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Conservation Assessments of Arboreal Mammals in Difficult Terrain: Occupancy Modeling of Pileated Gibbons (*Hylobates pileatus*)

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Abstract Long-term monitoring programs, wildlife surveys, and other research involving species population assessment require reliable data on population status. Given the logistically challenging nature of some species' habitats and cryptic behaviors, collecting these data can prove to be a considerable barrier. We used detection/nondetection data from pileated gibbons (*Hylobates pileatus*) in the Cardamom Mountains of southwest Cambodia to estimate their population occupancy and detectability. We modeled occupancy using elevation, tree height, tree density, tree diversity, and disturbance covariates. Modeling demonstrated that 83% of the sites are occupied by *Hylobates pileatus* and that the detectability of the species varies positively with elevation. No clear relationship between habitat quality covariates and occupancy of *Hylobates pileatus* emerged. Effort analysis based on model estimates demonstrated that at high elevations, less than half the number of site visits is needed to attain the same detectability estimate precision as across all elevations. We suggest that human activities at low elevations, which affect forest composition, are the central factors impacting the detectability and occupancy of *Hylobates pileatus*. Longer sampling durations and/or a higher number of site visits, especially at lower elevations, increase precision of the occupancy estimator for the least effort. For effective future monitoring and research for this and similar species, using this relatively simple method, applied with repeat site visits, would allow a longitudinal comparison of detection at sites in difficult terrain.

Keywords Cambodia · Covariates · Cryptic species · *Hylobates pileatus* · Maximum likelihood · Monitoring · PRESENCE

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Introduction

Population state variables, e.g., size, density, and growth and population requirements can inform research and land management plans for species and their habitats (Campbell *et al.* 2002; Carrette *et al.* 2002; Pollock *et al.* 2002; Tyre *et al.* 2003). These can be challenging to estimate in logistically difficult habitats, and study goals must be balanced with available resources. Occupancy assesses the proportion of sampled sites in which the local abundance of a species is greater than zero (MacKenzie *et al.* 2002). As a possible alternative for abundance or density estimates, which often require substantial effort, occupancy provides insight into species population distribution and status by determining species' habitat requirements as well as sources of disturbance (MacKenzie 2005; MacKenzie *et al.* 2006; Olson *et al.* 2005). Detection of a species is rarely perfect and it becomes more difficult to distinguish true and false absences as detection probability decreases, but spatial and temporal replication of survey efforts yields occupancy estimates that account for the probability of detection (MacKenzie *et al.* 2002; Tyre *et al.* 2003).

In an occupancy modeling framework, occupancy (ψ) and detection (p) probability parameters are estimated simultaneously from a detection history (repeat detection/nondetection data at multiple sites). Modeling ψ or p as a function of covariates on the logit scale assesses covariation between a species' occupancy or detectability and its environmental requirements (Donovan and Hines 2007; Elith *et al.* 2006; MacKenzie *et al.* 2002; Tyre *et al.* 2003). Occupancy modeling is based on several assumptions, including the following: the population in question is closed to changes in occupancy over the survey season; species are never falsely identified; and sites are independent, i.e., the probability of occupancy of one site is not affected by any other site (MacKenzie *et al.* 2002).

Gibbons are small, arboreal apes that inhabit the evergreen rain forests of Southeast Asia (Chivers 2005). Currently 16 species of gibbons are assessed on the IUCN Red List of threatened species as Vulnerable ($N = 1$), Endangered ($N = 11$), or Critically Endangered ($N = 4$). Many gibbon populations occur in habitats where terrain or the threat of hunting causes animals to flee from humans, making traditional line transects (especially when following roads: Hilario *et al.* 2012) impractical. The alternative method of triangulation requires substantial person-effort at few locations (Brockelman and Ali 1987). Aspects of gibbon ecology including territoriality, home range fidelity (Bartlett 2003; Gittins 1980), and loud predictable calls (Buckley *et al.* 2006; Geismann and Orgeldinger 2000) make gibbons well suited to investigation through occupancy modeling.

