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Estimating Site Occupancy for Four Threatened Mammals in Southeastern Laos

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Estimating Site Occupancy for Four Threatened Mammals in

Southeastern Laos

by

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Estimating Site Occupancy for Four Threatened Mammals in

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The tropical forests of Indochina harbor a suite of globally threatened tropical mammal species. These species are difficult to detect, and subsequently understudied. Noninvasive camera trapping was used to survey terrestrial mammals from a protected area in southeastern Lao PDR (Xe Sap National Protected Area). The presence-absence of four mammals (mainland serow *Capricornis milneedwardsii*, muntjac *Muntiacus spp.*, macaque *Macaca spp.*, and wild pig *Sus scrofa*) was modeled in an occupancy framework thereby accounting for detection probabilities. Our goals were to establish baseline occupancy data to assist with biological monitoring and to better understand the factors influencing the distribution of the target species. Naïve occupancy, or the proportion of sites at which the target species was detected, was 0.58 for muntjac, 0.55

for macaque, 0.38 for wild pig, and 0.30 for serow. True occupancy estimates ($\Psi \pm$ SE) from top-ranked models was 0.79 ± 0.21 for macaque, 0.74 ± 0.13 for muntjac, 0.51 ± 0.13 for wild pig, and 0.48 ± 0.18 for serow. The results underscore the importance of accounting for imperfect detection rates when studying rare or elusive species. I included two site covariates (forest type and distance to nearest village) in the occupancy models. Estimating occupancy as a function of site covariates improved model performance and provided insight into landscape-level factors that affect species occurrence. In the top-ranked models, serow occupancy was higher in hill evergreen forest (HEGF) than semi-evergreen forest (SEGF). Muntjac occupancy was higher in areas further from villages. Macaque occupancy was higher in areas closer to villages. Wild pig occupancy was higher in areas further from villages and in HEGF. I recommend using an occupancy framework to analyze occurrence data for difficult-to-study tropical mammal species. The results highlight the importance of Xe Sap NPA for large mammal conservation in the region.

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Introduction

The tropical forests of Indochina (*sensu* Cambodia, Lao PDR, Vietnam) contain one of the most threatened and least-explored mammal communities on the planet. Multiple factors have contributed to mammal population declines in the region. Rapid deforestation, caused by an increase in agricultural conversion and illegal logging, has greatly reduced the amount of suitable habitat (Kummer & Turner 1994). Between 1973 and 2009 the countries of the lower Mekong (Laos, Thailand, Cambodia, and Vietnam) lost almost one third of their forest cover (WWF 2013). Deforestation has been a major driver of mammal declines, and further declines due to habitat loss are projected (Brook et al 2003). Despite the negative impact such high levels of habitat loss have had on mammal populations, the primary threat to the long-term survival of most mammals in Indochina is overhunting (Robinson & Bennett 2000, Nooren & Claridge 2001). Heavy hunting pressure, fueled by local demand for bushmeat and international demand for the wildlife trade, has decimated mammal populations across the region (Corlett 2007). Widespread defaunation has resulted in a marked increase in "empty forest syndrome" (Redford 1992); numerous protected areas in Indochina have intact habitat but few mammals living in their forests. Large mammals in particular are vulnerable to overhunting because they often range over large areas, exposing them to more hunting areas, and are targeted by poachers, who want species that render the highest value per unit effort invested in hunting (Wilkie et al 2011). Low intrinsic rate of population increase further increases vulnerability of large mammals to extirpation (Wilkie et al

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2011). Combined, habitat loss and poaching have forced mammals in the region to persist in small, isolated, and increasingly fragmented populations (Duckworth & Hedges 1998).

To protect remaining large mammal populations in Indochina it is essential to establish baseline data that can be used to assess population status and monitor future trends. This information is lacking for many species in the region. Although flagship species such as the tiger (*Panthera tigris*) and Asian elephant (*Elephas maximus*) have received considerable scientific attention, other species, including diverse assemblages of even-toed hoofed ungulates and small carnivores, are understudied. Several species, including the large-antlered muntjac (*Muntiacus vuquangensis*) and Saola (*Pseudoryx nghetinhensis*), are endemic to Indochina. Extirpation of regional populations could thus lead to global extinction. Acquiring baseline data for these species is critical if conservationists are to make informed management decisions and monitor populations. The general lack of information on the mammals of Indochina is partly due to the difficulties of collecting data on mammals living in tropical forests. Many tropical mammals are elusive, nocturnal, or occur at low densities. Detecting these species remains a challenge (Linkie et al 2007a). Automatically triggered camera traps have revolutionized data collection for many tropical mammals, increasing detection rates far beyond that which could be achieved using traditional survey techniques, such as sign transects or distance sampling (Sanderson & Trolle 2005). Camera traps have therefore been widely used to gather data on otherwise difficult-to-study tropical mammal species. Even with increased detection rates, however, tropical mammals will always be detected imperfectly (i.e. detectability will be less than 1.0). Studies that assume perfect detection

rates will produce biased baseline data because the target species may have been present in an area but not detected (MacKenzie & Royale 2005). For species with individually recognizable markings, detectability can be incorporated into a capture-recapture statistical framework to estimate abundance in a given area (Pollock 1982, Nichols 1992). While this technique has been used to produce abundance estimates for several endangered tropical mammals (e.g. Karanth 1995, Silver et al 2004, Wilting et al 2012), its applicability is limited because most mammal species cannot be identified to individuals from photographs. An alternative state variable when abundance cannot be estimated is occupancy (Ψ), or the proportion of area occupied by a species (MacKenzie 2002). By incorporating imperfect detection rates into a modified capture-recapture framework it is possible to estimate the probability that a species was present but not detected in a survey area (MacKenzie et al 2002). Therefore, occupancy analyses allow one to distinguish, in a statistically robust manner, the difference between true and false absence. Furthermore, occupancy can be estimated as a function of site covariates, which can improve model performance and provide insight into factors that influence species occurrence (MacKenzie et al 2002, Bailey et al 2004). Site covariates can include habitat variables (e.g. forest type) or proxies of anthropogenic threat (e.g. distance to nearest village). For this study, camera trapping data was used to estimate occupancy of four tropical mammals (mainland serow *Capricornis milneedwardsii*, muntjac *Muntiacus spp.*, macaque *Macaca spp.*, and wild pig *Sus scrofa*) from a protected area in the Lao People's Democratic Republic (Lao PDR). Our primary objectives were to generate baseline data

and understand factors affecting occurrence of species of conservation concern in Indochina.

