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Temporal patterns of three sympatric pheasant species in the Nanling Mountains: *N*-mixture modeling applied to detect abundance

Fasheng Zou[1*], Qiang Zhang[1], Min Zhang[1], Myung-Bok Lee[1], Xincai Wang[1], Yuening Gong[2] and Changteng Yang[2]

Abstract

Background: The reliability of long-term population estimates is crucial for conservation and management purposes. Most previous studies assume that count indices are proportionally related to abundance; however, this assumption may not hold when detection varies spatially and temporally. We examined seasonal variations in abundance of three bird species (Cabot's Tragopan *Tragopan caboti*, Silver Pheasant *Lophura nycthemera*, and White-necklaced Partridge *Arborophila gingica*) along an elevational gradient, using *N*-mixture models that take into account imperfect detection in our bird data.

Methods: Camera-trapping was used to monitor temporal activity patterns of these species at Guangdong Nanling National Nature Reserve from December 2013 to November 2017 (4 seasons per year). For abundance analysis (*N*-mixture modeling), we divided a year into 4 seasons, i.e. 3 months per season, and performed the analysis by season. Elevation was incorporated into the *N*-mixture model as a covariate that may affect abundance. We compared the *N*-mixture model with a null model (no covariate model) and selected the better model based on AIC values to make an inference.

Results: From 24 sampling sites, we obtained 6786 photographs of 8482 individuals of 44 bird species and 26 mammal species. Silver Pheasant was photographed much more frequently and showed higher temporal activity frequency than White-necklaced Partridge or Cabot's Tragopan. Silver Pheasant was camera-captured most frequently in summer, and other two species in winters. All three species had two daytime activity peaks: between 6:00 a.m. and 10:00 a.m., and between 5:00 p.m. and 7:00 p.m., respectively. Our estimated abundance and detection probability from the *N*-mixture model were variable by season. In particular, all three species showed greater abundance in summer than in winter, and estimated abundance patterns of all three species were more similar with observed camera-trapping counts in summers. Moreover, in winter, elevation had a positive impact on abundance of Silver Pheasant and Cabot's Tragopan, but not on White-necklaced Partridge.

Conclusions: Our results demonstrate that the *N*-mixture model performed well in the estimation of temporal population abundance at local fixed permanent plots in mountain habitat in southern China, based on the modeling of repeated camera-trapping counts. The seasonal differences in abundance of the three endemic bird species and the

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*Correspondence: zoufs@giabr.gd.cn
[1] Guangdong Key Laboratory of Animal Conservation and Resource Utilization, Guangdong Public Laboratory of Wild Animal Conservation and Utilization, Guangdong Institute of Applied Biological Resources, Guangzhou 510260, China
Full list of author information is available at the end of the article

strong effect of elevation on abundance of two species in winter were only indicative of variations in spatio-temporal distribution within species and between species. In identifying suitable habitat for endemic pheasants, the positive elevational effect also suggests that more attention should be paid to conservation of areas with higher elevation in the Nanling Mountains.

Keywords: Abundance estimation, Camera-trapping, Imperfect detectability, Nanling Mountains, Spatio-temporal distribution, Sympatric distribution

Background

An interesting topic for population ecology is determining how sympatric species partition their activity patterns, including spatio-temporal niches to promote stable coexistence (Frey et al. 2017). Studying spatial and temporal partition of niches among sympatric species provides insight into the mechanisms that facilitate stable coexistence, especially for endangered pheasant species (Carothers and Jaksic 1984; Kronfeld-Schor and Dayan 2003). In southern China, Cabot's Tragopan (*Tragopan caboti*), White-necklaced Partridge (*Arborophila gingica*) and Silver Pheasant (*Lophura nycthemera*) have sympatric distributions in most native primary forests. Though formerly common, all three species have been trending dramatically downward due to habitat degradation and human disturbance or hunting over the last 50 years (Zhang et al. 2003). Cabot's Tragopan is considered Vulnerable (VU) according to the IUCN Red List, and is a nationally protected species in China (Category I). White-necklaced Partridge is listed as Near Threatened (NT) by IUCN, and Silver Pheasant is also a nationally protected species (Category II) in China. According to recent surveys by Xu et al. (2001) and Huang et al. (2003), Cabot's Tragopan and White-necklaced Partridge are at present rare and difficult to find in southern China. Based on our investigation over the last 10 years, populations of these pheasants in the Nanling Mountains, which may be the last refuge for these species, are relatively stable. Since all three species are sympatrically distributed in several national nature reserves in the areas, estimating their population abundances locally in the nature reserves is particularly important for their conservation management. Reliable long-term count data are crucial for conservation status assessment and spatio-temporal prediction of bird abundance or population size (Chandler et al. 2009; Jakob et al. 2014). This is particularly true for Galliformes species in China (e.g. partridges, pheasants, grouses) for which abundance estimates are essential for assessing degrees of threat, determining the species' conservation status (Lu 1991) and designing appropriate conservation strategies (Zhang et al. 2003). Currently, most monitoring programs for estimating endemic species population sizes assume that count indices are proportionally related to abundance (Carbone et al. 2001; Rovero and Marshall 2009). However, these data are rarely exhaustive and can only be regarded as an index of true abundance, rather than as abundance per se. Importantly, proportionality between an index and true abundance often cannot be assumed because individual detection probability varies spatially and temporally (Royle and Nichols 2003; Alldredge et al. 2007). Thus, pheasant population management policies require intensive sampling efforts and accurate estimating models, rather than mark–recapture or distance sampling.

