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Sampling mammalian carnivores in western Thailand: Issues of rarity and detectability

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Abstract. Many tropical mammalian carnivores are now threatened with extinction due to habitat loss and fragmentation, direct hunting pressure, and depletion of their prey reserves. Due to their cryptic behavior and relative rarity, we still know little regionally about baseline carnivore community composition and habitat preferences at individual sites across Southeast Asia, and consequently where and how best to study these communities, which further impedes conservation and management action. We sampled the mammalian carnivore community within diverse mosaic forest types of Thung Yai Naresuan Wildlife Sanctuary in western Thailand using camera traps augmented with direct observations from spotlighting and incidental daytime observations to assess our ability to effectively sample the carnivore community. The community of mammalian carnivores in Thung Yai revealed by this combination of camera trapping and direct sighting consisted of 20 species ranging in size from small (banded linsangs, <1 kg) to very large (tigers, ~200 kg). Community occupancy analysis based on camera trapping alone indicated that 66 ± 13% of the known community of carnivores (26 species) were detected during this survey. Detection probabilities of individual species varied from 0.01 to 0.34 with larger-bodied species having lower detection probabilities, possibly due to the small size of our trapping areas relative to their home range sizes. Effects of camera placement on species detection probability appeared to be subtle; however, terrestrial and large carnivores had higher detectability on the road, and semi-arboreal species seemed to have higher detection probabilities at cameras set on trails and trails by streams. The six species that went undetected included both terrestrial and semi-arboreal species. We attributed their non-detection to their behavior, natural rarity, and the limitations of our camera trap surveys. Spotlight surveys were useful in assessing strictly arboreal species, as we detected two additional species that went undetected by camera traps. Overall, this study suggests that surveys of carnivore assemblages via camera trapping can be improved by: (a) incorporating direct observations e.g., spotlight surveys; (b) surveying specific habitats or micro-habitats, particularly aquatic habitats, open forest/ non-forest edges; and (c) placing cameras on a range of trail sizes as well as off-trails.

Key words. Camera trapping, mammalian carnivores, Southeast Asia, spotlight surveys, Thailand

INTRODUCTION

Tropical Southeast Asia supports a rich assemblage of mammals of which approximately 10% (582 out of 5,506 species) are threatened with extinction due to habitat loss and degradation, prey depletion, and hunting for regional trade (Schipper et al., 2008a, b; IUCN 2013; Di Marco et al., 2014). Mammalian carnivores sit high on ecological pyramids and have major roles in maintaining ecosystem function (Croll et al., 2005; Crait & Ben-David, 2007); thus, their disappearance can have significant negative consequences for ecosystems (Berger et al., 2001; Ripple & Beschta, 2007). One impediment to carnivore conservation is that for many species status and distribution is often poorly known, as a consequence of their relative rarity and elusive behavior (Schreiber et al., 1989). This problem is particularly acute for small-bodied species, for which even appropriate field sampling protocols are underdeveloped, further impeding conservation and management action.

Thung Yai Naresuan Wildlife Sanctuary (Thung Yai, hereafter), together with adjacent Huai Kha Kaeng Wildlife Sanctuary, forms the core of one of the largest contiguous protected forest complexes in Thailand and Southeast Asia, known as the Western Forest Complex (18,000 km^2). Over the past 20 years a number of surveys have documented the status of wildlife here (Conforti, 1996; Steinmetz & Mather, 1996; Kanchanasaka, 1997; Steinmetz et al., 2008). These surveys, combined with compilations of secondary data and direct field observations (Lekagul & McNeely, 1988; Nakhasathien & Stewart-Cox, 1990; Supparatvikorn et al., 2012), indicate the occurrence of 26 species of mammalian carnivore from seven families in Thung Yai. In this paper we use this baseline of known species richness to assess the relative effectiveness of a given single survey to capture the richness of an entire carnivore community. We also compared detectability among species, and examined the effects of taxonomy, behavior, and study design on detection

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probability. This is one of the first studies to comprehensively evaluate these issues for a carnivore community.

Camera trapping is an effective method to document the occurrence of many elusive carnivores (e.g., Carbone et al., 2001; Mohamed et al., 2009; Wilting et al., 2010; Tantipisanuh et al., 2014). However, some carnivores, particularly viverrids and some felids, spend a significant proportion of their time in trees and therefore are rarely detected by cameras, which are typically placed <1 m above ground on existing roads or trails (Walston & Duckworth, 2003; Duckworth & Nettlebeck, 2007). This highlights the need to use multiple methodologies to account for species which are less likely or unlikely to be detected by standard camera trapping. For example, studies have shown that direct observation is required in order to detect strictly arboreal species such as small-toothed palm civet *Arctogalidia trivirgata* (Walston & Duckworth, 2003; Duckworth & Nettlebeck, 2007; Wilting et al., 2010).

In this study we used camera trapping augmented with spotlight surveys and daytime observations to document the carnivore community within the mosaic forests of Thung Yai. We estimated detection probabilities of carnivores based on camera trapping and tested whether their detection probabilities were biased towards species with larger body sizes (average weight >10 kg) or terrestrial behavior compared to those of smaller size (≤10 kg) or more arboreal in habit. Moreover, we also tested the effects of camera placement (such as trails and streams) on detection probabilities.

MATERIAL AND METHODS

Study site. Thung Yai covers 3,622 km^2 (15°00'–15°23'N, 98°30'–99°05'E). There are three seasons: cool dry (November–February), hot dry (March–May), and rainy (May–October). Mean annual temperature is 28°C (Thai Meteorological Department, 2005). Average annual rainfall is 2,337 mm (van de Bult, 2003), and is concentrated between July and September. Less than 100 mm of rain per month falls during December to April. The sanctuary is characterised by rugged mountainous terrain with elevations ranging from 250 m up to 1,800 m. Major forest types include mixed deciduous (45%), seasonal dry evergreen (28%; also known as semi-evergreen), and hill evergreen (15%). Secondary forest covers 4% of the sanctuary, and the remaining 5% consists of savanna, grassland, and dry dipterocarp forest (Nakhasathien & Stewart-Cox, 1990). Semi evergreen and mixed deciduous forests occur between 400 and 1,000 m elevation, as alternating patches in a mosaic determined largely by gradients of soil moisture (Nakhasathien & Stewart-Cox, 1990). Larger patches of seasonal evergreen and montane evergreen forests are confined to higher elevations (>1,000 m asl.). Details of forest structure and other characteristics can be found elsewhere (van de Bult, 2003; Webb et al., 2011, 2013).