Study area

Xe Sap National Protected Area (XS, approximately centered on 16°12' N, 107°02'E, Fig. 1) is located in southeastern Lao PDR along the Annamite mountain range. Its eastern boundary borders Vietnam. XS covers approximately 1335 km^2. Its topography is complex, with elevations varying from 400 to 2066 meters (WWF 2012). Approximately 35% of its total area is above 1000 m elevation (Davidson et al 1998). XS has a tropical monsoon climate. A general east-to-west moisture gradient exists across the protected
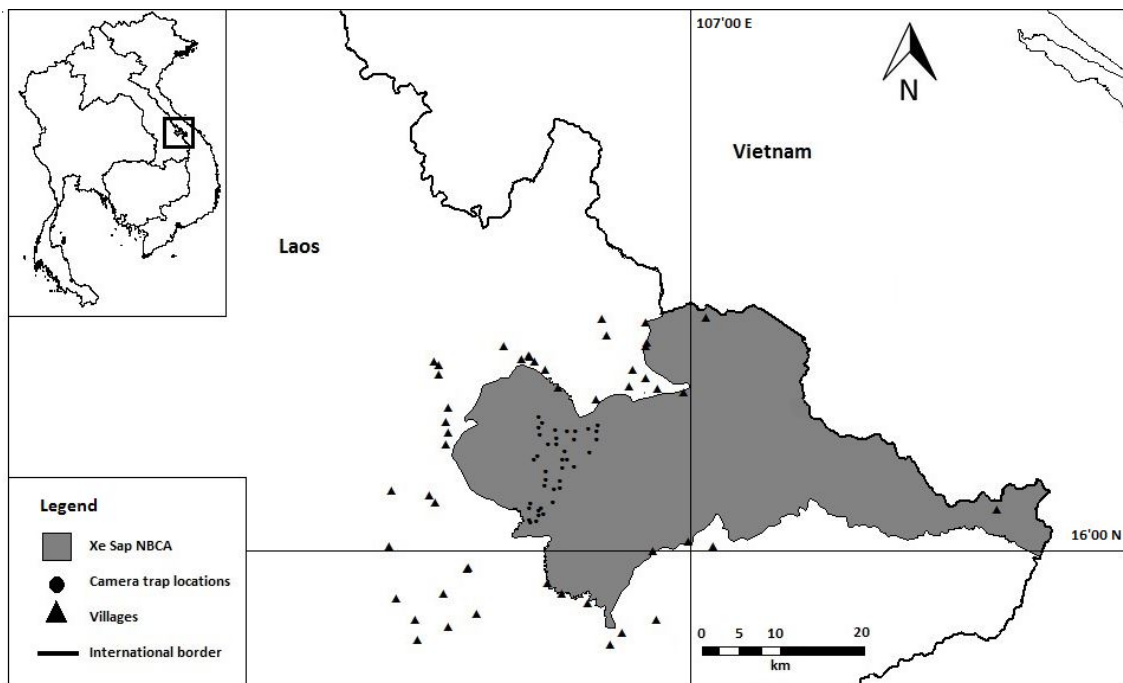

Figure 1: Xe Sap National Biodiversity Conservation Area. The inset shows the location of the protected within Southeast Asia. The detailed map shows the protected area boundary, nearby villages, and camera trap locations.

area (WWF 2012). The eastern region, in Xe Khong province, is comparatively wet, with a climate similar to the Hue and Quang Nam Saola Nature Reserves in neighboring Vietnam. The western region, in Salavan Province, is much drier. Hill evergreen (HEGF) and semi-evergreen forest (SEF) are the most common habitat types. At lower elevations open grassland interspersed with pine can be found, and the highest elevations (1800 > meters) are dominated by stunted growth montane forest. At least 30 villages are found within 5 km of the protected area boundary. Hunting, both for subsistence and for the wildlife trade, is common and has clearly depressed mammal populations (Timmins 2012).

Target species

XS contains a diverse mammal assemblage. However, because of access restrictions and the remoteness of the site, few scientific surveys have focused on its mammal community. Previous expeditions into XS have use sign surveys and interviews with local villagers to gather information on the mammal community (Davidson et al 1998, Steinmetz et al 1999). Our study is the first to use camera traps to systematically survey the mammals in the protected area. We conducted occupancy analyses for two species (serow and wild pig) and two species groups (macaque and muntjac).

The mainland serow (*Capricornis milneedwardsii*) is a large-bodied ungulate once abundant throughout Indochina. Populations are believed to be in significant decline, and the species is currently listed as Near Threatened by the IUCN (Duckworth et al 2008). Poaching is the primary cause of population declines. Serow meat is

frequently consumed in rural parts of Indochina. In Laos, serow bones, feet, teeth, and other body parts are used for medicinal purposes (Baird 1995). Furthermore, there is evidence of an active cross-border trade in serow parts from Laos into Thailand (Nash 1997). Relatively little is known about the basic ecology of the species. Serow feed on a variety of leaves and shoots, and frequents natural salt licks (Duckworth et al 2008). It is primarily associated with steep and rugged mountainous areas, but has also been recorded at lower elevations in gentler terrain (Lekagul & McNeely 1988, Duckworth et al 1999).