Using a maximum likelihood inferential approach, we assessed a population of *Hylobates pileatus* in southwest Cambodia, accounting explicitly for the probability of detection. The selected study site is mountainous, rendering transect data collection difficult. Although species are often detected visually during occupancy studies (Carrette *et al.* 2002; Guillera-Aroita *et al.* 2010; Keane *et al.* 2012), gibbons use high canopy and move quickly (Vereecke *et al.* 2006) and *Hylobates pileatus* are unhabituated in our study area, making direct counts nearly impossible. Predictable calling behavior noted from fixed points can be used for detections (MacKenzie *et al.* 2002; Pellet and Schmidt 2005) and gibbons can be detected accurately for distances up to 1 km by their loud calls (Buckley *et al.* 2006; Mitani 1985; Nijman

and Menken 2005), meaning that detection/nondetection data can be quickly collected over large geographical areas (Coudrat *et al.* 2011; Nijman and Menken 2005). Our aims were to: 1) assess the overall occupancy and detectability of *Hylobates pileatus* as estimated from repeated detection/nondetection surveys; 2) model occupancy and detectability as functions of human disturbance, tree diversity, tree height, tree density and elevation; and 3) assess the feasibility of occupancy modeling as an approach for long-term monitoring of gibbons and other vocal mammals in difficult terrain.

Methods

Survey Area

We conducted the research in Cambodia's Phnom Samkos Wilderness Sanctuary (PSWS). PSWS covers an area of *ca.* 3500 km². PSWS is dominated by evergreen hill forest with patches of high-elevation grassland, pine woodland, deciduous forest, gallery forest, bamboo groves, and open dipterocarp woodland (Grieg-Gran *et al.* 2008; Sarou 2009; Webb 2005) (Fig. 1). We collected data for *Hylobates pileatus* from three forested areas from April to July 2010 for a minimum of 14 d and a maximum of 25 d each: Stung Keo (12° 1'27.36"N, 103°7'46.60"E), Stung Ta Sok (12°24'52.66"N, 103°4'8.96"E), and Stung Delai (12°11'37.50"N, 102°57'41.44"E).

Data Collection

We collected detection/nondetection and habitat data using fixed-point sampling. We selected points using a stratified random method in which we ensured spatial independence by assuming an approximate home range size of 50 ha for *Hylobates pileatus* (Phoonjampa *et al.* 2010). Once we had passed a minimum distance of 700 m from the last point we placed the next point off the path using a preselected random distance and bearing. We used 22 points in Stung Keo and 20 points each in Stung Ta Sok and Stung Delai for both detection/nondetection and habitat data. We then added 12 points to Stung Keo, 14 points to Stung Ta Sok, and 7 points to Stung Delai for habitat sampling. We visited each fixed listening point five times at Stung Keo and Stung Ta Sok and four times at Stung Delai. During each 15-min fixed listening point visit we recorded the exact time, sex of caller, estimated distance, and direction of the calling gibbon as well as the estimated number of groups calling. We also recorded weather conditions and major weather changes using an ordinal index, in which we classified rainfall and wind as heavy, light, or absent.

To increase the probability of detection, we conducted all surveys between 08:00 h and 14:00 h (Coudrat *et al.* 2011; Traeholt *et al.* 2006). To mitigate the effect of time of day on the probability of detection per site we randomized the timing of repeated site visits. We restricted the survey period to a maximum of 25 d/ site to avoid temporal changes in singing behavior due to seasonal variation. As heavy precipitation affects the frequency of gibbons' singing negatively (Brockelman and Srikosamatara 1993), we did not collect singing data during heavy rain.

