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Modelling species distribution at multiple spatial scales: gibbon habitat preferences in a fragmented landscape

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Abstract

Conservation of Indochinese primates is hampered by a lack of knowledge of species ecology, habitat preferences and, locally, distribution. Predictive distribution and habitat suitability models, using predictors known to affect the distribution of similar species elsewhere, may, therefore be of great benefit to conservationists within the region. Yellow-cheeked crested gibbon *Nomascus gabriellae* is an IUCN-listed endangered primate distributed east of the Mekong River in Cambodia, southern Vietnam, and possibly southern Lao PDR. Within Cambodia, yellow-cheeked crested gibbon are naturally restricted to evergreen forest fragments within a landscape matrix of deciduous dipterocarp and semi-evergreen forests. During the 2008 dry season, auditory surveys for yellow-cheeked crested gibbon were conducted within Phnom Prich Wildlife Sanctuary, Mondulkiri province, Cambodia. Predictive distribution models, in which variables were included at the scale at which they best explained gibbon occurrence (multi-grain models), were constructed to examine the species' habitat associations and tolerance of habitat fragmentation within the wildlife sanctuary. Gibbon occupancy (φ) was higher in evergreen (0.43 ± 0.26–0.62) than in semi-evergreen forest (0.21 ± 0.09–0.4), with gibbon presence constrained by a critical amount of evergreen forest within 5 km radius of listening posts. Three patches of optimal habitat within Phnom Prich Wildlife Sanctuary were identified. These, and connecting habitats, should be the target of increased enforcement effort to limit hunting and habitat conversion. Similar multi-grain models are likely to be valuable for conservationists within mosaic habitats as they can facilitate identification of the minimum suitable fragment size for species of conservation concern.

Introduction

With high species diversity and exceptional levels of endemism, Indochina is globally significant for primate conservation (Groves, 2001; Polet & Ling, 2004; Sodhi *et al*., 2009). Indochinese primates are chronically threatened due to habitat loss, fragmentation and hunting (Johnson *et al*., 2005; Nadler *et al*., 2007; Duckworth, 2008). These processes are exacerbated by human population densities that are much higher than in many other tropical and subtropical regions (Sodhi *et al*., 2004). Consequently, proportionately more Indochinese primate species are globally threatened than from any other tropical region (Schipper *et al*., 2008). Efforts to address primate conservation issues in tropical Asia are, however, hampered by a lack of knowledge of species limits, taxonomy, population size and local distribution and habitat preferences (Timmins & Duckworth, 1999; O'Brien *et al*., 2004; Jablonski, 2005; Konrad & Geissmann, 2006; Duckworth, 2008).

Statistical species distribution models, which predict habitat suitability based on relationships between environmental variables and species' incidence or abundance, are increasingly used by conservationists to understand habitat requirements and clarify the distribution of species of conservation concern (Gibson *et al*., 2004; Jedrzejewski *et al*., 2008; Gray *et al*., 2009). Despite habitat and landscape variables often affecting wildlife populations at different scales (Wiens, 1989), habitat suitability models generally only include predictor variables at a single, constant scale. As a consequence, such models, and the resulting conservation management strategies, tend to focus on discrete 'habitat patches' and neglect the possible effects of the surrounding landscape. In contrast, multi-grain models, in which predictor variables are included at a scale at which they best explain observed species incidence, can allow an inference regarding the factors affecting species distribution across multiple scales (Cozzi, Muller & Krauss, 2008), therefore helping explore the influences of spatial scale on species distribution and abundance (Gray *et al*., 2009).

Predictive models may, therefore, be a valuable conservation tool for species within fragmented or mosaic landscapes where persistence may depend on critical amounts of different habitat within varying distance of the survey sites.