Camera trap surveys. We conducted surveys from November 2007 to August 2008 using passive film camera traps with white flash (DeerCam® - DC-100; Non Typical Inc., U.S.A. and Stealth Cam® Stealth Cam, LLC., U.S.A.). Camera traps were employed at four study sites: Tikong (no. of active cameras = 15); Sesawo (14); Headquarters (10); and Mae Gatha (14) (Fig. 1). Tikong and Headquarters covered mostly semi-evergreen forest with interspersed patches of dipterocarp and mixed deciduous (Tikong), while Sesawo and Mae Gatha were in open mixed deciduous and dry dipterocarp forest with large patches of grasslands and gallery evergreen forest along the many streams that bisect the area. We camera-trapped Tikong and Sesawo first, before shifting the cameras to Headquarters and Mae Gatha. Each site was surveyed for 127 days on average (range 106–142 days). Cameras were placed at each site at a density of 1–2 camera-traps km^{-2} with an average spacing of 600 m resulting in trapping polygons (by connecting outer camera traps together in a GIS) of 7.0, 7.5, 8.2, and 5.9 km^2 for Tikong, Sesawo, Mae Gatha, and Headquarters, respectively. We placed cameras at four different microhabitats where tracks and signs of small and large carnivores were found: on small animal trails (<1 m wide) along streams (2–5 m in width; *n*=33), on animal trails unrelated to streams (1–2 m wide; *n*=14), along streams with no trails (1–3 m wide; *n*=5), and on the main access road (*n*=1) which was unpaved (4–6 m wide). Cameras were mounted on trees or wooden poles at a height of *c.* 30–40 cm at a distance of 3–4 m to the target area. Each unit was programmed to operate 24

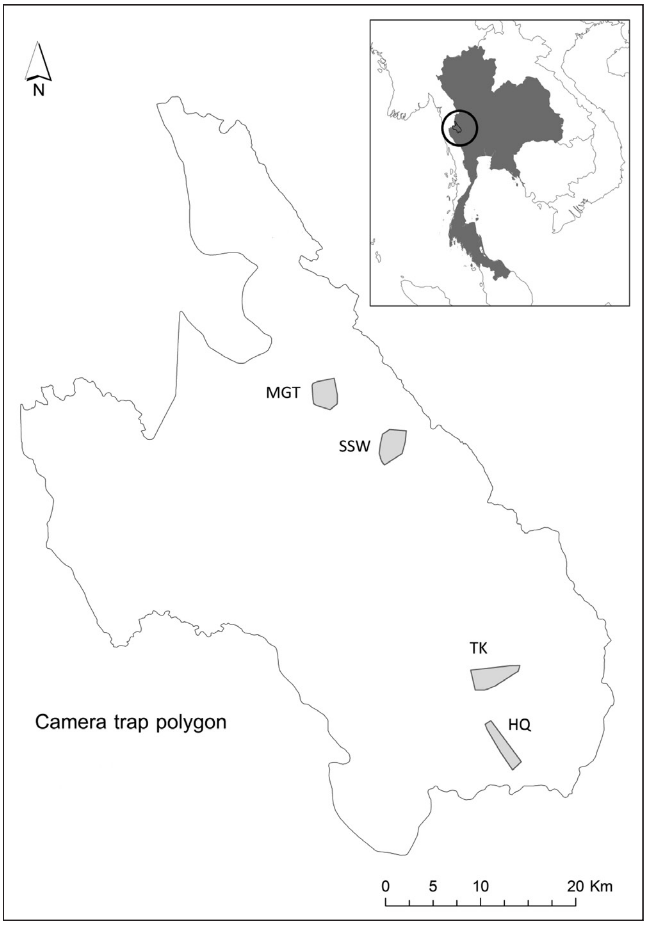

Fig. 1. Map of Thung Yai Naresuan Wildlife Sanctuary showing camera trap polygons in four study sites, from south to north, Headquarters (HQ), Tikong (TK), Sesawo (SSW), and Mae Gatha (MGT) between November 2007 and August 2008.

hours per day with a 1-minute delay between photographs. Time and date were recorded on photographs. We considered photos to be independent if: (1) consecutive photographs of different individuals were of the same or different species; or (2) consecutive photographs of individuals were of the same species taken more than 0.5 hour apart; or (3) nonconsecutive photos were of individuals of the same species (O'Brien et al., 2003). These independent events were used in our occupancy analyses (see below).

Spotlight surveys. We augmented camera trapping with spotlight surveys at Tikong and Sesawo. We walked along roads, trails, and streams at a slow pace (~1.5 hours km^{-1}) with 2–4 observers. We only report encountered animals that were confidently identified to species. Due to logistic constraints during the wet season, spotlight surveys were not possible at Headquarters and Mae Gatha.

Species discovery curves. We measured the rate at which new species of carnivores were discovered through camera trapping, using rarefaction with package BiodiversityR (Kindt & Coe, 2005). Data from all sites were combined for analysis. We graphed three different species discovery curves, one for all species combined, one for semi-arboreal species, and one for terrestrial species (defined below). Thus we could compare the rate at which the overall community was enumerated, as well as the effect of basic functional traits related to behavior on discovery rate. We were interested in the community of carnivores in the entire study area (i.e., Thung Yai as a whole), thus we did not compare carnivore discovery curves among sites. Additionally, camera trapping effort was different among sites thereby limiting comparisons.

Community completeness and detection probability. Our camera traps provided detection/non-detection data for each carnivore species. We analysed these data in an occupancy framework to (1) estimate community completeness (probability that a given member known to be present in the species pool is detected [MacKenzie et al., 2006]) and (2) estimate the detection probability of different species and species groups as a function of camera placement (MacKenzie et al., 2006). Data from all sites were combined for analysis. Data were lumped into 2-week periods resulting in eight sampling occasions.

For the first analysis, we compiled a list of carnivore species known to occur in Thung Yai and treated these as the baseline species pool potentially available for detection. In this case, our carnivore pool consisted of 26 species as noted above. Our interest was in the fraction of this species pool we could detect through our camera trap sampling, recognising that species might be present yet go undetected (MacKenzie et al., 2006). We constructed a detection matrix with the 26 species in rows (analogous to 'sites' in occupancy modeling of a single species) and sampling occasions in columns. Species detections (independent photos) and non-detections in each sample occasion at any camera location (n = 53) were coded '1' or '0', respectively. We modeled detection and occupancy probabilities as a function of specific traits (semi-arboreal versus terrestrial behavior) and average weight (kg) of males and/or females reported in Hunter (2011). We defined terrestrial species as those that spend most of their time on the ground whereas semi-arboreal were defined as those that spend part or much of their time in trees based on the literature (e.g., Lekagul & McNeely, 1988) and our own observations. The resulting occupancy estimate (ψ) represents the proportion of the available species pool actually present during our survey, analogous to 'relative species richness' of Cam et al. 2000 (MacKenzie et al., 2006; Conroy & Carroll, 2009).