To avoid spatial and temporal replication, a possible solution is to use recently developed models that simultaneously estimate abundance and detection probability using repeated count data (Royle 2004). These *N*-mixture models provide detectability-corrected abundance estimates when individual identification is impossible (i.e. the individual is not marked), as is mainly the case in large-scale endangered species monitoring. Therefore, these models have considerable potential for unbiased estimation of abundance in the case of large-scale species studies (Kéry et al. 2005; Kéry 2008). Although *N*-mixture models were initially developed in 2004, they have not found a wide use in ecological studies, despite their ability to model spatially and temporally repeated counts, a kind of data that is often collected in the field. Their use has been mainly restricted to studies of scrub–shrub bird species and certain game bird species (Chandler et al. 2009) or as a basis for subsequent methodological development (Joseph et al. 2009). For galliformes species, these models only have been used in studies of Red-legged Partridge (*Alectoris rufa*) (Jakob et al. 2014), because of the difficulty of monitoring these endangered pheasants, and the relative lack of reliable and cost-effective replicated counts. In this study, we explored the potential of *N*-mixture modeling for estimating population abundance and detection probability of three sympatric pheasant species with a spatial distribution and examined the associated major management implications.

Camera-trapping technology is increasingly used in wildlife research for spatiotemporal activities, and has become an effective tool to assess the biodiversity of terrestrial birds in China (e.g. phasianids, Li et al. 2010a, b; Si and Ding 2014). Technical advances have enabled camera units to provide long-term and continuous data collection, and camera-trapping also has the advantage of being a non-invasive way to record and monitor cryptic and reclusive terrestrial animals (Welbourne et al. 2016). Camera units have previously been used to observe spatial and temporal niche partitioning for sympatric species that facilitate their coexistence (Di Bitetti et al. 2010; Monterroso et al. 2014; Sunarto et al. 2015). In southern China, ground-feeding pheasant species are often photographed by camera traps (Xiao et al. 2014), including Silver Pheasant and White-necklaced Partridge, which are among the species most frequently photographed by camera trap in Guangdong Province, China (Zou et al. 2018). Despite their popularity, surprisingly few studies have examined camera-trapping survey results to offer guidelines for efficient study design, such as the minimum trapping effort required, estimated population abundance and detection probability (Si et al. 2014).

In this study, we investigated spatial and temporal activity patterns of these three sympatric pheasant species with a long-term dataset of spatially replicated counts by camera-trapping, and evaluated the reliability of using an *N*-mixture modeling approach for estimating population abundance and detection probability. We examined the following questions: (1) What is the observed temporal activity pattern of these three species of pheasants based on monthly and daily changes in relative abundance, as determined by photos? (2) Does *N*-mixture modeling provide precise estimates for population abundance and detection probability, that are correlated to our replicated count dataset based on camera-trapping? (3) Do environmental covariates (i.e. elevation, season) influence the estimated abundance and detection probability of some pheasant species at our fixed permanent plot?

Methods

Study area

The Nanling or “Southern” Mountains are the third-most important biodiversity ecoregion in China, and occupy the easternmost boundary between the Sino-Japanese and Oriental realms (Pang 2003). The mountain ranges are situated between 23°37′–27°14′N and 109°43′–116°41′E, straddling over 700 km from west to east. They represent an important boundary between the southern and central subtropical zones, and define the watersheds of the Yangtze and Pearl Rivers. Our survey was conducted in the central part of the Nanling Mountains along the southern slope of Nanling National Nature Reserve (hereafter, “Nanling”), which covers 584 km^2 (24°37′–24°57′N, 112°30′–113°04′E) and has a highest elevation of 1902 m on the summit of Shikengkong. The region has a subtropical monsoon climate, with a mean annual temperature of 17.4 °C. Mean monthly temperature ranges from 9 °C in January to almost 29 °C in July. Annual precipitation ranges from 1570 to 1800 mm, and mainly occurs between March and August. The elevational gradient of vegetation communities at Nanling encompasses mountain broadleaved evergreen forest, mixed evergreen and deciduous forest, coniferous and broadleaved mixed forest, mountaintop dwarf forest, and montane shrubs and herbs (Pang 2003).