Crested Gibbons (*Nomascus*) are one of four genera within the Gibbon family (Hylobatidae) and are represented by six recognised species occurring in the tropical evergreen and semi-evergreen forests of Indochina east of the Mekong river (Groves, 2001, 2007). All species are IUCN listed as Critically Endangered or Endangered (Geissmann *et al*., 2008), making the genus a priority for primate conservation. Yellow-cheeked crested gibbon *Nomascus gabriellae* occurs east of the Mekong River in north-eastern Cambodia, southern Vietnam, and possibly the extreme south of Lao PDR (Duckworth, 2008; N. T. Van, pers. comm.). Despite having the largest distribution range and presumed population size of any *Nomascus* gibbon, the species is considered Endangered based on an estimated population decline of over 50% within the past 45 years (three generations) primarily resulting from hunting and habitat loss (Geissmann *et al*., 2008). The largest extant populations of yellow-cheeked crested gibbon are believed to occur within evergreen and semi-evergreen forests in Mondulkiri and Ratanakiri provinces, Cambodia. In most of this range, suitable habitat is fragmented due to both the naturally patchy distribution of evergreen and semi-evergreen forests within the wider deciduous dipterocarp landscape matrix and the recent anthropogenic habitat loss and degradation (Stott, 1990; Tordoff *et al*., 2005). In common with the majority of globally threatened primate species within Indochina, conservationists lack knowledge of micro-distribution, accurate population size and habitat preferences, including tolerance of habitat fragmentation and degradation to effectively conserve the species (Traeholt *et al*., 2005; Nadler *et al*., 2007; Duckworth, 2008). The aims of this study were, therefore, to develop multi-grain habitat suitability models of yellow-cheeked crested gibbon within one protected area, Phnom Prich Wildlife Sanctuary, Mondulkiri province, Cambodia, in order to examine the species' habitat associations and tolerance of habitat fragmentation, and to model distribution patterns within the wildlife sanctuary for targeting field conservation actions.

Methods

Study area

Phnom Prich Wildlife Sanctuary (PPWS) is located in the west of Mondulkiri Province, east Cambodia (centred on 12.8°N, 106.5°E), and covers 2225 km^2. The terrain is characterised by higher elevation and relief (maximum 640 m a.s.l.) in the south-eastern section near the Mondulkiri plateau, sloping down towards the north and west to gently undulating lowlands with elevation *c*. 80–200 m a.s.l. PPWS forms part of one of the largest remaining relatively undisturbed landscapes in mainland south-east Asia and consists of a mosaic of deciduous dipterocarp forest (1027 km^2), semi-evergreen (808 km^2) and evergreen forests (262 km^2). Although the levels of human activity are relatively low throughout PPWS, large areas of the deciduous dipterocarp forest are annually burnt and it is unclear how this, and other anthropogenic activities, has affected the distribution of forest types.

Gibbon surveys

Yellow-cheeked crested gibbon within PPWS were sampled using auditory surveys recording the presence/non-detection of calling gibbon. Gibbons typically live high in the thick canopy of evergreen and semi-evergreen forest and are very wary, with responses to detection of humans ranging from noisy flight to quiet hiding (O'Brien *et al*., 2004). However, all gibbon species are known to produce loud, long and well-patterned song bouts (Geissmann & Orgelginger, 2000). Therefore, to counter the problems associated with the limited visibility of gibbons in the canopy, and the variable response of gibbons to detection of humans, auditory surveys are widely used for surveying gibbon populations (O'Brien *et al*., 2004; Traeholt *et al*., 2005; Rawson, Clements & Meng, 2009)

Previous observations of yellow-cheeked crested gibbon in Cambodia and Vietnam suggest that vocalizations are more frequent in the dry season (November–May), with heavy rainfall suppressing vocal activity (Rawson, Clements & Meng, 2009). Consequently, data collection was carried out during the dry season, with surveys conducted between January and April 2008. Yellow-cheeked crested gibbon sing almost exclusively in the morning, with social groups performing either solo (male/female or juvenile only) or duet (male and female) song bouts (Rawson, Clements & Meng, 2009). All surveys were therefore conducted between 05:00 and 12:00 h.