In the second analysis, we estimated detection probability for 15 out of the 17 carnivores detected by camera traps, excluding clouded leopard *Neofelis nebulosa* and leopard *Panthera pardus* which were photographed only once. We constructed a detection matrix with camera locations in rows (n = 53) and sampling occasions, as above, in columns. Detections at a site were coded '1' and non-detections coded '0' as above. Three models were compared: (1) a null model, in which occupancy probability and detection probability were free from effects of covariates, (2) detection probability modeled as a function of camera placement (4 categories; road, streams, trails, and trails by streams), and (3) occupancy and detection probabilities both modeled as a function of camera placement. For Asiatic golden cat *Catopuma temminkii*, dhole *Cuon alpinus*, and banded linsang *Prionodon linsang*, the saturated model (detection probability and occupancy probability modeled as a function of camera placement) failed to converge, thus only the first two models were considered.

We further estimated detection probabilities of species groups in order to assess the influence of two functional traits. For this analysis data from all 17 species detected by camera traps were used. We grouped species according to behavior, as either terrestrial or semi-arboreal, and according to body size based on Hunter (2011); small (average weight ≤10 kg) or large (>10 kg). Terrestrial included 10 species while semi-arboreal included seven species; small bodied carnivores consisted of nine species while large bodied included eight species (Table 1). We applied the same procedure as the previous single species models, testing whether detection probability of these different functional species groups was affected by camera placement. We averaged model predictions across all possible models to avoid constraining our inferences to a single best model (Burnham & Anderson, 2004). Occupancy analysis was performed using package 'unmarked' (Fiske & Chandler, 2011). All analyses were conducted in R version 3.0.1 (R Core Team, 2013).

We further examined the effect of body size on detection probabilities by plotting detection probability of the 15 carnivores estimated from the single species occupancy models as a function of species average weight (kg; log[base10]-transformed).

RESULTS

A total of 20 species of carnivores were detected from camera trapping and direct observations, ranging in size from

Table 1. Detections of 17 carnivores at different camera placements, with numbers of camera traps at each placement in parentheses (n = 53). Numbers refer to number of detections after independent events were lumped into eight 2-week periods (sampling occasions) occupancy analysis. Species are grouped based on traits (terrestrial, Terr, and semi-arboreal, Semi) and size class (small, ≤ 10 kg, S, and large, > 10 kg, L; see Methods). Percentage indicates proportion of total camera locations a given species was detected.

Species	Road (1)	Streams (5)	Trails (14)	Trails by Streams (33)	No. of Sampling Occasions Detected	Trait/Weight
Crab-eating mongoose (11%)		2		11	13	Terr, S
Common palm civet (6%)			6		6	Semi, S
Masked palm civet (15%)			3	9	12	Semi, S
Large Indian civet (45%)	2	2	9	35	48	Terr, S
Yellow-throated marten (4%)				4	4	Semi, S
Otter sp. (4%)				5	5	Terr, S
Ferret badger sp. (2%)				2	2	Terr, S
Leopard cat (11%)			2	6	8	Terr, S
Golden cat (2%)	2				2	Terr, L
Tiger (23%)	1		2	11	14	Terr, L
Dhole (4%)				2	2	Terr, L
Asiatic jackal (4%)			2		2	Terr, L
Banded linsang (4%)				2	2	Semi, S
Clouded leopard (2%)			1		1	Semi, L
Leopard (2%)				1	1	Terr, L
Sun bear (9%)			2	3	5	Semi, L
Asiatic black bear (9%)			1	3	4	Semi, L

banded linsangs (<1 kg) to tigers (~ 200 kg). Among these, 11 were terrestrial, seven were semi-arboreal, and two were entirely arboreal (Appendix 1). We did not detect at least four species previously recorded from this part of the Western Forest Complex: marbled cat *Pardofelis marmorata*, jungle cat *Felis chaus*, yellow-bellied weasel *Mustela kathiah*, and hog badger *Arctonyx collaris*. At least one species of otter was camera-trapped, but, based on the collective experiences of the authors, differentiating among otter species from photographs is possible only if they contain full shots of distinguishing features: heads and tails. Nevertheless, based on appearance particularly the characteristics of the tail and body size (relative to the size of known objects appearing in the photographs) it is likely the detected individuals were the smallest species—small-clawed otter *Aonyx cinerea*. Therefore, in addition, probably two otter species, smooth-coated *Lutrogale perspicillata* and Eurasian *Lutra lutra*, went undetected.

Camera trap surveys. From a total effort of 4,550 trap nights (average 86 ± 31 *SD* trap nights per location) we obtained 1,191 photographs of mammals. Photographs of mammalian carnivores accounted for 15% (n=181) of all mammal photographs taken and included 17 species from seven families (Appendix 1). Carnivores were recorded at 62% of camera trap locations and across the entire altitudinal range of the study (700–1,147 m asl.). Semi-arboreal and arboreal species combined were detected at 2–15% of camera locations while terrestrial species were detected at 2–45% (Table 1 and Appendix 1). Masked palm civet was the most widely detected species of the semi-arboreal group (15% of locations) and large Indian civet *Viverra zibetha* was the most widely detected terrestrial species (45%, Table 1 and Appendix 1). In contrast, ferret badger *Melogale* sp., leopard, clouded leopard, and Asiatic golden cat, all but one of which is terrestrial (clouded leopard is semi-arboreal), were only detected at a single camera location each (Table 1 and Appendix 1). We camera trapped otters but as noted above species identification could not be verified; three species are known to occur in Thung Yai (small-clawed, Eurasian, and smooth-coated otters; Kanchanasakha, 1997). We did not attempt to identify species of ferret badger as two species might occur in Thailand and both have similar pelage patterns, which cannot be resolved to species without examination of teeth (Duckworth et al., 2008).

Spotlight surveys. From 22 hours of spotlight surveys at Tikong and 21 hours at Sesawo, we observed six species of viverrids, and one species of prionodontid (Appendix 1). Small-toothed palm civet was the most frequently observed species (seven observations at each site), followed by common palm civet (five and two observations at Tikong and Sesawo, respectively), and masked palm civet (four and one observations) (Table 2). Most (92%) encounters of these three palm civets were in trees or woody climbers. Two out of 28 sightings of palm civets were uncertain for species identification. Ancillary observations made during daytime checks of camera traps yielded two sightings of binturong *Arctictis binturong*.

Species discovery curves. Species discovery curves appeared to reach asymptotes suggesting our sampling covered nearly the complete carnivore community of Thung Yai for all species combined as well as based on behavior (terrestrial vs. semi-arboreal) (Fig. 2).

Community completeness. The model averaged estimate of the proportion of species detected (ψ) by camera traps based on the known species pool of carnivores in Thung Yai (26 species) was 0.66 ± 0.13 *SE*. This is very close to the naïve estimate of 0.65 (17/26). Incorporating average body weight in the community occupancy models suggested only weak support relative to the null, although it was included in the top model (two models had ΔAIC < 2.0) (Arnold, 2010). Behavior (semi-arboreal or terrestrial) did not affect the proportion of species detected (Table 2A).