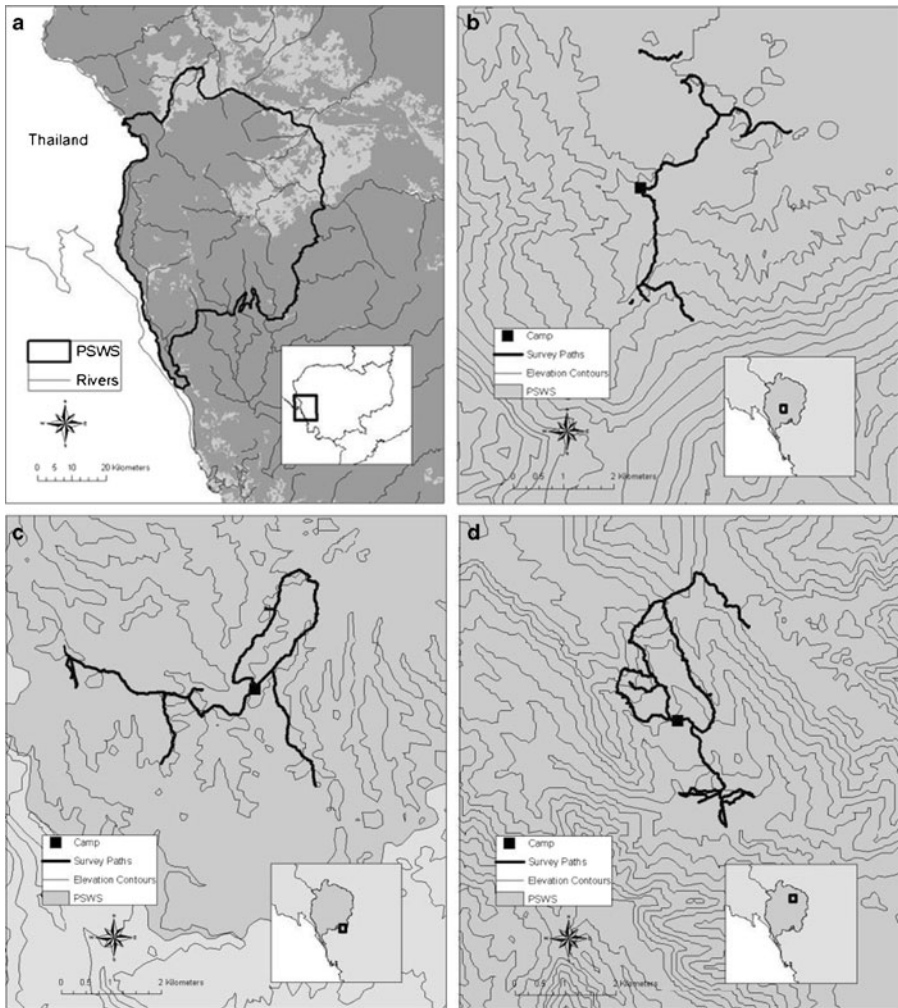


Fig. 1 Study site and survey areas for assessing occupancy of pileated gibbons in the Cardamom Mountains, southwest Cambodia, in April–July 2010. **(a)** Study site, the Phnom Samkos Wilderness Sanctuary, with the insert map denoting the location within Cambodia. **(b)** Stung Keo survey area. **(c)** Stung Ta Sok survey area. **(d)** Stung Delai survey area. For **(b)**, **(c)**, and **(d)** the black lines denote the paths traveled to get to sampling points. Fixed points (not shown) are situated along paths; inset maps denote the location of the larger maps within Cambodia.

We used point-quarter sampling (Ganzhorn 2003) to assess habitat variables. At each fixed point, we created four quadrats by plotting north/south and east/west lines converging on the point center. Within each, we calculated the distance between the tree (defined as diameter at breast height [DBH] > 10 cm) nearest to the point center and its nearest neighboring tree (McConkey *et al.* 2003). Project guides identified tree species. We calculated height using a clinometer. We estimated the canopy connectivity to the nearest neighbor tree by counting the number of trees contacted physically by the crown of the measured tree. We measured elevation, topography, slope, aspect, and GPS location at the point center. Within a 5×5 m plot placed in the northwest quadrant, we

used a DAFOR scale to derive seven measures of disturbance (DAFOR: Dominant = >75%, Abundant = 75–51%, Frequent = 50–26%, Occasional = 25–11%, Rare 10–1%) (Sutherland 2006). After removing disturbance measures that were correlated, we combined the remaining measures to create one index of disturbance covariate for analysis.