Surveys were conducted at randomly selected locations at the ground level (listening posts), with the restriction that no two listening posts were located closer than 2 km (the approximate maximum carrying distance of calling gibbon) from each other, within evergreen ($n = 28$) and semi-evergreen ($n = 25$) forest within PPWS. Based on prior knowledge of gibbon distribution and ecology within the study site, no listening posts were located within deciduous dipterocarp forest, where the lack of contiguous canopy makes the habitat unsuitable (Rawson, Clements & Meng, 2009).

Observations of focal yellow-cheeked crested gibbon groups have suggested that the probability of detecting calls over three survey days in the dry season exceeds 90% (Rawson, Clements & Meng, 2009); therefore, each listening post was visited on three consecutive mornings and the presence or the non-detection of calling gibbon was recorded. An occupancy framework (MacKenzie *et al*., 2002) was used in order to estimate the detection function and to correct for non-detection. The influence of habitat covariates (forest type) on gibbon occupancy (φ) and probability of detection (P) were modelled using the software Presence version 2.1 that implements the MacKenzie *et al*. (2002) model.

Predictive modelling

The probability of yellow-cheeked crested gibbon presence at listening posts was modelled using binary logistic regression with multi-model inference used to produce final models comprising averaged parameters for each variable (Burnham & Anderson, 2002). Model predictors were selected based on prior knowledge of gibbon ecology based on field studies within Cambodia (Traeholt *et al*., 2005; Rawson, Clements & Meng, 2009) and elsewhere in Indochina (Duckworth, 2008; N. T. Van, pers. comm.). However, we were constrained to using habitat and landscape variables available in GIS format for the entire study area. Based on these criteria, five predictor variables were selected, three habitat variables (cover of evergreen, semi-evergreen and deciduous dipterocarp forest) and two landscape variables related to human use of the wildlife sanctuary [distance to nearest village (m) and distance to nearest track (m)]. The three forest types (habitat variables) differ in the tree species composition, percentage canopy cover and understorey vegetation (Rundel, 1999). Habitat information was obtained from 2002 Cambodia-wide land-use cover (JICA, 2003), the most accurate land-cover classification for the study region, and landscape variables from internal WWF GIS datasets ground-truthed by field workers between 2002 and 2008.

To examine the spatial scale at which each predictor most strongly influenced gibbon presence/absence, univariate models were constructed for each habitat predictor variable at a range of grain sizes. Proportions of evergreen, semi-evergreen and deciduous dipterocarp forests cover were calculated within circular windows surrounding the centre of each listening post. Window size was increased stepwise from 500 to 10 000 m at increments of 500 m. The best grain size was taken as that for which the variable explained the greatest amount of variance in gibbon presence/absence, as assessed using Akaike's Information Criteria corrected for small sample size (AICc) (Gray *et al*., 2009). Subsequent multivariate models incorporated the percentage cover of each forest type surrounding each survey location at the scale at which it had performed best in these univariate tests. At these 'best scales,' no pairs of variables were strongly correlated ($r<0.7$); therefore, multicolinearity was sufficiently low for all five variables to be included in the final model (Freckleton, 2002).

Alternative models were constructed from all possible combinations of variables (Burnham & Anderson, 2002). Models were ranked based on their AICc and the Akaike weight (W_i) of each model was calculated (Burnham & Anderson, 2002). The Akaike weight represents the ratio of ΔAICc values for the whole set of candidate models, providing a measure of the strength of evidence for each model. A 95% confidence set of models was selected by sequentially summing Akaike weights until the total >0.95. This corresponds to a set of models in which there is 95% confidence that the best approximating model is included (Burnham & Anderson, 2002). We followed Burnham and Anderson (2002) to calculate model-averaged parameter estimates, and the unconditional standard error of each estimate, from this set of models. We calculated the relative importance for each variable included within the 95% confidence set by summing the Akaike weights for all models containing that variable.