Camera-trapping survey design

Our research using camera traps at Nanling was approved by the Guangdong Wildlife Management Authority and conducted under the relevant wildlife protection laws of the People’s Republic of China. We deployed camera traps in a permanent plot (6 km × 8 km) located in the old-growth broadleaved evergreen forest within the reserve where several pheasants often occurred together (Fig. 1, Additional file 1: Table S1). Twenty-four infrared digital cameras (Scoutguard SG550; Boly Media Communications Co., Ltd., Shenzhen, China) were set at random sites at an elevational range of 1066–1572 m in the plot from December 2013 to November 2017 (4 years and 4 seasons per year). The camera traps were sited along forest paths or woodland ways that were subject to little or no human disturbance and would in any case have been very difficult to find by people who did not know their exact locations. Cameras were placed at distances of 200 m from each other and mostly at 100 m or more from the forest edge. We chose the specific positions of camera sites to optimize the viewing angle from the tree on which they were mounted. Cameras were placed at heights of 20–30 cm above the ground on account of the relatively small body size of pheasant species compared to the larger mammalian species, and were also aligned to face north or south in order to reduce the influence of direct sunshine. Branches and grasses in front of the cameras were removed to prevent unwanted triggering of the cameras by moving vegetation, and protective waterproof covers were fitted to the cameras to keep them dry and minimize damage from the frequent rains in the area. A gap was also maintained between the camera and the tree to which it was attached. The cameras were set to take three photographs and 10 s of video after each trigger event, and the interval time was one second between two trigger events. Since individuals of the target species were unmarked, we defined a single detection of a species as a photo event separated by at least 30 min from the next photo event of the same species from the same camera. All cameras were set to work 24 h a day and memory cards and batteries were checked every 3 months (Si et al. 2014).

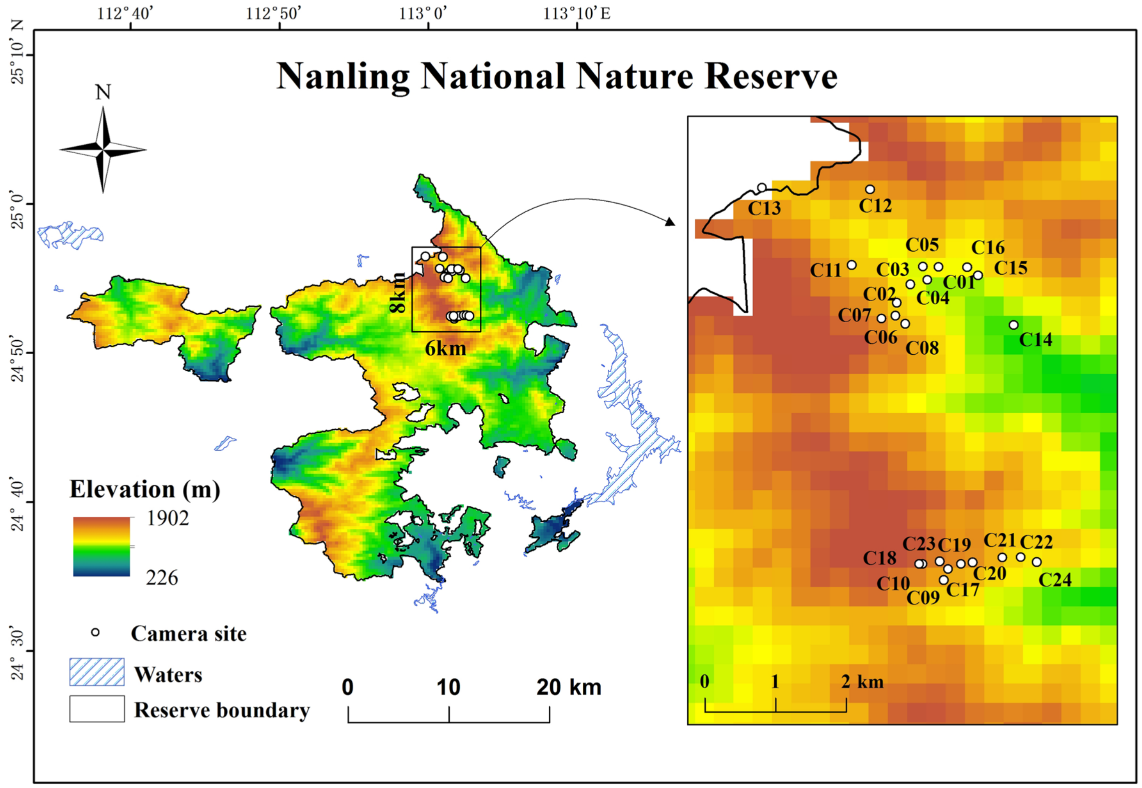

Fig. 1 The location of research areas in Nanling National Nature Reserve in Guangdong Province, southern China, and 24 camera trapping sites (white circles)

Temporal pattern and population estimation

We calculated the percentage ratio of photos recorded for each pheasant species and showed activity patterns of the three species pheasants in order to decrease absolute photo number differences. This minimized the impact of camera numbers and trapping period when comparing differences between months and hours, because all three species were recorded by the same number of cameras over the same amount of time. An index of the activity level for each hour or month was calculated by dividing the hourly or monthly number of occurrence events by the total number of occurrence events for each species. Hourly activity levels are expressed as percentages and depicted across 24 h, while monthly activity levels are expressed as percentages and depicted across 12 months. The monthly and daily changes in numbers of photos recorded by camera traps were analyzed by Kruskal–Wallis because of the abnormal distribution of data.