Data Analysis

We divided the three survey areas into a total of nine subareas split by geographic barriers (elevation, rivers, and overall distances). We used the mean for each covariate for each subgroup to characterize the area in which gibbons were detected. We derived a detection history for each fixed listening point, by assigning a 1 for visits where we heard *Hylobates pileatus* singing within 500 m and a 0 for visits where we heard calls from further away or not at all. A radius of 500 m is large enough to warrant survey point independence and to encompass an entire home range of *Hylobates pileatus*, thereby ensuring that any groups within the radius will be present for the entire survey, i.e., they are “occupying” the site, not just “using” it (MacKenzie 2005). As gibbon calls can be heard clearly over 1 km (Nijman 2001), a 500-m plot area radius also mitigated heterogeneity in individual detection from decreasing detection with increasing distance (Efford and Dawson 2012).

We first analyzed data from each area separately with constant occupancy and detectability and examined the proportion of sites where *Hylobates pileatus* was detected at least once (naïve estimate of occupancy) to assess general changes in detectability between survey areas. As no survey area had >22 points, we did not include covariates so as not to overparameterize the models (Donovan and Hines 2007; Elith *et al.* 2006). We combined data from the three survey areas to model occupancy and detection of *Hylobates pileatus* as functions of human disturbance, tree diversity, tree height, tree density, and elevation.

Initially, we ran a model holding ψ and p constant. We then modelled ψ and p as a function of different combinations of habitat covariates (Table I). We ranked the resulting models according to their Akaike Information Criterion (AIC), determined by

$$-2\log_e L + 2N$$

where L is the maximized likelihood and N is number of modeling parameters (Burnham and Anderson 2002). We back transformed overall estimates of probability of occupancy and detection and their standard errors from the outputted regression coefficients using the delta method (Cooch and White 2010). We obtained model-averaged estimates from top-ranking models, from models within two delta AIC units of the top-ranked model for convenience (Donovan and Hines 2007), using

$$\hat{\theta}_A = \sum_{i=1}^R w_i \hat{\theta}_i$$

where $\hat{\theta}_i$ is estimated probability of occupancy or detection for model i and w_i is the adjusted AIC weight of model i and we obtained model-averaged standard errors using

$$SE(\hat{\theta}_A) = \sum_{i=1}^R w_i \sqrt{\text{var}(\hat{\theta}_i | g_i) + (\hat{\theta}_i - \hat{\theta}_A)^2}$$

Table 1 Measured covariates used for modeling probability of detection and probability of occupancy of pileated gibbon *Hylobates. pileatus* in the Cardamom Mountains of southwest Cambodia in April–July 2010

Name	Type	Description	Covariate calculation in each subarea
Elevation	Continuous	Mean elevation in the subarea	Mean
Tree diversity	Continuous	Shannon–Wiener index of tree species diversity/ subarea	$H = -\sum P_i(\ln P_i)$ where P is the proportional frequency of each tree species (Molles and Cahill 1999)
Tree height	Continuous	Average tree height/ subarea	Mean
Tree density	Continuous	Density of individual trees per hectare in each subarea	$d=1/m^2$ where m = average distance between the tree closest to a random point and its nearest neighbor within each of four quadrants centered around the random point (Zhu and Zhang 2009)
Disturbance	Continuous	Index of human impact/subarea	collapsed into one index through addition of noncorrelated DAFOR measures/ fixed point

where $\text{var}(\hat{\theta}_i|g_i)$ is the variance of $\hat{\theta}$ in model i and R is the number of models averaged in the set (Burnham and Anderson 2002). We assessed model fit for the most parameterized (global) model and the top-ranking model using a bootstrap χ^2 test comparing the model-observed history probabilities to histories randomly generated from the model parameters (Burnham and Anderson 2002; Donovan and Hines 2007; MacKenzie and Bailey 2004).

We used the sum of AIC weights for each covariate from models within two AIC units of the top-ranking model to assess their relative contribution to either occupancy or detectability (Burnham and Anderson 2002; Guillera-Arroita *et al.* 2010; MacKenzie *et al.* 2006).

