication
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Competing interests
The authors declare that they have no competing interests.

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