For estimating population size or abundance, we stacked yearly data of 24 sites by season (a total of 4 seasons). Although stacking data can be considered a pseudo replication, we used it because detection rates were low during the whole survey periods. However, it should be noted that there were variations in the period of camera trap surveys among sites and years, resulting in different sample sizes between seasons: Winter (Dec–Feb) = 65, Spring (Mar–May) = 67, Summer (Jun–Aug) = 67, and Autumn (Sep–Nov) = 60 samples.

Spatial autocorrelation

Before the final analysis, we determined spatial autocorrelation in the data. We performed a Morans' I test and examined the correlogram using the residuals from a generalized linear model with Poisson distribution in R ("spdep" package; Bivand et al. 2013). The model includes elevation and sampling effort (number of months when camera trap surveys were conducted) as explanatory variables and maximum number of individuals detected during each season as a response variable, i.e., abundance. Spatial autocorrelation was weak in most cases: the Moran's I value was ≤ 0.10 (0.02–0.10) in all cases (3 species × 4 seasons) except three that also showed low values (0.12, 0.13 and 0.18). Thus, we considered spatial autocorrelation to be negligible.

Abundance analysis

To investigate the relationship between elevation and abundance of the three species and seasonal variation in these relationships, we used an *N*-mixture model, accounting for imperfect detection in the estimation of abundance (Royle 2004). *N*-mixture models require repeated counts (temporal replicates) during a survey period. In general, the *N*-mixture model is composed of two model parts: an abundance model part estimating the local abundance at a site i, i.e., N_i, which is assumed to follow a Poisson distribution with mean local abundance λ; and an observation model part linking N_i with p (detection probability), i.e., $y_{ij} \sim$ binomial (N_i, p) where y_{ij} represents the observation state at a site i during replicate survey j. Effects of covariates are incorporated into the model part associated with λ and p through a log-link and a logit-link function, respectively. Due to the low number of detections in our camera trap survey, we used a month as a replicate, generating 3 replicates per season and considered the maximum number of individuals captured by camera during a month as a count (observed abundance) for the month. However, during winter, the observed abundance of Cabot's Tragopan was recorded as 1 at any site where Cabot's Tragopan was detected. We used *N*-mixture models based on presence/absence data for this case (Royle and Nichols 2003).

We constructed four models for each species and season except Cabot's Tragopan in winter; three models with elevation as a covariate for the abundance part [covariate models: Poisson, zero-inflated Poisson (ZIP), and negative binomial (NB)] and one model with only intercept (null model). We included two variants of the Poisson *N*-mixture model, i.e., ZIP and NB *N*-mixture models because a model fit of the Poisson *N*-mixture model was poor in most cases. Count data with many zero values, which are common, can cause overdispersion that affects the estimates of standard error or confidence intervals and a model fit. ZIP and NB *N*-mixture models are often used to account for the overdispersion and improve the model fit (Kéry and Royle 2016). Both models are also implemented in an "unmarked" package (Fiske and Chandler 2011). For Cabot's Tragopan in winter, we compared two models, i.e., the covariate model and the null model. No covariate was incorporated into detection probability, assuming constant detection probability. Elevation data were standardized to have a mean of 0 and a standard deviation of 1 to improve model fit. A model with lowest AIC (Akaike's Information Criterion) was selected as a final model for analysis (Burnham and Anderson 2002; see Additional file 1: Table S2 for AIC values of all models). However, if differences in AIC values between the model and the null model were less than 2, we considered there was no significant effect of elevation on the species' abundance. Using 1000 parametric bootstraps, we tested a model fit of the selected model for each species and season. Abundance analyses were conducted using "occuRN" function for Cabot's Tragopan during winter and "pcount" function for other cases in "unmarked" package. All statistical analyses were performed in R version 3.3.2 (R Core Team 2016).

Results

Comparison of numbers of photos that recorded the three pheasant species

A total of 6786 photographs of 8482 individuals were obtained at the 24 sampling sites between December 2013 and November 2017 (35,040 camera-days), with 44 bird species and 26 mammal species recorded. Numbers of photos of the three focus species varied, as follows: Silver Pheasant (682 photographs), White-necklaced Partridge (170 photographs), and Cabot's Tragopan (231 photographs) were recorded during the 4-year survey, respectively. Camera traps recorded a mean of 12.48 ± 1.67 photos per month and 14.51 ± 1.25 photos per hour for Silver Pheasant, 2.69 ± 0.36 photos per month and 3.53 ± 0.43 photos per hour for White-necklaced Partridge, and 4 ± 0.44 photos per month and 2.18 ± 0.25 photos per hour for Cabot's Tragopan (Fig. 2). There were significant differences in number of photos recorded by camera trap per month ($\chi^2 = 30.86$, df = 2, $p < 0.001$; Fig. 2a) and per hour ($\chi^2 = 78.258$, df = 2, $p < 0.001$, Fig. 2b) among the three species. These findings indicated a much greater abundance of Silver Pheasant than White-necklaced Partridge and Cabot's Tragopan at Nanling Mountains.