Detection probabilities. Camera placement appeared to influence detection probabilities for three of four functional groups. Top models (ΔAIC = 0.0) for the terrestrial, semi-arboreal, and large-bodied carnivore groups included camera placement as a covariate for detection probability and had AIC weights > 0.71 (Table 2B). Specifically, detection probabilities (p) for large carnivores, and for terrestrial carnivores, were up to 10 times higher on the road (p = 0.38 and 0.68 for large and terrestrial, respectively; Fig. 3) versus other locations (p = 0.03 and 0.18 for streams, 0.13 and 0.24 for trails, 0.14 and 0.38 for trails by streams; Fig. 3). However, for small-bodied carnivores effect of camera placement appeared to be negligible; the top model did not include this covariate (w_i = 0.76 for the null model; Table 2B). In addition, there were relatively small differences among placement sites for this group (0.37 road, 0.35 streams, 0.41 trails, 0.41 for trails by streams; Fig. 3). For individuals species, presumably due to small numbers of captures and recaptures the models indicated weak to minimal effects of placement (models with ΔAIC < 2.0 compared to the null; Table 2C). Nonetheless, based on visual inspection, the data did suggest some possible trends for two or three species including common palm civets, tigers, and perhaps golden cats (Fig. 3). For example, tigers and golden cats appeared

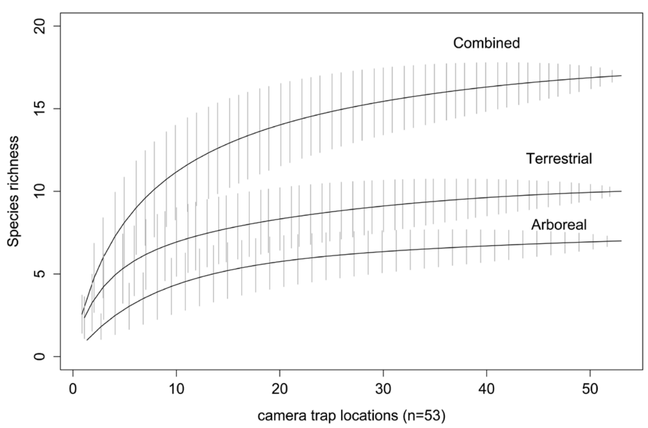

Fig. 2. Species discovery curves generated from rarefaction for mammalian carnivores based on camera trap surveys at four study sites within mosaic forest types of Thung Yai between November 2007 and August 2008. Bars represent 95% confidence intervals of the estimates scaled by survey effort (camera trap nights) combined across all active camera locations (n = 53). Curves were estimated using package *BiodiversityR* in program R.

to have higher detection probabilities on the road, although precision was poor as noted above (Fig. 3).

Estimated detection probabilities controlling for effects of camera placement were relatively low for both grouped traits and single species (< 0.5; Fig. 4). Large differences were observed between small and large-bodied carnivores whereas semi-arboreal and terrestrial species appeared not to differ. For single species the precision was also low (wide confidence intervals), particularly for otter, ferret badger, common palm civet, and yellow-throated marten.

The overall relationship between detection probability and log average body weight was non-linear (Fig. 5), however there appeared to be two distinct patterns; for the lightest nine species (lg weight ≤1.0 kg) the relationship appeared linearly positive (beta = 0.305, R^2 = 0.757), while for the largest six species there appeared to be little or no correlation. This suggested that detection probability increased with size up to a 'middle' weight level, but then declined for the larger carnivores (lg weight >1.0) including Asiatic golden cats, Asiatic jackals, dholes, sun bears, Asiatic black bears, and tigers. The overall weak relationship (R^2 = 0.245) indicates that detection probability was likely influenced by other factors in addition to weight, such as home range size as we discuss below.

DISCUSSION

Camera trapping alone detected 65% of the carnivores known to occur in Thung Yai; combined with direct sighting, this yielded 77% of carnivores known to occur in the study area. At the community level, the species discovery curves suggested that the community of carnivores was nearly completely sampled by camera trapping during our survey. In contrast, the community occupancy analyses suggested that we only detected two-thirds (66 ± 13%) of the known community via camera trapping. This discrepancy suggests sufficient sampling of some habitats and conditions, while other species-specific habitats or micro-habitats were poorly sampled or missed completely. However, this probably only accounts for some, but not all of the non-detection of the six 'missing' species (marbled cat, jungle cat, yellow-bellied weasel, hog badger, and possibly two otter species—smooth-coated and Eurasian) during our study (see below). Furthermore, three species (small Indian civet, small-toothed palm civet, and binturong) were only detected by direct observation and not with camera traps presumably due to their largely arboreal behavior. All of the larger known carnivores (e.g., tiger, leopard, Asiatic black bear etc.) were detected, but their detection rates were typically low.

Behavior. For some species we can be more confident that absence or low detection rates by camera traps were most likely caused by their arboreal behavior. For example, we regularly encountered small-toothed palm civets, but only in trees during spotlight surveys. Indeed, the species has not been detected during any camera trap survey we are aware of across the region (Appendix 2). Clearly, strict arboreality severely precludes detection by ground-level camera traps (Walston & Duckworth, 2003). In Sabah, Borneo, small-toothed palm civets were likewise only observed during spotlight surveys (Wilting et al., 2010; Appendix 2). Masked palm civets, common palm civets, and binturongs were commonly observed in trees although they are known to travel on the ground (WC pers. obs.), resulting in at least occasional camera trap records (Appendix 2). Likewise, the low detection of banded linsangs in our cameras was in concordance with other studies (Appendix 2). It is still unclear whether their partially arboreal behavior (Van Rompaey, 1993) and probably limited trail usage may cause their low camera trap detection probability. However, surveys that use spotlighting frequently detect this species (Wilting et al., 2010). Nevertheless, spotlight surveys would be of limited use for species that are partially diurnal and mainly terrestrial (e.g., hog badgers [Than Zaw et al., 2008],