Model accuracy and fit was assessed using the area under receiver operating characteristic curve (AUC) and true skill statistic (TSS) (Allouche *et al*., 2006). Receiver operating characteristic plots evaluate the performance of a model, independent of a threshold probability value for judging presence/absence. The AUC is a single measure of model fit; a value of 0.5 is equal to random allocation of presence/absence, and a value of 1.0 is the perfect prediction at all possible cut-off values (Gray *et al*., 2007). TSS is derived from Cohen's κ and measures the actual agreement minus the agreement expected by chance while allowing for prevalence, which may be a particular problem when modelling rare species because the number of presence records can be limited (Allouche *et al*., 2006; Gray *et al*., 2009). To calculate TSS, it is necessary to define a threshold of predicted probability above which a species is considered present. We calculated the optimized threshold (TSS^{opt}), determined as the probability threshold yielding the highest TSS value of all possible threshold values from 0.01 to 0.99. Values of TSS can be classified as <0.4 poor; 0.4–0.7 moderate; >0.7 good (Allouche *et al*., 2006). Statistical analysis was conducted in STATA statistical software (Stata, 2005).

The final model-averaged logistic regression equation was used to predict the distribution of yellow-cheeked crested gibbon (at TSS^{opt}) within PPWS. Arc View GIS (ESRI, 1999) was used to compare this with the total extent of evergreen forest within the wildlife sanctuary.

Results

Occupancy and univariate analysis

Yellow-cheeked crested gibbons were detected from 17 of the 53 surveyed listening posts (0.32). Occupancy analysis suggested that true occupancy varied between habitat types and was greater within evergreen forest [$\varphi = 0.43 \pm 0.26–0.62$ 95% confidence interval (CI)] than semi-evergreen forest ($\varphi = 0.21 \pm 0.09–0.4$ 95% CI). The probability of detection during one visit was constant between the habitat types ($P = 0.84 \pm 0.71–0.91$ 95% CI). In univariate logistic regression, the three habitat predictors best explained variance in gibbon occurrence at different scales. Cover of semi-evergreen forest had the highest influence at relatively small scales (greatest reduction in deviance at 1500 m radius), deciduous dipterocarp forest cover at an intermediate scale (3000 m radius) and evergreen forest cover over a larger scale (5000 m radius). At these scales, gibbons showed a positive preference for evergreen forest ($t = 5.3$, d.f. = 51, $P<0.001$) and avoidance of semi-evergreen ($t = 2.8$, d.f. = 51, $P = 0.008$) and deciduous dipterocarp forests ($t = 3.2$, d.f. = 51, $P<0.003$). Listening posts where gibbons were recorded were located further away

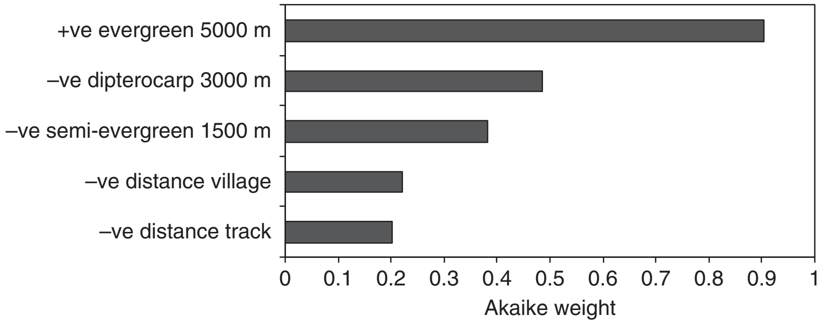

Figure 1 Ranking of habitat and landscape variables included in 95% set of models by sum of Akaike weights (ΣW_i). +ve or −ve symbol indicates the direction of effect of variable on the probability of gibbon presence.