The Eurasian wild pig (*Sus scrofa*) occurs across the region. It is found in a variety of habitat types, from temperate to tropical forest, and can thrive in heavily degraded areas (Oliver & Leus 2008). The species is highly omnivorous, consuming a range of plant and animal matter (Bruinderink et al 1994, Baubet et al 2004, Pinna et al 2007). This habitat and diet-based flexibility, combined with higher reproductive rates than other sympatric ungulates, has contributed to the persistence of the species across large parts of Indochina. The wild pig is currently listed as Least Concern by the IUCN (Oliver & Leus 2008). As a species the wild pig is not endangered. However, wild pigs are not immune to hunting pressure, and at the local level populations may be severely depressed or extirpated. Hunting, both for subsistence and to supply meat for the bushmeat trade, is the primary threat to wild pigs in Indochina (Steinmetz et al 2006).

Both the pig-tailed macaque (*Macaca nemestrina*) and the stump-tailed macaque (*Macaca arctoides*) are terrestrial group-living primate species distributed widely across Indochina. Although both species remain locally abundant in parts of their ranges, habitat loss and overhunting have caused overall numbers to decrease, and both primates are

listed as Vulnerable (Richardson et al 2008, Htun et al 2013). Pig-tailed macaque group sizes in Laos tend to be many times smaller than group sizes in unexploited populations in other Indochinese countries (Duckworth 1999). Although earlier surveys in Laos recorded the stump-tailed macaque in several protected areas, numbers at each survey site were low (Duckworth 1999), providing additional evidence of overexploitation. Both species have been recorded in a variety of habitat types. The pig-tailed macaque can been found in evergreen, deciduous, pine, and dry dipterocarp forests (Duckworth 1999, Nadler et al 2007). The stump-tailed macaque inhabits semi-deciduous, deciduous, and limestone forests (Nadler et al 2007).

At least four sympatric muntjac species are likely to occur in XS: red muntjac (*Muntiacus vaginalis*), large-antlered muntjac (*Muntiacus vuquangensis*), and at least two species from the Truong Son / Roosevelt's muntjac complex (*Muntiacus truongsonensis / rooseveltorum*). (Schaller 1995, Timmins and Vongkhamheng 1996). The red muntjac is found across Southeast Asia. It is listed by the IUCN as Least Concern (Timmins et al 2008a), though may be locally scarce, especially in the more heavily poached areas of Indochina. In XS, populations have undoubtedly been much reduced from historic levels (Timmins 2012). The Large-antlered muntjac is endemic to the Annamite mountain range that straddles the border between Laos and Vietnam (Timmins et al 1998). This restricted distribution, combined with heavy hunting pressure throughout its known range, makes it one of the highest large mammal conservation priorities in Indochina, and it is listed as Endangered (Timmins et al 2008b). Taxonomic uncertainties within the Truong Son / Roosevelt's muntjac complex, combined with a general lack of information on range and

population status, prohibit an accurate conservation assessment. Truong Son / Roosevelt's muntjac is currently listed as Data Deficient (Timmins et al 2008c, Timmins et al 2008d).

Methods

Camera trapping took place between July 2012 and January 2013 within a 200 km^2 area of the Taoy district in western XS (Fig. 1). Commercially available infrared, remote-trip cameras (Bushnell Trophy Cam, Kansas City, Missouri) were used to survey the mammal community. The survey area was divided into 1km^2 grid-cells. Thirty-nine grid-cells were randomly chosen for sampling. A single camera trap was non-randomly placed in each grid-cell. Cameras were located in places identified by local survey teams as having a high probability of detecting large mammals—these were generally along animal trails and rivers. All camera trap units were programmed to take a three-picture burst when triggered and each photograph was stamped with the date and time. Pictures of the survey team were taken during camera setup and removal and used to verify that the unit was operational for the duration of the sampling period. All cameras were placed on trees between 20 and 130 cm above the ground (mean = 45, standard deviation = 24.76) and operational throughout the 24-hour cycle. Camera traps were operational between 95 and 288 nights (mean = 151, standard deviation = 60). Elevation was measured at each camera trap station with a handheld GPS, and ranged from 737 to 1387 m (mean = 1096, standard deviation = 217). Forest type within the vicinity of each camera was classified in the field by the survey team; sixteen sites were in HEGF, twenty-three in SEGF. Linear distance from each camera to the nearest local village was calculated *post hoc* in *ArcGIS v. 10.1* (ESRI 2013, Redlands, USA) using a remotely sensed data set.

Two biologists familiar with the region's mammals independently identified the camera trap photographs to species or species group. Photographs that could not be

identified were not included in the analysis. Macaque photographs were identified as either pig-tailed macaque (*Macaca nemestrina*) or stump-tailed macaque (*Macaca arctoides*). However, because detection probabilities were low for both primates, the two species were combined for the occupancy analysis. It was not possible to identify with confidence the muntjac photographs to the species level. Muntjac photographs were also combined for the occupancy analysis.

Encounter histories for each species or species group were constructed in an "X-matrix" format with rows representing encounter histories at each site and columns representing captures at each sampling occasion (Otis et al 1978). A detection for a site at a given sampling occasion was represented with a "1" and a non-detection with a "0." Sampling occasions were twenty-night periods starting from the date the camera was set and ending on the twenty-night period closest to when the camera was removed. Thus, a camera operating for eight-five nights would result in four sampling occasions with the remaining five nights dropped from the analysis. A sampling period consisting of 20 camera trapping nights was chosen to avoid zero inflation in the encounter history data. Occupancy models require a minimum number of detections, and therefore minimum level of detection probability, to converge on reliable estimates (O'Connell et al 2006). I ran models using sampling periods of 5, 10, and 15 nights, but at these values the models failed to converge on reliable occupancy estimates for all target species. Convergence was attained for all models using a 20-night sampling period.