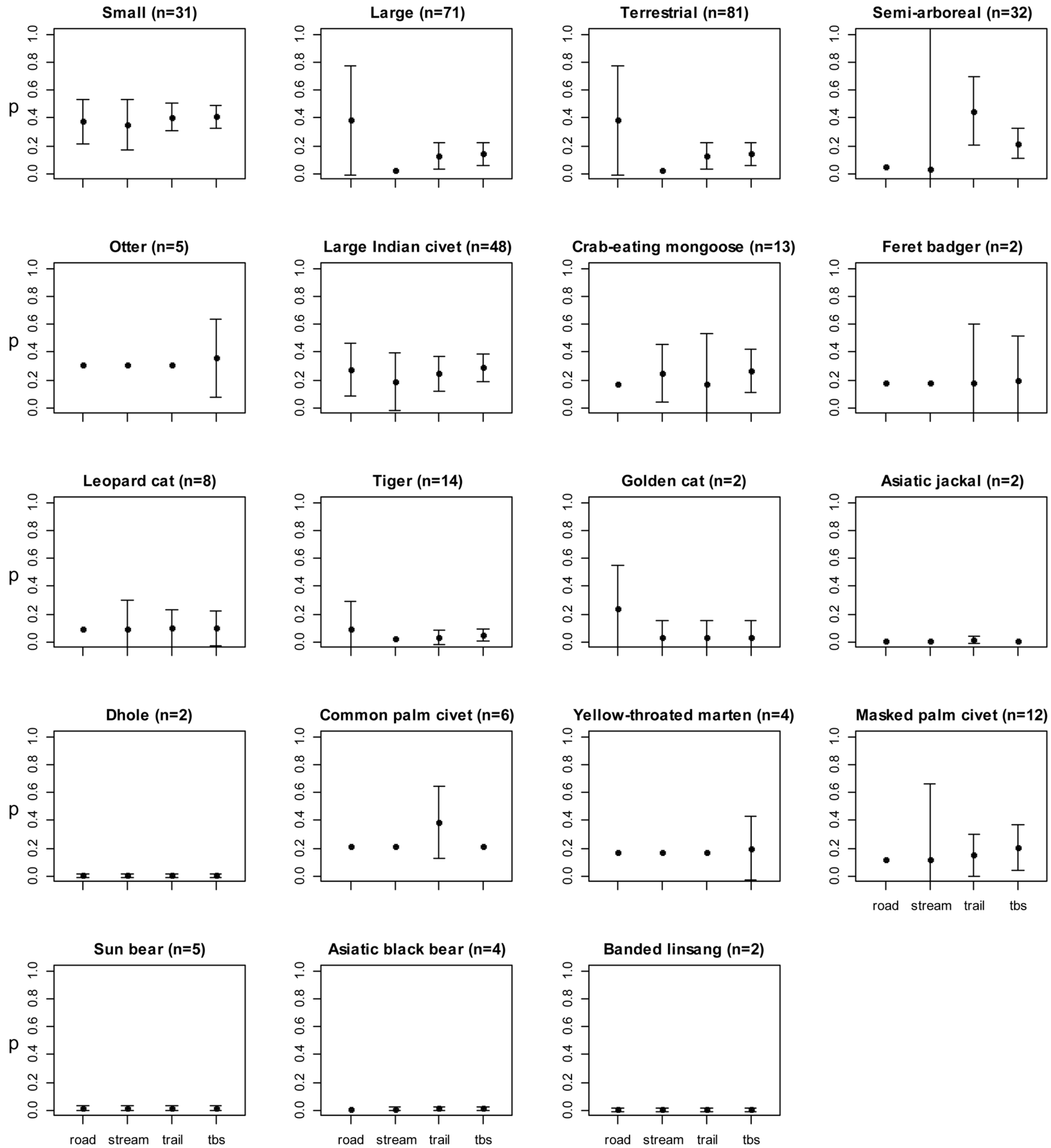

Fig. 3. Model averaged estimates of detection probability of four functional groups of carnivores (top row) and for each of 15 species separately. Detection probabilities are estimated as functions of camera placement categories (road [no. cameras = 1], streams [5], trails [14], & trails by streams [tbs; 33]). Error bars represent 95% confidence intervals. Estimates were presented without error bars when standard errors could not be estimated. Estimates with 95% confidence intervals less than zero and/or greater than one indicate a lack of model convergence. *n* refers to the number of independent photographs used to estimate detection probabilities.

yellow-bellied weasels [Supparatvikorn et al., 2012]), and/or extremely rare, at least in this region, such as jungle cats (Duckworth et al., 2005).

Behavior may partly explain non-detection by camera traps for yellow-bellied weasels. Based on our field observations at numerous sites in the region, we believe these species rarely use trails. Though we had some off-trail camera locations, most of our cameras were installed on small trails by streams. Thus, we might also have missed the micro-habitat that these species prefer. For example, extensive camera trap surveys in Borneo (>40,000 trap-nights) only detected

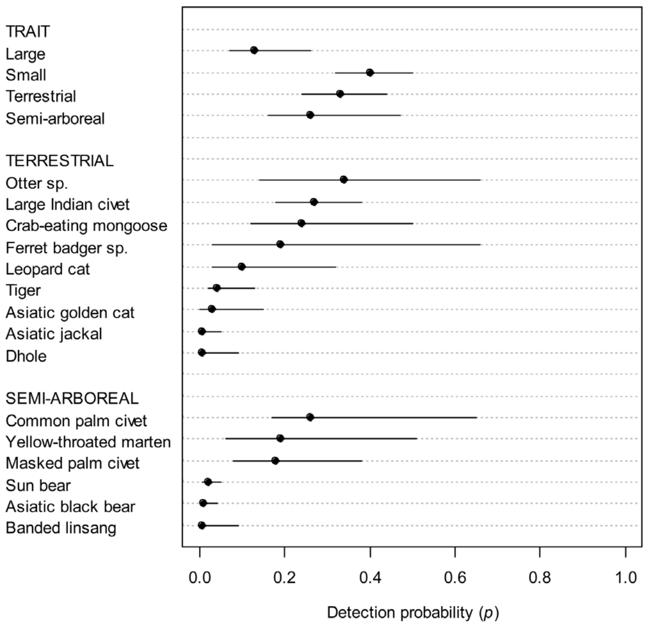

Fig. 4. Model averaged estimates of detection probability across the models shown in Tables 2B and 2C for species functional groups (TRAIT; large vs small and terrestrial vs semi-arboreal behavior). Estimated detection probabilities of each species are also shown for TERRESTRIAL and SEMI-ARBOREAL species. Error bars represent 95% confidence intervals.

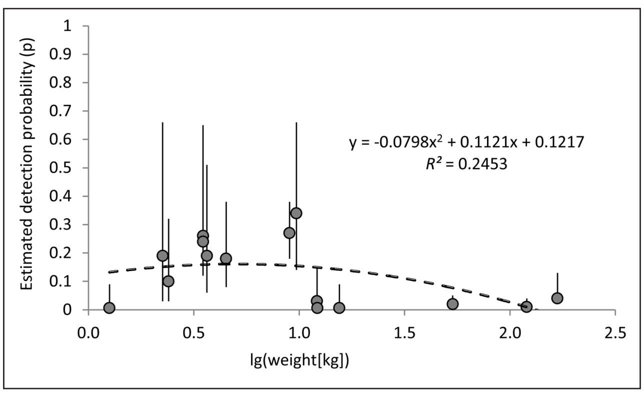

Fig. 5. Model averaged estimates of detection probability for 15 carnivore species by camera trapping plotted as a function of $\log_{10}$(weight in kg). Error bars represent 95% confidence intervals. Fitted line is derived from a second-order polynomial which described the best fit of the data. R^2 is the coefficient of determination of the fitted line. The six species with lg(weight) greater than 1.0 are Asiatic golden cat, Asiatic jackal, dhole, sun bear, Asiatic black bear, and tiger, from left to right.