from both villages and roads than listening posts with no gibbons; however, the differences were non-significant ($P = 0.16$–0.32)

Model averaging and predictive model

The single 'best' logistic regression model contained one predictor variable: evergreen forest cover; however, the relatively low Akaike weight of this model (0.2) indicated uncertainty relative to alternative models, therefore supporting the use of a model-averaging approach. Two alternative models (both containing evergreen forest cover with deciduous dipterocarp forest cover and distance to track, respectively) were within $<2\ \Delta\mathrm{AIC}$ of the best model, indicating substantial support. A further 13 models were within $<5\ \Delta\mathrm{AIC}$ of the best model. The sum of Akaike weights of these 16 models was 0.96; these were, therefore, considered the 95% CI set. All five predictor variables were included in this final model set with the positive relationship with evergreen forest cover included in all but three models. The high sum of Akaike weights for this variable (0.904) indicates the overwhelming importance of evergreen forest cover on the probability of gibbon presence. Additional variables were ranked −ve deciduous dipterocarp forest cover >−ve semi-evergreen forest cover >−ve distance to the nearest village >−ve distance to the nearest track (Fig. 1).

The final model-averaged regression equation (Table 1) fitted the data well with high AUC (0.88 ± 0.79–0.98 95% CI) and TSS scores (0.7 at $\mathrm{TSS}^{\mathrm{opt}} = P > 0.26$). Plotting the frequency distribution of observed data against predicted probabilities of gibbon presence from the logistic regression equation (Smart *et al*., 2004) demonstrates the clear positive influence of evergreen forest cover within 5000 m of listening posts (Fig. 2a) and the negative influence of deciduous dipterocarp forest within 3000 m (Fig. 2b) on the probability of gibbon presence.

At $\mathrm{TSS}^{\mathrm{opt}}$ (0.26), 123 km^2 of PPWS were predicted as an optimal habitat for yellow-cheeked crested gibbon, with three separate patches of suitable habitat within the south of the wildlife sanctuary (Fig. 3). The mean patch size of the suitable habitat was 40.4 km^2 (range 15.8–56.2 km^2). Additional smaller patches of evergreen forest within the sanctuary (mean size 5 km^2; range 0.7–14 km^2) were predicted as being unsuitable for the species. This suggests that $>15\ \mathrm{km}^2$ of evergreen forest cover within the vicinity of listening posts is necessary to support yellow-cheeked crested gibbon within the deciduous forest matrix of PPWS.

Table 1 Final model-averaged parameter coefficient estimates and the unconditional standard error of each estimate for gibbon presence/absence at listening posts within the Phnom Prich Wildlife Sanctuary

Predictor variable	Average coefficient	Standard error
Evergreen forest cover 5000 m	11.635	4.9
Semi-evergreen forest cover 1500 m	−0.961	1.4
Deciduous dipterocarp forest cover 3000 m	−3.746	3.1
Distance to village (m)	0.001	<0.001
Distance to road (m)	0.001	<0.001
Constant	−2.563	1.5

Discussion

Conservation activities within tropical regions are often hindered by lack of knowledge of the local distribution, ecology and habitat preferences of focal species. Statistical predictive distribution and habitat suitability models can, therefore, benefit conservationists through predicting species distributions at both local (Gibson *et al*., 2004; Jegannthan *et al*., 2004) and regional scales (McShea *et al*., 2005; Gray *et al*., 2009) and improving understanding of the ecological factors influencing distribution (Lane, Alonso & Martín, 2001; Gray *et al*., 2007). We have demonstrated the utility of such habitat suitability models for the conservation of poorly known species by providing important information on the local distribution and habitat preferences, including identification of possible minimum fragment size, for the globally Endangered yellow-cheeked crested gibbon within PPWS, Mondulkiri, Cambodia.