Occupancy models were developed in the program *PRESENCE v.6.2* (Hines 2006) for all four mammals. *PRESENCE* uses likelihood-based methods to estimate

detection probabilities (*p*) and proportion of sites occupied (Ψ). Covariates can be incorporated into occupancy models to reduce variance in parameter estimates (Mackenzie et al 2006). We used two site-level covariates in our analysis: forest type and distance to nearest village. Forest type, recorded as either HEGF or SEGF, was a categorical variable; distance to nearest village, measured in meters, was a continuous variable. Forest type was chosen based on *a priori* expectations that large mammals living in a heterogeneous landscape may show preferences for certain habitat types; large mammal habitat preferences have been demonstrated in other parts of Indochina (e.g. Koy et al 2005, Gray & Phan 2011, Gray 2012). Distance to nearest village was chosen as a proxy for poaching pressure, based on the assumption that poaching will be higher in areas more accessible to hunters. In neighboring central Vietnam, accessibility is the primary factor influencing snare density in protected areas (Tilker *unpublished data*). Distance to nearest village values were measured in ArcGIS 10.1. Before running the models, these values were standardized to *z*-scores. Standardizing continuous variables has been shown to optimize model convergence (Mackenzie 2006).

Models were first developed to determine if site covariates significantly affected detection probability. A null model was created in which detection probability was held constant (*p.*) with respect to site covariates. This model was compared to models detection probability estimated as a function of site covariates ($p_{habitat}$, $p_{distance}$, $p_{habitat+distance}$). For all species or species groups the null model was more strongly supported based on Akaike Information Criterion (AIC) values. In the final models, detection probability was therefore held constant (*p.*). Final models estimated occupancy

without covariates ($\Psi_{\cdot}$) or with covariates ($\Psi_{habitat}$, $\Psi_{distance}$, $\Psi_{habitat+distance}$). AIC values were used to rank candidate models and calculate their Akaike weights (ϖ_i) (Burnham & Anderson 2002). A model averaging technique was used to estimate final occupancy in situations where there were multiple top-ranked candidate models (i.e. models with ΔAIC weights less than 2.0) (Burnham & Anderson 2002).

Results

In 5900 camera trap nights we obtained a total 191 photographs of the four target mammal species and species groups. Muntjac was the most commonly encountered mammal with seventy-three photographs across twenty-two camera trap sites, followed by macaque with forty-eight photographs across twenty-one sites, wild pig with forty-five photos across fifteen sites, then serow with twenty-five photographs across twelve sites. Overall detectability was low ($p < .20$) for all four target mammals but robust enough for model convergence (Table 1). Naïve occupancy, defined as the proportion of sites that recorded at least one photograph of the target species, was 0.5750 for muntjac, 0.5500 for macaque, 0.3846 for wild pig, and 0.3000 for serow. Modeled occupancy estimates, which incorporate detectability (p) and the influence of site covariates, gave a different ranking. Averaged occupancy ($\Psi \pm$ SE) from top-ranked models was 0.7922 ± 0.2090 for macaque, 0.7411 ± 0.1294 for muntjac, 0.5103 ± 0.1386 for wild pig, and 0.4829 ± 0.1849 for serow (Fig. 2).

Table 1: Camera trapping data from Xe Sap National Protected Area.

Species	Number of encounters	Number of sites[1]	Naïve occupancy[2]	Detectability[3]
Serow	25	12	0.3000	0.1202
Muntjac	73	22	0.5800	0.1670
Macaque	48	21	0.5500	0.1379
Wild pig	45	15	0.3846	0.1659

[1] Number of sites at which the target species was detected
[2] Defined as the proportion of sites at which the target species was detected
[3] Averaged detectability across all sampling periods

Based on AIC values, two models, Ψ and Ψ_{forest}, had strong support for serow (Table 2). In the Ψ_{forest} model, predicted occupancy was higher in HEGF than SEGF. $\Psi_{distance}$ and Ψ. were the top-ranked models for muntjac. In the $\Psi_{distance}$ model, distance to nearest village

was positively correlated to muntjac occurrence, with occupancy estimates higher in the more remote parts of the survey area. $\Psi_{distance}$ and $\Psi.$ were also the best models for macaque. However, unlike muntjac, macaque occurrence was negatively correlated to distance from nearest village, with occupancy estimates higher near human settlements. $\Psi., \Psi_{forest},$ and $\Psi_{distance}$ had strong support for wild pig. In the Ψ_{forest} model, occupancy estimates were higher in SEGF than HEGF. As with serow and muntjac, occupancy estimates in the $\Psi_{distance}$ model were negatively correlated with distance to nearest village.
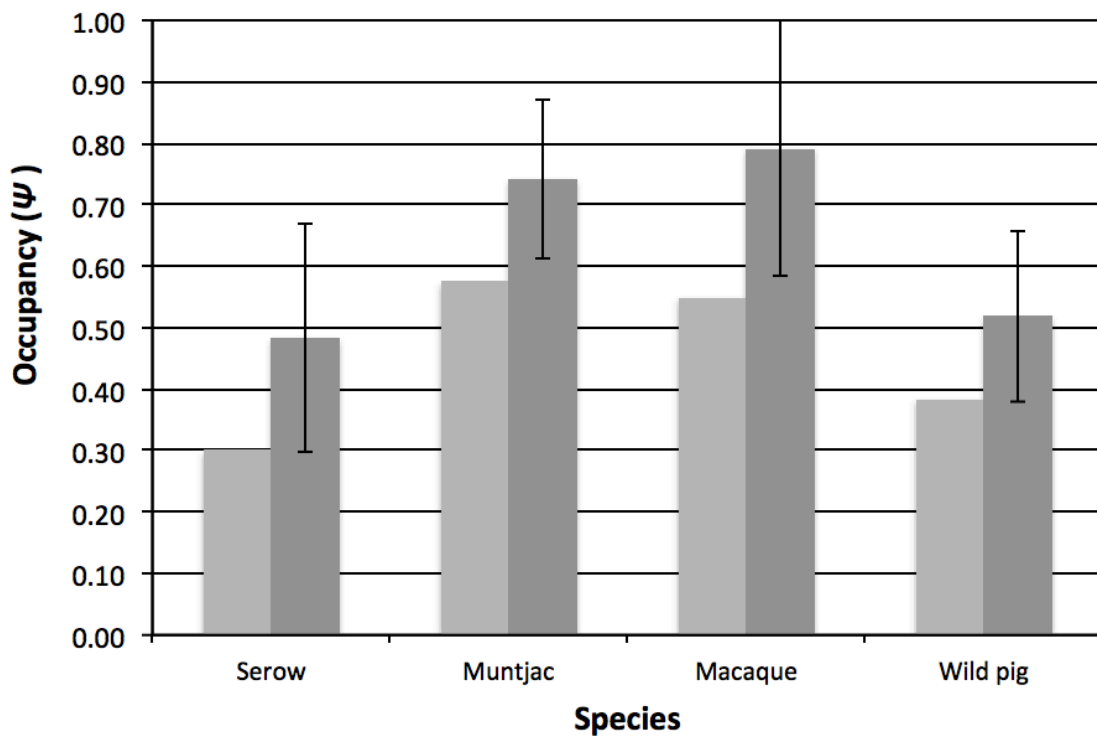