We calculated the minimum number of site visits (N_{\min}) required to be 95% confident that the species is detected where present given the estimated probability of detection using the formula

$$N_{\min} = \frac{\log(C)}{\log(1-p)}$$

where p is the estimated model averaged detection probability and C is the confidence level (either 0.05 or 0.15) (MacKenzie 2005; Pellet and Schimdt 2005). We calculated total effort requirements for achieving various desired levels of precision (0.05, 0.075, 0.1, 0.15) in the model probability of occupancy estimator by identifying where the number of sites (s) multiplied by the number of site visits (K) is minimized. K was allowed to vary between 1 and 50 and s was calculated using the formula

$$s = \frac{\Psi}{\text{Var}(\Psi)} \left[(1-\Psi) + \frac{(1-p^*)}{p^* - Kp(1-p)^{K-1}} \right]$$

where p^* , the probability of detecting a species at least once after K surveys, was calculated as $p^* = 1 - (1 - p)^K$ (Guillera-Arroita *et al.* 2010). We used PRESENCE

(Hines 2006) 3.0 for all occupancy modeling and SPSS 17.0 for all supplemental statistical analysis.

Results

We heard *Hylobates pileatus* sing more than once at 34% of sites where we detected them at least once. Modeling occupancy for each survey area on its own demonstrated a low probability of detection. At Stung Keo, the probability of detection was 0.13 (SE \pm 0.07). With a naïve estimate of occupancy of 45%, $\hat{\psi}$ was quite high for the area (90% \pm 0.39). The naïve occupancy at Stung Ta Sok was 35%, $\hat{p} = 0.18$ (\pm 0.08), and $\hat{\psi}$ was only 55% (\pm 0.24). Detections were more frequent at Stung Delai ($\hat{p} = 0.34 \pm 0.09$), which produced a closer naïve (60%) and estimated occupancy (0.75 \pm 0.16).

Across all three survey areas, we detected *Hylobates pileatus* at 29 of 62 sites producing a naïve probability of occupancy of 0.47. In the simplest model combining all three areas in which occupancy and detectability were held constant their estimated values were 0.67 and 0.23, respectively (Table II). Both the constant and survey-specific estimation of p models were ranked rather low among the models ($w_i = 0.0$ and 0.0).

We found no evidence of lack of fit for the most parameterized model (five covariates) ($\chi^2 = 29.63$, $\hat{c} = 0.72$, probability test statistic \geq observed = 0.78) and the top-ranking model ($\chi^2 = 31.44$, $\hat{c} = 0.77$, probability test statistic \geq observed = 0.74). We removed three models that did not converge in the likelihood maximization from the top-ranking models. The lack of convergence was likely due to the combination of parameters in those models as changing the initial estimate values did not affect convergence. The probability of detection in the top-ranking model was quite low (0.18, SE \pm 0.036). Correspondingly, the naïve occupancy in the top-

Table II Occupancy models for pileated gibbons *Hylobates pileatus* in the Cardamom Mountains, southwest Cambodia in April–July 2010, with AIC values within 2 units of the top-ranking model

#	Model	AIC	D.AIC	N	w_i	A. w_i	ψ (\pm SE)	p (\pm SE)
1	$p(\text{ele}), \psi$	232.34	0	3	0.100	0.210	0.85(0.150)	0.18(0.036)
2	$p(\text{ele}), \psi(\text{div})$	233.17	0.830	4	0.066	0.138	0.79(0.149)	0.19(0.039)
3	$p(\text{ele}, \text{div}), \psi$	233.26	0.920	4	0.063	0.132	0.87(0.142)	0.18(0.034)
4	$p(\text{ele}), \psi(\text{dist})$	233.75	1.410	4	0.050	0.104	0.81(0.147)	0.19(0.039)
5	$p(\text{ele}), \psi(\text{hei})$	234.04	1.700	4	0.043	0.090	0.81(0.159)	0.18(0.040)
6	$p(\text{ele}, \text{dens}), \psi(\text{div})$	234.05	1.710	5	0.043	0.089	0.77(0.146)	0.20(0.042)
7	$p(\text{ele}), \psi(\text{ele})$	234.26	1.920	4	0.038	0.080	0.81(0.201)	0.19(0.042)
8	$p(\text{ele}, \text{hei}), \psi$	234.28	1.940	4	0.038	0.079	0.85(0.149)	0.2(0.036)
9	$p(\text{ele}), \psi(\text{dens})$	234.33	1.990	4	0.037	0.078	0.84(0.158)	0.18(0.037)
10	p, ψ	243.29		2		0.0004	0.67 (0.122)	0.22(0.047)