Monthly and daily changes in numbers of camera trap photos

For temporal activity frequency, Silver Pheasant presented a higher value than other two species for both monthly ($\chi^2 = 18.122$, df = 2, $p < 0.001$) and daily change ($\chi^2 = 29.729$, df = 2, $p < 0.001$). Silver Pheasant was most frequently recorded from April to August during the 4 years of monitoring (Fig. 3a), and higher daytime activity peaks occurred in the morning from 6:00 a.m. to 7:00 a.m., and in the evening from 6:00 p.m. to 7:00 p.m. (Fig. 3b). However, the temporal patterns of activity frequency of White-necklaced Partridge and Cabot's Tragopan were similar, and there were not significant differences among months ($\chi^2 = 10.063$, df = 11, $p = 0.525$) and daily hours ($\chi^2 = 19.483$, df = 13, $p = 0.147$). For instance, White-necklaced Partridge was most frequently recorded in January and February, and a higher daytime activity peak occurred from 6:00 p.m. to 7:00 p.m. Similarly, Cabot's Tragopan was most frequently recorded in January and February, and a higher daytime activity peak occurred from 8:00 a.m. to 10:00 a.m. and from 4:00 p.m. to 5:00 p.m.

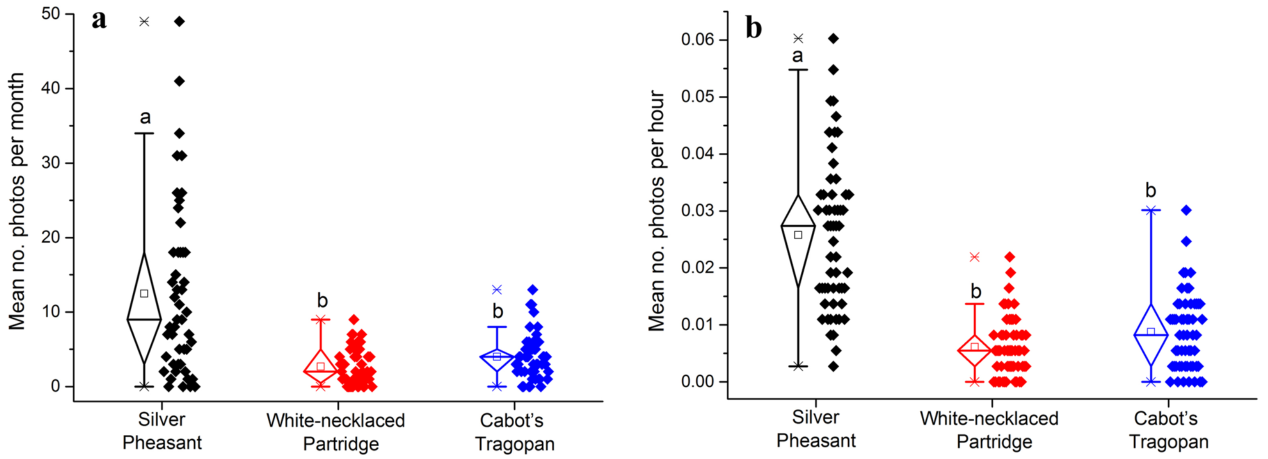

Fig. 2 Mean numbers of photos trapped per month (**a**) and per hour (**b**) for Silver Pheasant, White-necklaced Partridge and Cabot's Tragopan. Box plots show medians (horizontal lines), means (rectangle), 95-percentiles and extreme values

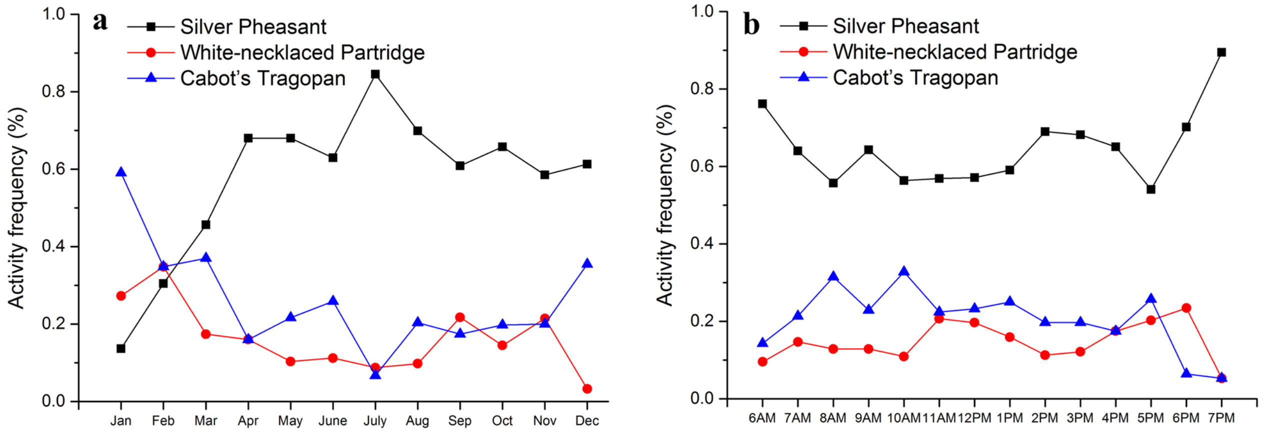

Fig. 3 Monthly (**a**) and daily (**b**) change in percent activity frequency for Silver Pheasant, White-necklaced Partridge and Cabot's Tragopan