Figure 2: Naïve (light gray) and modeled (dark gray, with standard error bars) occupancy estimates for serow, muntjac, macaque, and wild pig in Xe Sap National Biodiversity Conservation Area.

Species	Model[1]	ΔAIC[2]	ϖ_i[3]	Model likelihood	Ψ (SE)[4]	K[5]
	$(\Psi.)(p.)$	0.00	0.5330	1.0000	0.4681 ± 0.1521	2
Serow	$(\Psi_{habitat})(p.)$	1.98	0.1918	0.3716	0.5002 ± 0.2178	3
	$(\Psi_{distance})(p.)$	2.00	0.3679	0.3679	0.4681 ± 0.1806	3
	$(\Psi_{habitat+distance})(p.)$	3.98	0.1367	0.1367	0.4721 ± 0.2091	4
	$(\Psi_{distance})(p.)$	0.00	0.5635	1.0000	0.7266 ± 0.1337	3
Muntjac	$(\Psi.)(p.)$	1.34	0.2883	0.5117	0.7485 ± 0.1251	2
	$(\Psi_{habitat})(p.)$	3.07	0.1214	0.2155	0.7486 ± 0.1763	3
	$(\Psi_{habitat+distance})(p.)$	6.09	0.0268	0.0476	0.7586 ± 0.1932	4
	$(\Psi.)(p.)$	0.00	0.6008	1.0000	0.7894 ± 0.1539	2
Macaque	$(\Psi_{distance})(p.)$	1.78	0.2467	0.4107	0.7934 ± 0.2642	3
	$(\Psi_{habitat})(p.)$	3.37	0.1114	0.1854	0.7921 ± 0.2921	3
	$(\Psi_{habitat+distance})(p.)$	5.37	0.0410	0.0682	0.7982 ± 0.3105	4
	$(\Psi.)(p.)$	0.00	0.5108	1.0000	0.5023 ± 0.1187	2
Wild pig	$(\Psi_{distance})(p.)$	1.72	0.2161	0.4232	0.5258 ± 0.1449	3
	$(\Psi_{habitat})(p.)$	1.97	0.1907	0.3734	0.5028 ± 0.1521	3
	$(\Psi_{habitat+distance})(p.)$	3.65	0.0823	0.1612	0.5063 ± 0.1777	4

Table 2: Occupancy model results for serow, muntjac, macaque, and wild pig from Xe Sap National Protected Area.

[1] *Habitat* refers to forest type (HEGF or SEGF) and *distance* refers to linear distance from camera trap to nearest village
[2] Difference in AIC value relative to the top model
[3] AIC weight
[4] Averaged occupancy and SE values
[5] Number of parameters estimated

Discussion

The results reaffirm the efficacy of using camera trapping to noninvasively gather data on elusive mammals living at low densities in tropical forest. Even with improved detection rates, however, probabilities of detection (p) were less than 1.0 for all four mammals. Naïve occupancy, which assumes perfect detectability, was found to underestimate true occupancy, highlighting the importance of accounting for non-detections when analyzing camera trapping data. Not accounting for the discrepancy between naïve occupancy and informed estimates can have profound implications for conservation and management decisions. In the past, conservation assessments have routinely used the presence or absence of focal species to gauge the relative value an area contributes to existing conservation goals. If non-detections of target species are unaccounted for, the total area occupied by the species, and therefore the potential conservation value of the area, will be underestimated.

Standard occupancy analyses must meet several key assumptions, one of which is that occupancy state at a site does not change during the course of the repeat sampling (MacKenzie et al 2002). This condition is likely to be violated if the area sampled is smaller than the average home range size of the target species. Information on the home range sizes of the four target species in the Indochina region is lacking. However, studies from other regions and on closely related species suggest that our camera traps spacing may have been smaller than the likely home-ranges of serow (Kishimoto & Kawamichi 1996), muntjac (McCullough et al 2000), macaque (Makwana 1978) and wild pig (Russo et al 1997). MacKenzie et al (2006) suggests that the closure assumption may be relaxed

as long as movement of the target species in and out of the sampling unit occurs at random. If movement between sites occurs non-randomly the occupancy estimator will likely be biased. As Gray (2012) points out, when survey areas are smaller than the home range of the target species, the correct interpretation of Ψ is not proportion of sites occupied by the target species, but the proportion of sites used. Thus intensity of use at camera trapping station can provide insight into habitat preferences. However, researchers must be careful about drawing inferences between occupancy and abundance.