Model names include the covariate that was modeled with the probability of occupancy (ψ) and the probability of detection (p). Covariates included in the top-ranking models are elevation (ele), Shannon–Wiener index of tree diversity (div), tree density (dens), disturbance (dist) and tree height (hei). Delta AIC (D. AIC) is the difference in AIC between model i and the top-ranking model. N is the number of parameters in model i . The adjusted AIC weight (A. w_i) is the proportional weight of model i for this model set.

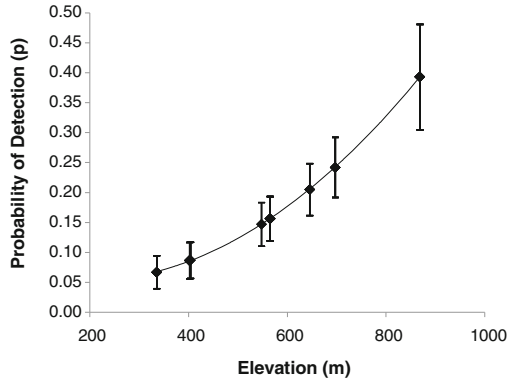


Fig. 2 Changes in the average estimate of probability of detection of pileated gibbons *Hylobates pileatus* in the Cardamom Mountains, southwest Cambodia, in April–July 2010 as predicted by elevation. Error bars represent standard errors. Detection probabilities are from the top-ranking model.

ranking model (47%) was much lower than the associated $\hat{\psi}$ (0.85 ± 0.150), indicating that the gibbons went undetected at sites where they were present (Pellet and Schmidt 2005). Model-averaged $\hat{\psi}$ and \hat{p} (0.83 ± 0.157 and 0.18 ± 0.039) were only nominally different from those of the top-ranking model.

Elevation (ele) was the strongest predictor of the probability of detection when the species was present, as demonstrated by the sum of the adjusted AIC weights from of all models in the top-ranking set containing $\hat{p}(\text{ele})$ (1.00). The effect of elevation was both positive and significant (i.e., the confidence interval does not cross 0). The regression coefficient and 95% confidence interval of $\hat{p}(\text{ele})$ from the top-ranking model were 0.698 ± 0.372 (Fig. 2). No single covariate emerged as an essential predictor of occupancy but tree species diversity was the most important in the top-ranking models (Table III). The poor precision of estimate for the tree diversity regression coefficient with $\hat{\psi}$ and its low summed AIC from the top-ranking models (0.228) weaken its predictive power. In the top-ranking model containing tree diversity covariation with ψ , the regression coefficient value and 95% confidence interval for $\hat{\psi}(\text{div})$ was 0.716 ± 1.435 .

Table III Tree species richness (number of species with dbh >10 cm) and Shannon–Wiener index of diversity (SW) for each of the subareas examined in Stung Keo (SK), Stung Ta Sok (ST), and Stung Delai (SD) in the Cardamom Mountains, southwest Cambodia in April–July 2010

Subarea	SW diversity	Richness
SK 1	3.05	25
SK 2	2.94	25
SK 3	2.92	24
ST 1	2.90	27
ST 2	2.56	19
ST 3	2.56	19
SD 1	3.24	31
SD 2	2.83	24
SD 3	2.63	19

Based on the model-averaged estimate of p , up to 15 site visits are needed to ensure with 95% confidence that *Hylobates pileatus* is not missed at an occupied site. If the confidence is lowered to 85%, the number of site visits required reduces to nine. At 95% confidence, only six visits are needed at elevations >800 m. Assessment of total effort revealed only a slight increase in sites required for the same estimate precision between high elevation areas and the model averaged estimate of p at the point of least effort (Fig. 3). The number of sites required for a desired level of estimate precision ranged from 8 to 73 in low-elevation areas and 8 to 79 in high-elevation areas.