Effect of elevation on estimated abundance and seasonal variation

Among the three covariate models (i.e., Poisson, ZIP, and NB *N*-mixture model), the NB *N*-mixture mode was often selected as the best model for all three species, particularly Silver Pheasant and Cabot's Tragopan (Table 1). Detection probability was low, ranging 0.01–0.14 depending on season and species. Compared to other seasons, Silver Pheasant and White-necklaced Partridge showed relatively higher detection in summer than in other seasons, whereas Cabot's Tragopan showed relatively higher detection in autumn (but its estimate was not significant). Elevation had a significant impact on the abundance of two species (Silver Pheasant and Cabot's Tragopan) during winter: both showed greater abundance at high rather than low elevation (Table 1 and Fig. 4). In contrast, White-necklaced Partridge did not show a clear association with elevation in any season (Table 1). All species showed lower abundance in winter than other seasons. In particular, the abundance of Cabot's Tragopan was the lowest among the three species in winter (Table 1 and Fig. 5a), which is consistent with the observation that there were no cases of ≥ 2 individuals caught by camera across the sites in winter. For Silver Pheasant and Cabot's Tragopan, abundance was greater in summer (Table 1 and Fig. 5b), whereas the abundance of White-necklaced Partridge was greater in autumn. Back-transformed detection probability presented similar pattern with estimated abundance (Table 1 and Fig. 6).

Discussion

Studying spatial and temporal partition of sympatric species provides insight into the mechanisms that facilitate stable coexistence (Carothers and Jaksic 1984; Kronfeld-Schor and Dayan 2003). Wilson and Martin (2008)

Table 1 Parameter estimates (± standard errors) of the model selected for each species and season

Season	Species	Abundance		Detection
		Intercept	Elevation	Intercept
Winter	Silver Pheasant	*1.42* ± 0.58	*0.89*± 0.28	− *3.09* ± 0.56
	White-necklaced Partridge	*1.94* ± 0.80	–	− *3.82* ± 0.81
	Cabot's Tragopan	*0.39*± 0.94	*1.20* ± 0.30	− *3.18* ± 0.91
Spring	Silver Pheasant	*2.67* ± 0.81	–	− *3.26* ± 0.84
	White-necklaced Partridge	2.78 ± 4.79	–	− 3.57 ± 4.80
	Cabot's Tragopan	2.23 ± 1.24	–	− 3.39 ± 2.72
Summer	Silver Pheasant	*2.73* ± 0.35	–	− *2.95* ± 0.33
	White-necklaced Partridge	*2.03*± 0.58	–	− *3.35*± 0.56
	Cabot's Tragopan	*2.24* ± 0.75	–	− *3.50* ± 0.77
Autumn	Silver Pheasant	*2.58* ± 0.47	–	− *3.12* ± 0.47
	White-necklaced Partridge	*4.18* ± 1.05	–	− *4.59* ± 1.07
	Cabot's Tragopan	1.29 ± 1.41	–	− 1.80 ± 1.45

Values are not back-transformed: estimates related to abundance and detection are on log and logit scale, respectively

Standard errors are calculated based on parametric bootstrap method

Estimates with *p*-value < 0.05 are in italic

Note that there are only two cases that the covariate model with elevation was better than the null model (no covariate) based on AIC values: Silver Pheasant and Cabot's Tragopan during winter. See Additional file 1: Table S2 for the summary of model selection (AIC values and weights of all models)

studied breeding habitat selection of three coexisting species, White-tailed Ptarmigan (*Lagopus leucura*), Rock Ptarmigan (*L. muta*) and Willow Ptarmigan (*L. lagopus*) in the southern Yukon Territory, Canada. White-tailed Ptarmigan tends to occur at higher elevations, and on steeper slopes, and selects drier habitats dominated by lichens, rock, and dwarf shrubs; Rock Ptarmigan prefers lower elevations with higher more graminoid-covered meadows and scattered woody shrubs; and Willow Ptarmigan nests in areas with dense, woody shrubs at lower elevations and on flatter slopes. Differences in habitat preference therefore allow the three species to coexist. In a study of three sympatric cormorants in India, Mahendiran (2016) showed that Little Cormorant (*Phalacrocorax niger*) and Indian Cormorant (*P. fuscicollis*) share the same foraging habitat, but they tend to forage at different time: Little Cormorant forages in the morning, and Indian Cormorant forages in the afternoon. Additionally, Little Cormorant and Great Cormorant (*P. carbo*) share the same foraging time but tend to use different foraging habitats: Little Cormorant uses lentic habitat and Great Cormorant uses lotic habitat. Consequently, this niche divergence results in resource partitioning. Furthermore, two sympatric deer species may mitigate competition for similar space and food resources through differences in their activity patterns (Ferreguetti et al. 2015), and time can be considered a resource (Halle 2000).