Malay weasel *Mustela nudipes* 28 times (one detection per >1400 trap-nights) (Ross et al., 2013). This low detection rate was presumably because cameras were only placed on trails and roads. Previous studies assumed that the lack of camera trap records for most weasels was a result from their morphology and habits—fast moving and low slung (Giordano & Brodie, 2012), behaviors which might affect detectability during standard camera-trap surveys (Duckworth & Robichaud, 2005; Duckworth et al., 2006; Abramov et al., 2008; Ghimirey & Acharya, 2012). Nonetheless, our study which specifically targeted small carnivores, placing more traps on small animal trails rather than roads and manmade trails, still failed to detect yellow-bellied weasel although it is known to occur in Thung Yai (Supparatavikorn et al., 2012), though we regularly photographed much smaller, fast-moving rodents. Thus, we currently attribute the lack of weasel records primarily to small numbers of cameras being placed off-trail (see also Ross et al., 2013).

Rarity. Natural rarity is the most likely explanation for the non-detection of jungle cat and marbled cat, both known to be present. Marbled cats are semi-arboreal with great climbing ability (Mohamed et al., 2009), which likely reduces their detection probability and could partially account for their non-detection during our study. But comparisons with other small bodied carnivores with similar behavior, for example, common palm civets, masked palm civets, or even more so like binturongs, all were detected fairly frequently in our and other camera trap studies (Appendices 1 and 2). Thus we doubt the absence of marbled cat is due to their semi-arboreal behavior alone. A recent compilation of camera trap records across Thailand of over 14 protected areas with a combined survey effort > 40,000 trap nights resulted in only 10 photographs (one detection per >4000 trap-nights) (Lynam et al., 2013; Tantipisanuh et al., 2014). This suggests a condition of naturally low abundance not just in Thung Yai but throughout their Thai range and Indochina (Cambodia, Laos, and Vietnam; Duckworth et al., 2005). Combined with their semi-arboreal behavior, this would result in extremely few detections, whether by camera trapping or spotlighting (e.g., Mohamed et al., 2009).

The lack of jungle cat records from our study and elsewhere in SE Asia (Appendix 2), also appears to be the result of genuine rarity and perhaps a preference for open habitats (Duckworth et al., 2005). An assessment of jungle cat status from Indochina suggested it was indeed extremely rare and mostly occurred in secondary/degraded deciduous (e.g., dry dipterocarp; Duckworth et al., 2005; Gray et al., 2012) habitats where hunting pressure was very high (Duckworth et al., 2005). In addition, most field surveys focused on old growth forest within protected areas whereas jungle cats might actually prefer open, disturbed, agricultural, and settlement areas (as in India, Duckworth et al., 2005). This is probably the case for our study where all our cameras were installed in the inner part of Thung Yai (closest human settlement to any camera was >15 km), although a large proportion of cameras were in open habitats, we failed to detect this species. Alternatively jungle cat may have been extirpated from the area for unknown reasons. The most recent

Table 2. Model selection for: A, community occupancy models; B, species grouped by trait (terrestrial and semi-arboreal) and average body weight (small, ≤ 10 kg and large, > 10 kg); and C, single species occupancy models for 15 carnivores, based on camera trap surveys during 2007/2008 in Thung Yai (4 sites were pooled resulting in 53 sampling units, i.e., camera traps). *n* refers to numbers of sampling occasions detected within eight, two-week periods. The effect of camera placement (camera) including road, trails, trails by streams, and streams was modeled for functional groups (B) and specific species (C).

A. Community occupancy models (top 3 models) of the 26 possible carnivore species combined (n = 62).

Model	K	AIC	ΔAIC	w_i
ψ(weight) p(weight)	4	220.62	0.00	0.36
ψ(.) p(weight)	3	221.61	0.99	0.22
ψ(.) p(weight+trait)	4	222.70	2.08	0.13

B. Functional trait occupancy models (top 3 models, unless otherwise noted) for terrestrial (10 species; n = 81) versus semi-arboreal (7 species; n = 32) and small (9 species; n = 77) vs. large (8 species; n = 31). Model of the form 'ψ(.) p(.)' represents the null model where no covariate was modeled.

Model	K	AIC	ΔAIC	w_i
Terrestrial				
ψ(.) p(camera)	5	347.26	0.00	0.83
ψ(.) p(.)	2	351.54	4.28	0.10
ψ(camera) p(camera)	8	352.28	5.02	0.07
Semi-arboreal				
ψ(.) p(camera)	5	184.94	0.00	0.72
ψ(camera) p(camera)	8	187.96	3.02	0.16
ψ(.) p(.)	2	188.43	3.49	0.13
Small-bodied carnivores				
ψ(.) p(.)	2	319.11	0.00	0.76
ψ(.) p(camera)	5	321.66	2.55	0.21
ψ(camera) p(camera)	8	325.71	6.60	0.03
Large-bodied carnivores				
ψ(.) p(camera)	5	200.98	0.00	0.78
ψ(.) p(.)	2	204.04	3.07	0.17
ψ(camera) p(camera)	8	206.29	5.31	0.05

C. Single species occupancy models

Model	K	AIC	ΔAIC	w_i
Crab-eating mongoose (n = 13)				
ψ(.) p(.)	2	91.97	0.00	0.67
ψ(.) p(camera)	5	93.46	1.49	0.32
ψ(camera) p(camera)	8	99.38	7.41	0.02
Common palm civet (n = 6)				
ψ(.) p(.)	2	40.99	0.00	0.56
ψ(.) p(camera)	5	41.53	0.54	0.42
ψ(camera) p(camera)	8	47.53	6.54	0.02
Masked palm civet (n = 12)				
ψ(.) p(.)	2	94.54	0.00	0.69
ψ(.) p(camera)	5	96.74	2.20	0.23
ψ(camera) p(camera)	8	98.85	4.31	0.08
Large Indian civet (n = 48)				
ψ(.) p(.)	2	258.78	0.00	0.57
ψ(.) p(camera)	5	259.64	0.86	0.37
ψ(camera) p(camera)	8	263.22	4.44	0.06
Yellow-throated marten (n = 4)				
ψ(.) p(.)	2	37.94	0.00	0.87
ψ(.) p(camera)	5	41.88	3.94	0.12
ψ(camera) p(camera)	8	47.88	9.94	0.01
Otter sp. (n = 5)				
ψ(.) p(.)	2	37.94	0.00	0.88
ψ(.) p(camera)	5	41.94	4.00	0.12
ψ(camera) p(camera)	8	47.93	10.00	0.01

Table 2. Cont'd.