Estimating occupancy as a function of site covariates provided insight into the factors that influence mammal occurrence in XS. Estimated serow occupancy was higher in HEGF than SEGF. Our results are consistent with other studies on serow that have documented habitat associations in heterogeneous landscapes (Endi 2004, Chen et al 2009). Understanding habitat use can have important implications for on-the-ground conservation decisions (Law and Dickman 1998). In XS, anti-poaching resources are limited. Because anti-poaching teams can only cover a fraction of the landscape, conservation and management officials must prioritize areas for patrolling. Knowledge of habitat associations can be used to make more informed area prioritization decisions and ultimately may be used to meet species-specific conservation goals.

It is also important to note that habitat associations may not be fully explained by biotic factors. Topography, for example, may influence the ability of a prey animal to escape predators. A study on another forest-dwelling ungulate, the bongo (*Tragelaphus eurycerus*), found terrain ruggedness to be a more important predictor of habitat use than vegetative characteristics (Estes et al 2011). The fact that in other areas serow have also

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been found to prefer areas with steeper slopes (Chen et al 2009) may indicate that this species also selects areas that facilitate escape. Overall, our results provide insight into one factor that influences serow occurrence in XS. To better understand serow distribution in the area we recommend that future studies investigate seasonal variation in habitat use and take into account additional landscape-level variables.

Distance to nearest village was the most important factor influencing muntjac occurrence. It is not surprising that muntjac occupancy was higher at sites further away from villages. In XS, as in other areas in the region, hunting is primarily accomplished through the setting of wire foot-hold snares. Because snares need to be routinely monitored, poaching pressure is usually higher near human settlements. To preserve viable muntjac populations in XS it is essential that remote areas with high muntjac occupancy be protected from future encroachment by poachers. After securing these core sites, enforcement efforts could focus on areas that currently have higher poaching pressure and lower muntjac occupancy. Fortunately, muntjac have been shown to recover relatively rapidly from low population numbers (Steinmetz et al 2010). Areas near villages cannot be reoccupied, however, without viable source populations.

No evidence was found for muntjac habitat associations. However, this does not necessarily indicate that such habitat associations do not exist at the species level. Previous studies on sympatric ungulate communities have provided evidence that habitat segregation is linked to niche partitioning and therefore may facilitate coexistence of similar species (Hanley and Hanley 1982, Namgail et all 2004, Darmon et al 2012). Because muntjac photographs could not be distinguished to species with confidence, we

grouped all muntjac together for the occupancy analysis. To investigate possible species-specific habitat associations we recommend future studies in XS use survey techniques capable of identifying muntjac to the species level. Species-specific muntjac studies would first require a revision of the Truong Son / Roosevelt's complex.

Distance to nearest village was also the most important factor influencing wild pig occupancy within the survey area. As with muntjac, the negative correlation between occupancy and village proximity probably reflects higher hunting pressure in more accessible areas. In Laos, wild pigs are targeted as food both for subsistence and sale to local restaurants (Duckworth 1999). Although not a threatened species, and therefore not a high conservation priority for the region, wild pigs are an important component of tropical forest ecosystems. Wild pigs are a food source for large predators such as dhole (*Cuon alpinus*), leopard (*Panthera pardus*), and tiger (*Panthera tigris*) (Karanth & Sunquist 1995, Stoen & Wegge 1996, Andheria et al 2007). Maintaining healthy wild pig populations is therefore critical to large carnivore persistence in XS. Furthermore, wild pigs can have significant effects on tropical forest plant dynamics. Through soil-rooting and seed predation, wild pigs alter understory vegetation structure and diversity (Ickes et al 2001, Siemann et al 2009). In the $\Psi_{distance}$ model, wild pig occupancy was higher in HEGF than SEGF. Other studies have shown wild pig habitat preferences in heterogeneous landscapes (Singer et al 1981, Welander 2000), which may be linked to food availability (Spitz & Petrucci-Fonseca 2004).

Predicted occupancy for macaque was negatively related to distance from nearest village. At first this result seems counterintuitive given the fact that snaring levels tend to

be higher closer to villages. One possible explanation is that as semi-arboreal mammals macaques are less susceptible to snaring. Another explanation, well documented in the literature, is that macaques benefit from being in close proximity to human habitations by exploiting food resources from settlements (Priston & McLennan 2013). In other parts of Asia, macaques thrive in suboptimal habitat by subsisting off of anthropogenic food sources. Macaques have also been known to raid crops. In Sumatra, macaques were found to be one of the most destructive crop pests, second only to wild pig (Linkie et al 2007b). The association of pig-tailed and stump-tailed macaques in XS with human settlements surrounding the protected area could have important conservation implications. Macaques may be directly persecuted when they come into conflict with humans. To ensure the protection of these threatened primates I recommend investigating possible human-macaque conflict in XS and taking steps to mitigate problems. The lack of evidence for SEGF / HEGF habitat associations in XS is consistent with observations in other parts of the species ranges.

By analyzing camera trapping data within an occupancy framework, I have provided occupancy estimates for four threatened mammals in XS. These estimates can be used as a baseline to assess population status and monitor future population trends whilst keeping in mind the caveats, mentioned above, regarding the unproven correlation between occupancy / intensity of use and genuine abundance. However given the limited data on species status in XS, and many other tropical forested protected areas, this information is likely to be important for conservation managers. The results are consistent with other studies that have shown large discrepancies between naïve and

informed occupancy estimates (Gray 2012), and emphasize the importance of accounting for imperfect detection rates when analyzing occurrence data. By incorporating site covariates into our models we also obtained insight into the factors that influence large mammal occurrence in XS. Finally, our research highlights the importance of XS for mammal conservation in the region. The widespread poaching that occurs throughout the tropical forests of Indochina shows no sign of abating. The importance of XS as a refuge for threatened mammals will only increase in the future. Steps should be taken now to protect its mammal community and further research should investigate species-specific conservation needs.