In our study, Silver Pheasant was most frequently recorded during the breeding season, and higher daytime activity peaks occurred in morning and evening (Fig. 3), which was consistent with other studies. For instance, Wu et al. (2017) surveyed yearly activity patterns of Silver Pheasant at Fengyangshan-Baishanzu National Nature Reserve in Zhejiang, and showed that activity increased in May, decreased in September, and that there were peaks in June and August. Peak daytime activity also occurred between 05:00 and 07:00 a.m. in spring and summer, and 07:00–09:00 a.m. in winter in Zhejiang. The monthly peak activity increased dramatically during the breeding season at both study sites, which indicates that Silver Pheasants have a more fixed home range area in summer. The species has been recorded migrating

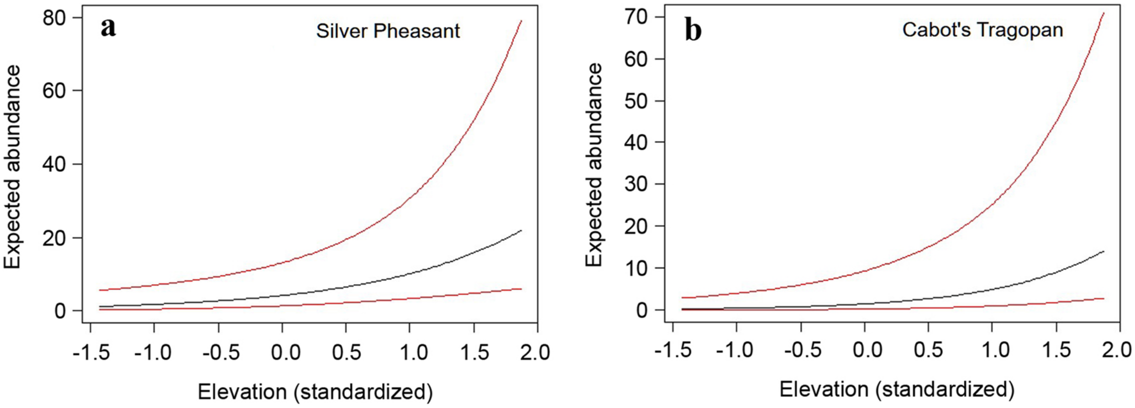

Fig. 4 Effect of elevation on estimated abundance of Silver Pheasant (**a**) and Cabot's Tragopan (**b**) during the winters. The red lines represent the smoothed 95% confidence interval

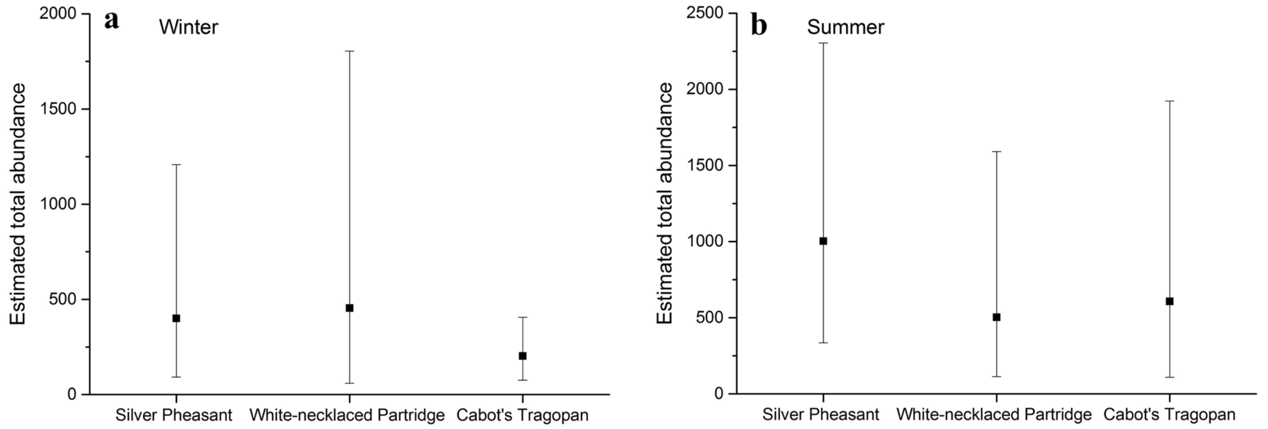

Fig. 5 Estimated total abundance across 24 sampling camera sites during winter (**a**) and summer (**b**)