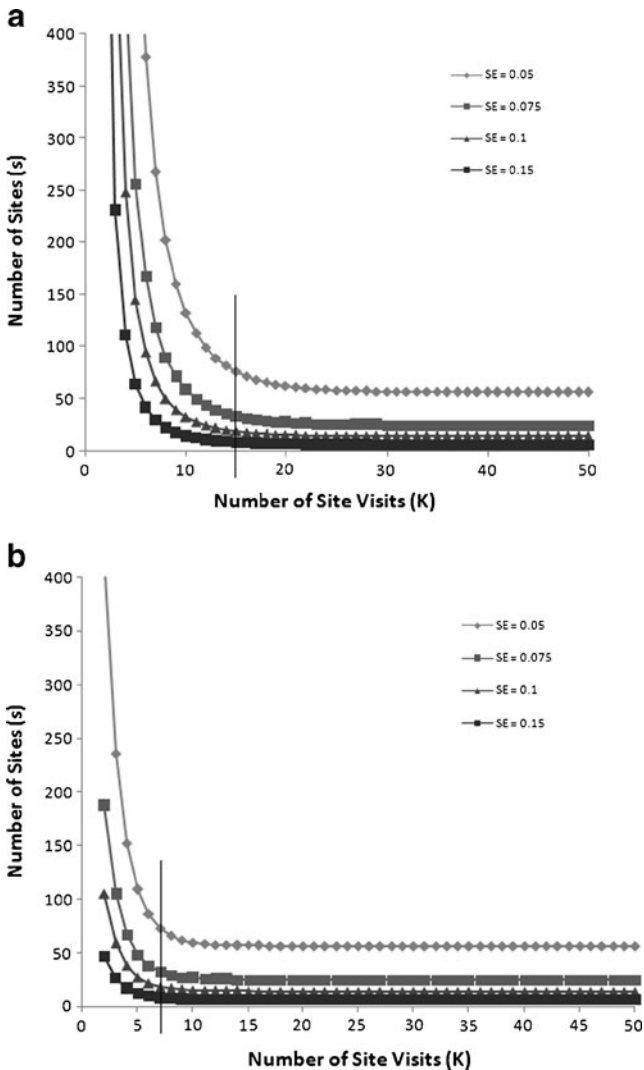


Fig. 3 Number of sites (s) needed per site visit repetitions (K) for varying levels of precision given model estimates of probability of occupancy and the probability of detection of pileated gibbons *Hylobates pileatus* in the Cardamom Mountains, southwest Cambodia, in April–July 2010. We calculated optimal survey effort by minimizing $s * K$. We generated curves (a) using the overall model averaged estimates of p ($p = 0.183$ and $\psi = 0.825$) and curves (b) from the model averaged estimate of p at high elevation (>800 m) fixed points ($p = 0.39$ and $\psi = 0.825$). Single vertical line represents the point of least effort for an SE of 0.05.

Discussion

Our results support the use of occupancy modeling as a means of surveying highly vocal but rare arboreal mammal species in difficult habitats. Detection/nondetection data proved to be a useful approach for describing the relationship between elevation and the spatial distribution of a vocal mammal in mountainous habitat, in this case *Hylobates pileatus*. When estimating other state variables, such as density, using distance sampling, the recorded distance between sighted individuals and the survey transect or point must be measured precisely (Buckland *et al.* 1993; Ross and Reeve 2003). This would have been nearly impossible in our study owing to the difficult terrain and cryptic behavior of *Hylobates pileatus*. Occupancy sampling requires only that individuals are detected within a set distance rather than precise measurements of distance. It is possible that our analysis included detections from outside a 500-m radius sampling circle, which would have overestimated the probability of detection or occupancy. Whenever possible, the sampling team visited the location of singing gibbons to increase confidence in estimating distances and it is unlikely that our analysis included numerous detections beyond 500 m. Because our surveying method required only a relatively short visit to each fixed point, repeated visits were possible, allowing the incorporation of detectability into our analysis. Detection rates and the corresponding modeled probability of detection of *Hylobates pileatus* were low in all three study areas, indicating that occupancy and other measurable state variables would probably be underestimated without an assessment of detectability. Further, establishing transects would have consumed considerable time in the mountainous field site. Randomly placed fixed points are far more time efficient (Nijman and Menken 2005).