Although yellow-cheeked crested gibbon has been regarded as a habitat generalist occurring within evergreen, semi-evergreen, mixed deciduous and bamboo forests (Rawson, Clements & Meng, 2009), our results suggest that, at least during the dry season within the mosaic landscape of PPWS, the species is strongly dependant on the extent of evergreen forest cover. Percentage cover of evergreen forest

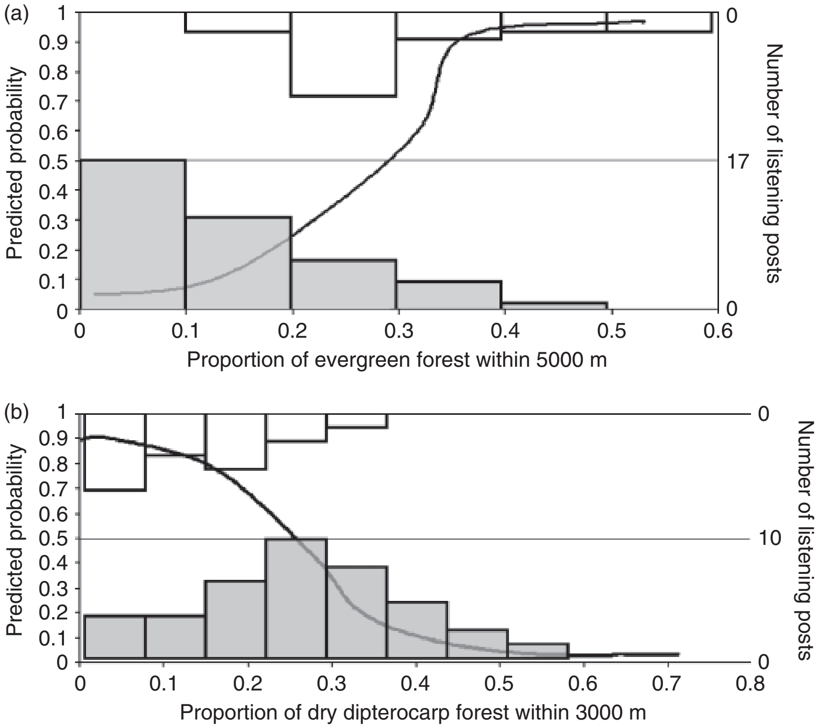

Figure 2 The probability of gibbon presence at listening posts in relation to (a) proportion of evergreen forest within 5000 m and (b) proportion of deciduous dipterocarp forest within 3000 m. Bars shows the frequency distribution of observed data for occupied (white bars) and unoccupied (grey bars) locations and the line shows the fitted logistic regression curve (see Smart *et al.*, 2004).