Model	K	AIC	ΔAIC	w_i
Ferret badger sp. (*n* = 2)				
ψ(.) *p*(.)	2	22.34	0.00	0.92
ψ(.) *p*(camera)	5	27.34	5.00	0.08
ψ(camera) *p*(camera)	8	33.34	11.00	0.00
Leopard cat (*n* = 8)				
ψ(.) *p*(.)	2	75.49	0.00	0.88
ψ(.) *p*(camera)	5	79.72	4.23	0.11
ψ(camera) *p*(camera)	8	84.52	9.03	0.01
Golden cat (*n* = 2)				
ψ(.) *p*(camera)	5	19.00	0.00	0.85
ψ(.) *p*(.)	2	22.48	3.49	0.15
Tiger (*n* = 14)				
ψ(.) *p*(.)	2	119.60	0.00	0.50
ψ(.) *p*(camera)	5	119.71	0.10	0.48
ψ(camera) *p*(camera)	8	125.71	6.10	0.02
Dhole (*n* = 2)				
ψ(.) *p*(.)	2	28.35	0.00	0.88
ψ(.) *p*(camera)	5	32.34	3.99	0.12
Asiatic jackal (*n* = 2)				
ψ(.) *p*(.)	2	28.35	0.00	0.57
ψ(.) *p*(camera)	5	29.00	0.65	0.41
ψ(camera) *p*(camera)	8	35.00	6.65	0.02
Asiatic black bear (*n* = 4)				
ψ(.) *p*(.)	2	47.13	0.00	0.91
ψ(.) *p*(camera)	5	51.96	4.83	0.08
ψ(camera) *p*(camera)	8	57.96	10.83	0.01
Sun bear (*n* = 5)				
ψ(.) *p*(.)	2	55.67	0.00	0.89
ψ(.) *p*(camera)	5	60.06	4.39	0.10
ψ(camera) *p*(camera)	8	66.06	10.39	0.01
Banded linsang (*n* = 2)				
ψ(.) *p*(.)	2	28.35	0.00	0.88
ψ(.) *p*(camera)	5	32.34	3.99	0.12

record for jungle cat near our study area was a sighting in a transition of semi-evergreen and bamboo dominated mixed deciduous forest at about 400 m asl in 1995 (Steinmetz & Mather 1996; detailed in Duckworth et al., 2005).

Spatial coverage. One of the limitations of this study was the spatial coverage which was often considerably smaller than the home range sizes of the larger carnivores (dholes, bears, tigers, golden cats, clouded leopards, and leopards). Small camera trapping areas may cause large carnivores to be 'absent' most of the survey period when they would be presumably occupying other larger parts of their home ranges. This likely reduced the number of detections and precision of our detection probability estimates at least for the larger species. For example, our estimated detection probability for tiger was very low, suggesting that the tigers spent most of the survey period outside the camera trapping areas. In addition, this may explain the weak relationship between detection probability and weight for the species weighing over 10 kg (i.e., species with lg weight > 1.0 in Fig. 5). On the other hand, the spatial coverage appeared to be sufficient for carnivores less than 10 kg. This resulted in a greater number of detections and relatively higher precision of detection probability estimates particularly for large Indian civets, and for some of the other smaller-bodied animals (Fig. 3 and Fig. 5). Thus, future camera trapping surveys to assess community richness should take into account the scale of species ranges (e.g., home range size) to ensure that the probability of detecting species or the community of concern is maximised (MacKenzie et al., 2006).

Missing habitats. Although we camera-trapped otters, we could not be entirely certain as to species identification. Nevertheless, based on appearance it is likely the detected individuals were small-clawed otter. In addition, previous studies suggested that the two larger species, Eurasian and smooth-coated otters, appeared to be either restricted to larger and slow flowing rivers (smooth-coated) or faster flowing rivers (Eurasian) (Kruuk et al., 1994; Kanchanasakha, 1997), thus, we believe that the species we camera-trapped in the small streams were small-clawed and that we probably under-sampled the other two otters' habitats.

Study limitations. Although we recorded 17 species of carnivores from camera trapping over 4,500 trap nights in a range of habitats, the study had four limitations that might have affected the species detected and their capture frequencies: (1) as noted above, deploying a small number of camera_traps (10–15) in small trapping areas (5.9–8.2 km^2) in each study site. This perhaps limited our ability to repeatedly detect certain species that have large home ranges (e.g., tigers); (2) limited ability to detect species that are mostly arboreal. As we noted, increasing camera trap effort may not guarantee that additional species will be detected. This was clearly demonstrated by the two mostly arboreal viverrids—small-toothed palm civets and binturongs, which were only encountered by direct observations at Tikong and Sesawo despite more than 3,000 trap nights of camera-trapping in these two areas; (3) lack of off-trail cameras may have hindered our ability to detect some carnivores which may avoid trails of any size, such as hog badgers and weasels; and (4) we probably greatly under-sampled some habitats of specialist carnivores such as those used by Eurasian and smooth-coated otters.

Conclusions. The occurrence of 20 carnivores in the study area determined from camera trapping and direct observations highlights the importance of large intact forested landscapes such as this for carnivore conservation. Of the six species considered threatened, we detected five by camera trapping and one (binturong) by direct sighting, confirming the effectiveness of camera trapping for detecting elusive and low density carnivores (e.g., Carbone et al., 2001). However, for the six species known to be present but not detected we attribute this to either their extreme rarity at the site and/or their preference for habitats and/or micro-habitats that we did not survey. Owing to different behaviors, habitat requirements, and rarity, multiple methods are required to detect the entire community, particularly the semi-arboreal and arboreal species as well as riverine specialists such as otters. For some species, we speculate that more targeted surveys in specific microhabitats are needed, while baited camera traps and setting cameras off-trail may be more effective for other species e.g., hog badger and yellow-bellied weasel (Ross et al., 2013). Together the results highlight the fact that even in relatively undisturbed habitats using intensive sampling, many mammalian carnivores can be relatively rare and difficult to detect. Future surveys targeting a range of carnivore species that vary greatly both in size, behavior, and degree of rarity should also take into account camera placement.

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Appendix 1. Detection and non-detection of mammalian carnivores in four study sites of Thung Yai (Table 1) between November 2007 and August 2008 based on three different detection methods; CT – camera trap, NS – direct observation made during night surveys, and DO – direct observation made during daytime. IUCN (2013) status (EN Endangered; VU Vulnerable; NT Near Threatened) in parentheses. Night surveys were not conducted in Headquarters and Mae Gatha. Shown are number of independent events, number of camera trap locations, and percentage of total camera trap locations (n = 53), and mean altitude and range (meters) where carnivores were detected by camera traps.