Previous studies have used gibbon vocal behavior to estimate their densities and distribution through triangulation. However, triangulation represents increased effort over occupancy modeling for several reasons. First, Brockelman and Srikosamatara (1993) included a correction factor to mitigate variability-induced error of singing into density estimates. Correction factors require knowledge of group composition and singing behavior, which is difficult to collect from unhabituated groups during short studies. Second, like distance sampling, distance estimates are required to plot group detections (Brockelman and Srikosmatara 1993). Third, triangulation requires more than one group of researchers, unlike occupancy modeling, allowing us to sample a larger area in a short period. Finally, collecting detection/nondetection data from single points is straightforward and requires limited training when compared to the three points and subsequent training needed for triangulation.

Elevation was important for predicting the probability of detection of *Hylobates pileatus*. The probability of detection was at least three times larger at altitudes >700 m than at lower elevations. This contrasts with the results of other researchers who found that detection and the corresponding abundance of gibbons decrease with elevation (Caldecott 1980; Fan and Jiang 2010; Nijman 2004). As altitude increases forest structure changes, including smaller basal area and tree girth, creating less habitable conditions for gibbons (Caldecott 1980). Forest characteristics including tree DBH, connectivity, and height did not change substantially with elevation at our study site, suggesting that p decreased at lower elevation for other reasons. A likely contributor to this decreased p in low-lying areas is a change in the singing behavior of *Hylobates pileatus*. Increased human presence and habitat disturbance have been shown to change

gibbon singing behavior (Fan and Jiang 2010; Johns 1985; Nijman 2001), affecting their detectability rather than their occupancy. In all survey areas, as elevation increased, roads built for selective logging decreased, and vehicles and direct evidence of hunting were more common in low-lying areas. Roads were not built higher than 680 m at Stung Delai and Stung Ta Sok, while they did not extend >340 m in elevation at Stung Keo.

We also found some weak indication that the probability of occupancy may increase with tree diversity. Tree diversity has been found to be an important habitat requirement of gibbons (Caldecott 1980; Cheyne *et al.* 2012; Fan and Jiang 2010; Phoonjampa *et al.* 2010). Low tree-species diversity in our survey areas indicates that some intergroup resource competition may occur and that the probability of gibbon occupancy increases in areas of high tree diversity (Brockelman and Srikosmatara 1993; Fan *et al.* 2009; Mitani 1985; Nijman 2004). The lack of significance of the ψ -tree diversity relationship is probably due to the relatively small sample of tree species frequencies contributing to the Shannon–Wiener indices in each area. A small sample size increases the variance of the measure of tree species diversity in sampling subarea, which would, in turn, increase the standard error around the model-estimated tree diversity regression coefficient (Guillera-Arroita *et al.* 2010). The prevalence of nondetection in the sampling histories also tends to introduce bias and reduce precision in covariate coefficients (Gu and Swihart 2004).

The effort analysis provides further guidelines for long-term monitoring of *Hylobates pileatus*. Only a small increase in the number of sites from high to average elevation sites was needed to achieve the same estimate precision. However, half the number of site visits was necessary to arrive at occupancy estimates of the same precision from overall estimates. In addition, because the probability of detection decreases at lower elevations, surveys of low-lying areas should use longer sample durations and/or a higher number of site visits to ensure adequate detections for modeling (Geissmann *et al.* 2009; Pellet and Schmidt 2004). The simplicity of occupancy data collection allows for the increased costs incurred. The Ministry of Environment and PSWS rangers that patrol the forest regularly could conduct long-term monitoring based on detection/nondetection data using repeated site visits with multiple teams. Once fixed points have been designated for site visits, very little training and no additional equipment is necessary to generate detection histories over several seasons. To ensure informative results from future occupancy monitoring programmes in the area, covariate values could be obtained from multiple sources such as habitat sampling at gibbon detection locations and remote sensing data (Guillera-Arroita *et al.* 2010).

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