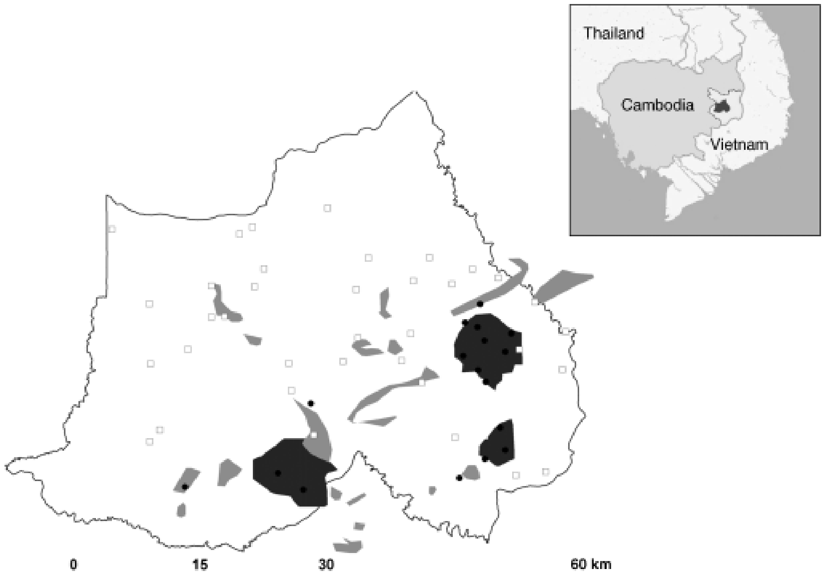

Figure 3 Predicted distribution of yellow-cheeked crested gibbon (dark grey) within the Phnom Prich Wildlife Sanctuary at TSS^{opt} ($P > 0.26$) based on listening post surveys. Listening posts, circles, filled where gibbon present and empty when absent. Evergreen forest patches in which gibbon were predicted are in light grey.

within 5000 m of listening posts was identified as the most important predictor variable within the model-averaged logistic regression equation, with an Akaike Weight almost double that of the second most important predictor (avoidance of deciduous dipterocarp forest). The large spatial scale at which evergreen forest cover affected gibbon distribution is likely to reflect the necessity for a minimum amount of this habitat in order to provide the necessary year-round resources to support gibbon. By developing a multi-grain model, incorporating the effects of the surrounding landscape upon the probability of gibbon presence, we were able to identify this potential minimum threshold of evergreen forest. This was 15 km^2; smaller fragments, representing $> 50\%$ of the evergreen forest cover within the study area, were predicted as being unsuitable for gibbon. A similar minimum fragment size, of *c.* 20–30 km^2, has been identified for the long-term persistence of the larger western hoolock gibbon *Hoolock hoolock* in north-eastern India (Kakati *et al.*, 2009). In contrast, the smaller scale at which semi-evergreen and deciduous dipterocarp forest affected gibbon distribution is likely to reflect a general avoidance of these forest types in the more immediate vicinity of survey locations.

Despite the strong internal model validation statistics, four of the 17 occupied listening posts were located in areas predicted as being unsuitable for gibbon. These listening posts were located within smaller blocks of evergreen forest between 1 and 8 km away from areas predicted as being suitable. While these records may relate to the detection of gibbons that were actually singing within nearby evergreen forest predicted as suitable, or single young males dispersing between larger evergreen forest patches, it is likely that individuals may seasonally make use of smaller evergreen and semi-evergreen forest patches in relation to changes in fruit availability. However, these habitats may not provide sufficient year-round resources to support gibbon through resource-poor bottle necks (e.g. the late dry season) in the absence of larger evergreen forest patches within the landscape.

Based on listening post surveys, yellow-cheeked crested gibbon densities have been estimated at between 0.2 and 0.7 groups km^{-2} within evergreen and semi-evergreen forests in Mondulkiri (Rawson, Clements & Meng, 2009; P. Channa & T. N. E. Gray, unpubl. data). At these densities, the minimum fragment size identified by the model (i.e. 15 km^2) could support between three and 10 gibbon groups. However, while evergreen forest fragments within PPWS are natural, it is possible that the long-term viability of populations within smaller fragments depends on the presence of larger evergreen forest blocks nearby, allowing dispersal of new individuals and maintaining populations that would not be viable if there was no outside recruitment. Maintaining connectivity for dispersing gibbons between evergreen forest patches, probably through gallery forest along rivers, may be critical.

The low Akaike weights for the two predictor variables related to human use of the landscape (distance of tracks and villages to listening posts) suggest that current levels of human activity, particularly hunting, are not strongly affecting gibbon distribution within PPWS. This is supported by information from local hunters that suggests that while other primate species of higher trade value, predominantly long-tailed macaque *Macaca fascicularis* and Loris spp. *Nycticebus*, are hunted, gibbon are rarely targeted (pers. obs.). This contrasts with large areas of Vietnam, Laos and China where hunting-driven local extinctions of *Nomascus* gibbon populations, even when considerable habitat remains, are widely documented (Geissmann *et al.*, 2000; Zhou *et al.*, 2005; Jiang *et al.*, 2006; Duckworth, 2008). Given the synergistic affects of hunting and fragmentation on species persistence (Peres, 2001; Pattanavibool & Dearden, 2002), it is unlikely that yellow-cheeked crested gibbon could remain in forest fragments as small as 15 km^2 in large parts of species' range. However, our model suggests that, at least within PPWS, hunting is not having a major impact on gibbon distribution and the results genuinely reflect a minimum threshold fragment size for the species in the absence of hunting.