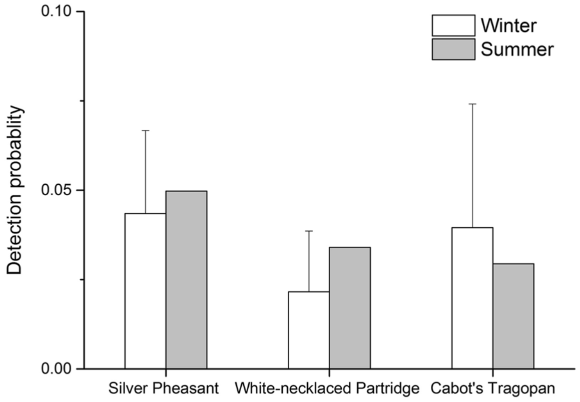

Fig. 6 Back-transformed detection probability (mean + SE) of each of three species in winter and summer

altitudinally with season (Gao 1991). In contrast, White-necklaced Partridge and Cabot's Tragopan were most frequently recorded by camera in winter, and there was no variation in monthly activity detection probability. One explanation for this is that these two species have a fixed or smaller home range, and do not migrate altitudinally with season (Zhao 2001). Alternatively, the results may reflect that compared to Silver Pheasant both White-necklaced Partridge and Cabot's Tragopan have much lower "true" abundance and detection probability in our permanent study plot (Fig. 2), or that four years of survey are not long enough to adequately record similar differences in monthly activity between the two species. It is a matter of urgency to assess the endangered status of these two species, and to establish protection strategies for White-necklaced Partridge and Cabot's Tragopan at Nanling. In summary, monthly activity peaks of Silver Pheasant were different from the other two species, which indicated that temporal activities were distinct for these three pheasant species as studies of Little Cormorant and Indian Cormorant have shown in India (Mahendiran 2016). Such activity differences facilitate the coexistence of endangered sympatric species, reflect niche diversification, and expand knowledge of coexistence in species ecology.

The study of spatial and temporal variation in population abundance is central to ecology (Bivand et al. 2013). For instance, bird counts are important organismic indicators in biodiversity monitoring programs, where the population sizes of specific species or functional guilds are used to evaluate environmental health (Zhang et al. 2015). For some endemic species, bird counts are also used to measure the efficiency of nature-protection actions. However, estimation of abundance for animal populations involves two basic issues (Royle and Nichols 2003). First, the investigator is sometimes interested in areas that are too large for ground surveys to be conducted over the entire area of interest. Secondly, many species are so widespread or so inconspicuous, or have such low population densities, that their abundance cannot be assessed without error, but instead must be estimated using methods that account for detectability. In order to address these drawbacks, Royle (2004) and Kéry et al. (2005) have developed a *N*-mixture model for accounting for heterogeneous detection probabilities in replicated presence–absence data (i.e., 'occupancy surveys') where the heterogeneity arises as a result of variation in abundance among sites. This model enables abundance estimation without individual identification, based simply on temporally and spatially replicated counts. The motivating result of our study is that we identified covariate effects and obtained estimates of detectability and abundance that were largely consistent with our expectations. Moreover, the *N*-mixture model was able to distinguish complex covariate relationships (i.e. season and elevation), and the parameters of this relationship are identifiable under this model.

Conclusions

To conclude, this study demonstrates that the *N*-mixture models have performed well for the estimation of temporal population abundance at local a fixed permanent plot in mountain habitat in southern China, based on the modeling of repeated camera-trapping counts of three pheasant species. The heterogeneity in detection can be modeled easily using environmental covariates, such as seasonal and elevational factors. Notably, summer, when breeding occurs, is more suitable for the population estimation of pheasants than other seasons. In assessing suitable habitat of endemic pheasants for conservation purposes, more attention should be paid to higher elevational areas at Nanling. We suggest that the *N*-mixture model is a promising approach for camera-trapping data for endemic forest pheasants, or other species with similar life histories, and for estimating abundance for management purposes.

Moreover, the use of camera-trapping and *N*-mixture models for monitoring is more cost efficient than classical observation methods. A further point is that potential sources of detection heterogeneity are systematically surveyed and included in the model (Jakob et al. 2014). In cases where local abundance is highly heterogeneous, different habitat covariates might be related to abundance to reduce the confidence interval of the estimates. Lastly, this approach would be useful for conservation policy applications (e.g. to assess the vulnerability of a population to extinction, true population trajectory, and metapopulation dynamics), because estimates of "true abundance that are free of any potentially distorting effects of detection probability" are required, and simple counting indices of "relative abundance" are not sufficient.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s40657-019-0181-6.

Additional file 1: Table S1. Location of camera-trapping sites distributed in Nanling National Nature Reserve, Guangdong Province, China. **Table S2.** Location of camera-trapping sites distributed in Nanling National Nature Reserve, Guangdong Province, China.

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Authors' contributions

FZ designed the project and wrote the manuscript, aided by QZ, MZ and MBL, who also performed the data analysis. XW, YG and CY were responsible for camera set-up and conducted the camera-trapping. 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 request.

Ethics approval and consent to participate

Our research using camera traps at Nanling was approved by the Guangdong Wildlife Management Authority and conducted under the relevant wildlife protection laws of the People's Republic of China.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

[1] Guangdong Key Laboratory of Animal Conservation and Resource Utilization, Guangdong Public Laboratory of Wild Animal Conservation and Utilization, Guangdong Institute of Applied Biological Resources, Guangzhou 510260, China. [2] Guangdong Nanling National Nature Reserve, Ruyuan 512727, China.

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