Bibliography

Andheria, A.P., et al. "Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India." *Journal of Zoology*. 273.2 (2007): 169-175.

Bailey, L.L., et al. "Estimating site occupancy and species detection probability parameters for terrestrial salamanders." *Ecological Applications* 14.3 (2004): 692-702.

Baird, I. G. Lao PDR: an overview of traditional medicines derived from wild animals and plants. TRAFFIC Southeast Asia, 1995.

Brook, B. et al. "Catastrophic extinctions follow deforestation in Singapore." *Nature*. 424.6947 (2003): 420-426.

Burnham, K. P. and D. R. Anderson. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, 2002.

Chen, et al. "Habitat use and separation between the Chinese serow (*Capricornis milneedwardsi*) and the Chinese goral (*Naemorhedus griseus*) in winter." *Mammalia* 73.3 (2009): 249-252.

Corlett, R. T. "The impact of hunting on the mammalian fauna of tropical Asian forests." *Biotropica* 39.3 (2007): 292-303.

Darmon, G., et al. "Spatial distribution and habitat selection in coexisting species of mountain ungulates." *Ecography* 35.1 (2012): 44-53.

Davidson, P., et al. A Wildlife and Habitat Survey of the Southern Border of Xe Sap National Biodiversity Conservation Area and the Dakchung Plateau, Xe Kong Province, Lao PDR: Final Report. Wildlife Conservation Society, 1998.

Duckworth, J. W. et al. Wildlife in Lao PDR: 1999 status report. World Conservation Union, 1999.

Duckworth, J. W., and S. Hedges. A review of the status of tiger, Asian elephant, gaur and banteng in Vietnam, Lao, Cambodia and Yunnan Province (China), with recommendations for future conservation action. World Wide Fund for Nature Indochina Program, Hanoi, Vietnam. 1998.

Duckworth, J. W., et al. (2008). *Capricornis milneedwardsii*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Downloaded on 09 May 2014.

Endi, U. P. Z. "Habitat selection and its seasonal change of serow (*Capricornis sumatraensis*) in Cibagou Nature Reserve, Tibet." *Acta Theriologica Sinica* 1 (2004): 002.

Estes, L. D., et al. "Predictive distribution modeling with enhanced remote sensing and multiple validation techniques to support mountain bongo antelope recovery." *Animal Conservation* 14.5 (2011): 521-532.

Gray, T. N. & C. Phan. "Habitat preferences and activity patterns of the larger mammal community in Phnom Prich Wildlife Sanctuary, Cambodia" *Raffles Bulletin of Zoology* 59.2 (2011): 311-318.

Gray, T.N. "Studying large mammals with imperfect detection: status and habitat preferences of wild cattle and large carnivores in eastern Cambodia." *Biotropica* 44.4 (2012): 531-536.

Hanley, T. and K. A. Hanley. "Food resource partitioning by sympatric ungulates on Great Basin rangeland." *Journal of Range Management* (1982): 152-158.

Hines, J. E. (2006). PRESENCE- Software to estimate patch occupancy and related parameters. USGS-PWRC. http://www.mbr-pwrc.usgs.gov/software/presence.html.

Htun, S., et al. 2008. *Macaca arctoides*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Downloaded on 12 April 2014

Ickes, K. et al. "Effects of native pigs (*Sus scrofa*) on woody understory vegetation in a Malayan lowland rain forest." *Journal of Tropical Ecology.* 17.02. (2001): 191-206.

Karanth, K U. and M. E Sunquist. "Prey selection by tiger, leopard, and dhole in tropical forests. *Journal of Animal Ecology* (1995): 439-450.

Karanth, K. U. "Estimating tiger (*Panthera tigris*) populations from camera-trap data using capture—recapture models." *Biological Conservation* 71.3 (1995): 333-338.

Kishimoto, R. and T. Kawamichi. "Territoriality and monogamous pairs in a solitary ungulate, the Japanese serow, *Capricornis crispus*." *Animal Behaviour* 52.4 (1996): 673-682.

Koy, K., et al. "Percentage canopy cover–using Landsat imagery to delineate habitat for Myanmar's endangered Eld's deer (*Cervus eldi*)." *Animal Conservation* 8.03 (2005): 289-296.

Kummer, D. M. and B. L. Turner. "The human causes of deforestation in Southeast Asia." *Bioscience* (1994): 323-328.

Law, B. S., and C. R. Dickman. "The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management." *Biodiversity & Conservation* 7.3 (1998): 323-333.

Lekagul, B. and J. A. McNeely. *Mammals of Thailand*. Bangkok: White Lotus Press, 1977.

Linkie, M., et al. "Estimating occupancy of a data deficient mammalian species living in tropical rainforests: sun bears in the Kerinci Seblat region, Sumatra." *Biological Conservation* 137.1 (2007a): 20-27.

Linkie, M., et al. "Patterns and perceptions of wildlife crop raiding in and around Kerinci Seblat National Park, Sumatra." *Animal Conservation* 10.1 (2007b): 127-135.

MacKenzie, D. I., and J. A. Royle. "Designing occupancy studies: general advice and allocating survey effort." *Journal of Applied Ecology* 42.6 (2005): 1105-1114.

MacKenzie, D. I., et al. "Estimating site occupancy rates when detection probabilities are less than one." *Ecology* 83.8 (2002): 2248-2255.

MacKenzie, D. I., et al. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence.* Academic Press, 2006.

Makwana, S. C. "Field ecology and behaviour of the rhesus macaque (*Macaca mulatta*): I. Group composition, home range, roosting sites, and foraging routes in the Asarori Forest." *Primates* 19.3 (1978): 483-492.