Common name (by family)	**Tikong**	**Sesawo**	**Headquarters**	**Mae Gatha**	**No. Independent Events**	**No. Camera Locations Detected (%)**	**Mean Altitude (Range; m)**
Canidae							
Asiatic jackal	CT	–	–	–	3	2 (4)	1,010 (976–1,045)
Dhole (EN)	CT	–	–	CT	2	2 (4)	766 (700–832)
Mustelidae							
Yellow-throated marten	DO	CT, DO	–	–	5	2 (4)	909 (889–929)
Ferret badger sp.[€]	–	CT	–	–	16	1 (2)	940
Otter sp.[€]	–	CT	–	–	8	2 (4)	890 (840–940)
Viverridae							
Small Indian civet	NS	–	–	–	–	–	
Large Indian civet (NT)	CT, NS, DO	CT, NS, DO	CT	CT	62	24 (45)	842 (700–977)
Masked palm civet	CT, NS	CT, NS	–	–	13	8 (15)	921 (840–1,046)
Common palm civet	CT, NS	NS	–	–	8	3 (6)	943 (840–1,045)
Small-toothed palm civet	NS	NS	–	–	–	–	
Binturong (VU)	DO	DO	–	–	–	–	
Prionodonidae							
Banded linsang	CT, NS	–	–	CT	2	2 (4)	790 (740–840)
Herpestidae							
Crab-eating mongoose	CT	CT	–	CT	23	6 (11)	839 (702–940)
Felidae							
Leopard cat	–	CT	–	CT	8	6 (11)	855 (700–930)
Asiatic golden cat (NT)	–	CT	–	–	2	1 (2)	827
Clouded leopard (VU)	CT	–	–	–	1	1 (2)	840
Leopard (NT)	–	CT	–	–	1	1 (2)	860
Tiger (EN)	CT	CT	–	–	18	12 (23)	907 (820–1,147)
Ursidae							
Asiatic black bear (VU)	CT	CT	–	CT	5	5 (9)	828 (700–920)
Sun bear (VU)	CT	CT	–	CT	5	5 (9)	850 (702–930)

[€] Species identification for ferret badger sp. and otter sp. could not be verified from camera trap photographs.

Appendix 2. Camera trap studies conducted in South and Southeast Asian countries showing number of camera trap photographs or independent events of mammalian carnivores. Studies are: A, Eastern Cambodia (Gray & Phan, 2011); B, Cambodia (Holden & Thy, 2006); C, Northern Laos (Johnson et al., 2006, 2009); D, Central Vietnam (Long & Minh Hoang, 2006); E, Northern Myanmar (Rao et al., 2005); F, Myanmar (Than Zaw et al., 2008); G, NE India (Datta et al., 2008a,b); H, Western Thailand (Ngoprasert, 2004); I, NE Thailand (Grassman et al., 2006); J, NE Thailand (Jenks et al., 2011); K, Southern Thailand (Kitamura et al., 2010); L, Peninsular Malaysia (Lynam et al., 2007); M, Peninsular Malaysia (Mohd.-Azlan, 2006); N, Peninsular Malaysia (Kawanishi & Sunquist, 2004); O, Malaysian Sabah (Brodie & Giordano, 2011, 2012); P, Malaysian Sabah (Mohamed et al., 2009; Wilting et al., 2010); Q, Central Kalimantran, Indonesia (Cheyne et al., 2010; Cheyne & Macdonald, 2011); and R, this study. Some surveys augmented detection methods using spotlight surveys (studies B, D, P, R), examination of skins, skulls, track/sign, roadkill, and opportunistic sightings (B, D, F, G, M); therefore care should be taken when comparing results.

Family/Species	A	B	C	D	E[§]	F	G	H	I	J	K	L	M	N	O	P	Q	R
CANIDAE																		
Asiatic jackal	7							2		6								3
Dhole	17		1		42			67	11	8		17	13	16				2
FELIDAE																		
Leopard cat	21		24		48		1	31	3	4	13	31	86	62	20	288	25	8
Asiatic golden cat			48		20		1	1	2	5	43	69	38	37				2
Clouded leopard[¥]	1		1		77		1		2	8	4	25	13	16	59	19	29	1
Leopard	20		1					167			2	70	103	150				1
Tiger			13					10	3		5	51	151	61				18
Marbled Cat			39				1	1		1		10	1	16	3	2	4	
Jungle cat																		
Fishing cat								1										
Flat-headed cat															1	4	7	
Bornean bay cat																2		
HERPESTIDAE																		
Crab-eating mongoose		28	13	4		46	5	14		11								23
Small Asian mongoose	1	1									1							
Collared mongoose																17	8	
Short-tailed mongoose																30	14	
mongoose spp.												4	16		9			
MUSTELIDAE																		
Yellow-throated marten	1	5	90	1	84	54	5	6	1		17	9	2	7	1	1	5	5
Small-toothed ferret badger				1														
Large-toothed ferret badger																		
Ferret badger sp.		2		9		5	4											16
Smooth-coated otter		1				1										5		
Oriental small-clawed otter			1			1										1		
Hairy-nosed otter		5														1		
Eurasian otter																		
Otter sp.												1	1			2	8	
Hog badger	4	15	25	1		33	1	72	2	3								
Yellow-bellied weasel				1		1												

Appendix 2. Cont'd.

Family/Species	A	B	C	D	E[§]	F	G	H	I	J	K	L	M	N	O	P	Q	R
Siberian weasel																		
Stripe-backed weasel			1			4												
Malay weasel														1				
Sunda stink badger																107		
PRIONODONTIDAE																		
Banded linsang						5					7	4	3	1	3	6	1	2
Spotted linsang		1	7	1	7	8												
URSIDAE																		
Asiatic black bear			1					8	7	21								5
Sun bear	5		1		42			9	3	16		82	167	225		1		5
VIVERRIDAE																		
Large Indian civet	45	18	34	2		128	15	77	9	37		13	3	7				62
Masked palm civet		3	39	12	34	10	5				21	17	2	6	2			13
Common palm civet	23	24	31	9		38	5	33	2	2	1	3	16	4	1	1	5	8
Small Indian civet	6	22	3			8												1
Small-toothed palm civet*				1												23		14
Binturong			1	7	13			2	2	7	8	1	3	2	1		1	
Large-spotted civet	1	13				2				3								
Banded civet											13	2		5		44		
Malay civet												10	28	81	18	326	16	
Owston's civet			1	1														
Hose's civet															3			
Otter civet															10	2		
AILURIDAE																		
Red Panda						7												
Survey effort	2717	3661	8499	6337	1238	7955	1983	4493	1224	6260	11106	6259	5972	14054	2915	1916	6025	4550
No. species detected	13	13	20	14	9	17	11	15	12	14	12	17	17	18	11	20	12	20

We caution here that direct comparison of numbers of photographs and independent events are not advised owing to the fact that different surveys used different criteria. For example, study A assigned independent events for photographs taken > 20 minutes apart whereas study C used 30 minutes, while study H and N reported all photographs taken. Moreover, some studies did not state explicitly how camera trap photographs were assigned.

[§] Number of events reported here were back-calculated from relative abundance indexes (no. independent photos/100 trap nights) indicated in the study.

* Detections came solely from spotlight surveys. [¥] Sunda clouded leopard *Neofelis diardi* for studies O, P, and Q.