Conservation implications for the Lower Mekong Dry Forest Ecoregion

Conservation effort for gibbons within PPWS should be focused on larger evergreen forest fragments (>15 km^2) and these, and their key access points, should be priorities for law enforcement patrols to reduce degradation of the evergreen forest fragments and hunting. While smaller evergreen patches have considerable conservation value, particularly for maintaining connectivity, the very limited resources available for conservation within the landscape (government support for PPWS is $<$US\$0.05 per hectare) necessitate targeted conservation interventions and patrolling. Although evergreen forests within the forest landscape matrix of northern Cambodia are naturally fragmented (Stott, 1990), human activity is likely to be reducing fragment size through fire regimes and logging, thereby affecting the extent of a suitable habitat for species dependent on this forest type. Evergreen forest fragments are particularly attractive to commercial logging operations and, while long-term effects of logging on primates have largely demonstrated a surprising resilience to habitat alteration (Plumptre, 1994; Chapman *et al.*, 2000; Guo *et al.*, 2008), these have not investigated the effect in mosaic landscapes where evergreen patches are small. Moreover, infrastructure developments associated with logging can ease access to remote forest areas, thereby facilitating hunting, permanent settlements and further habitat degradation or conversion (Schwartzman *et al.*, 2000; Laurance *et al.*, 2008). Additional activities that may contribute to reductions in the size of evergreen forest fragments such as agricultural land and mining concessions and anthropogenic changes in burning regimes along the deciduous dipterocarp–evergreen forest ecotone must also be regulated.

Our findings provide further support for the conservation value of medium to large evergreen forest patches within the Lower Mekong Dry Forest Ecoregion outlined by Tordoff *et al.* (2005). This habitat may also be important for a number of additional threatened mammal species with globally significant populations within the ecoregion including Asian elephant *Elephas maximus*, black-shanked douc *Pygathrix nigripe* and gaur *Bos gaurus* (Tordoff *et al.*, 2005). Such forest patches also act as refuges and source populations for other species more easily hunted in open deciduous forest (Duckworth *et al.*, 2005). Given the potential threats, together with the conservation value of larger fragments of evergreen forest for key species such as yellow-cheeked crested gibbon, these Cambodian forests should be considered priorities for conservation planning across the Lower Mekong Dry Forest Ecoregion. This is particularly imperative, given the high hunting pressure within the more biologically diverse evergreen and semi-evergreen forests of southern Vietnam.

Habitat loss and fragmentation is a major threat to global biodiversity (Brooks *et al.*, 2002; Leimgruber *et al.*, 2003). Understanding species' responses to habitat fragmentation is, therefore, a critical topic for conservation biologists (Harcourt & Doherty, 2005). Examining the occurrence of species of conservation concern within naturally non-contiguous habitats may have broader implications for understanding the conservation value of fragments (Tutin, White & Mackanga-Missandzou, 1997). By developing multi-grain models, in which predictor variables were included at the scale at which they best explained the variance in gibbon presence/non-detection, we were able to identify a minimum size of evergreen forest patches necessary to support yellow-cheeked crested gibbon. As with many tropical protected areas, comprehensive surveys of PPWS to map the distribution of focal species are difficult due to lack of resources, capacity and logistical problems. Therefore, accurate predictive models may be a useful tool for identifying portions of protected areas containing key populations of species of conservation concern. Our modelling approach may be particularly valuable when designing conservation strategies for species for which it is important to identify minimum fragment sizes suitable for conservation activities.

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