McCullough, D. R., et al. "Home range, activity patterns, and habitat relations of Reeves' muntjacs in Taiwan." *The Journal of Wildlife Management* (2000): 430-441.

Nadler, T., et al. "Conservation status of Vietnamese primates." *Vietnamese Journal of Primatology* 1.1 (2007): 7-26.

Namgail, T., et al. "Habitat segregation between sympatric Tibetan argali *Ovis ammon hodgsoni* and blue sheep *Pseudois nayaur* in the Indian Trans‑Himalaya." *Journal of Zoology* 262.1 (2004): 57-63.

Nash, S., ed. Fin, feather, scale, and skin: observations of the wildlife trade in Laos PDR and Vietnam. Selangor: TRAFFIC, 1997

Nichols, J. D. "Capture-recapture models." *BioScience* (1992): 94-102.

Nooren, H. & G. Claridge. Wildlife Trade in Laos: the End of the Game. Amsterdam: Netherlands Committee for IUCN, 2001.

O'Connell Jr, A. F., et al. "Estimating site occupancy and detection probability parameters for meso-and large mammals in a coastal ecosystem." *Journal of Wildlife Management* 70.6 (2006): 1625-1633.

Oliver, W. & K. Leus. 2008. *Sus scrofa*. In: IUCN 2014. IUCN Red List of Threatened Species. Version 2014.1. <www.iucnredlist.org>. Downloaded on 02 July 2014.

Otis, D. L., et al. "Statistical inference from capture data on closed animal populations." *Wildlife Mongraphs* (1978): 3-135.

Petrucci-Fonseca, F. "Habitat selection by wild boar *Sus scrofa* in Alentejo, Portugal." *Galemyz* 16 (2004) 167-184.

Pinna, W., et al. "Vegetable and animal food sorts found in the gastric content of Sardinian Wild Boar (*Sus scrofa meridionalis*)." *Journal of Animal Physiology and Animal Nutrition* 91.5‑6 (2007): 252-255.

Pollock, K H. "A capture-recapture design robust to unequal probability of capture." *The Journal of Wildlife Management* (1982): 752-757.

Priston, N.E.C, and Matthew R. McLennan. "Managing Humans, Managing Macaques: Human–Macaque Conflict in Asia and Africa." *The Macaque Connection*. Springer New York, 2013. 225-250.

Redford, Kent H. "The empty forest." *BioScience* 42.6 (1992): 412-422.

Richardson, M., et al. 2008. *Macaca nemestrina*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Downloaded on 12 April 2014

Robinson, J.G. & E.L. Bennett, eds. *Hunting for Sustainability in Tropical Forests*. New York : Columbia University Press, 2000.

Russo, L., et al. "Daily home range and activity of wild boar in a Mediterranean area free from hunting." *Ethology Ecology & Evolution* 9.3 (1997): 287-294.

Sanderson, J. and M. Trolle. "Monitoring elusive mammals—unattended cameras reveal secrets of some of the world's wildest places." *American Scientist* 93.2 (2005): 148-155.

Schaller, G.B. A wildlife survey of the Annamite Mountains of Laos, December 1994-January 1995. Unpublished report to the Wildlife Conservation Society, Vientiane. 1995

Siemann, E. et al. "Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US." *Forest Ecology and Management*. 258.5 (2009): 546-553.

Silver, S., et al. "The use of camera traps for estimating jaguar Panthera onca abundance and density using capture/recapture analysis." *Oryx* 38.02 (2004): 148-154.

Singer, Francis J. et al. "Home ranges, movements, and habitat use of European wild boar in Tennessee." *The Journal of Wildlife Management* (1981): 343-353.

Steinmetz, R., et al. "Collaborating to conserve large mammals in Southeast Asia." *Conservation Biology* 20.5 (2006): 1391-1401.

Steinmetz, R., et al. "Population recovery patterns of Southeast Asian ungulates after poaching." *Biological Conservation* 143.1 (2010): 42-51.

Steinmetz, R., et al. Ecological survey of habitats, wildlife, and people in Xe Sap National Biodiversity Conservation Area, Saravan Province, Lao PDR. WWF, 1999.

Stoen, O.G., and P Wegge. "Prey selection and prey removal by tiger (*Panthera tigris*) during the dry season in lowland Nepal." *Mammalia* 60.3 (1996): 363-374.

Timmins, R. J. et al. "Status and conservation of the giant muntjac *Megamuntiacus vuquangensis*, and notes on other muntjac species in Laos." *Oryx* 32.01 (1998): 59-67.

Timmins, R. J. Xe Sap Mammal and Bird Survey, May-June 2012. Vientiane: WWF, 2012.

Timmins, R.J. and C. Vongkhamheng. A preliminary wildlife and habitat survey of Xe Sap National Biodiversity Conservation Area and mountains to the south, Salavan Province, Lao PDR. Final report to CPAWM, Department of Forestry. Vientiane: Wildlife Conservation Society. 1996

Timmins, R.J., et al. 2008a. *Muntiacus vaginalis*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Downloaded on 09 May 2014.

Timmins, R.J., et al. 2008b. *Muntiacus vuquangensis*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Downloaded on 12 April 2014.

Timmins, R.J., et al. 2008c. *Muntiacus truongsonensis*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Downloaded on 12 April 2014.

Timmins, R.J., et al. 2008d. *Muntiacus rooseveltorum*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Downloaded on 12 April 2014.

Welander, J. "Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape." *Journal of Zoology*. 252.02 (2000): 263-271.

Wilkie, David S., et al. "The empty forest revisited." *Annals of the New York Academy of Sciences* 1223.1 (2011): 120-128.

World Wildlife Fund. 2012. Management plan for Xe Sap National Protected Area Lao PDR 2012-2016.

World Wildlife Fund. 2013. Ecosystems in the Greater Mekong: Past trends, current status, possible futures.