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HOW USEFUL ARE TRANSECT SURVEYS FOR STUDYING CARNIVORES IN THE TROPICAL RAINFORESTS OF BORNEO?

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ABSTRACT. — Transect surveys are a widely used tool in the study of wildlife populations. Here, we review different forms and objectives of transect surveys, discuss the need for and briefly describe principles of good study design, and discuss various biological measurements employed in the study of carnivores in the rainforests of Borneo. We discuss the conservation value of these measurements, underlying assumptions in using different approaches, and why these assumptions cannot often be met in the study of Bornean carnivores. We argue that transect surveys are of little use as a stand-alone technique for carnivore studies in Borneo; numbers of encounters from genuinely random transects are too low to be amenable to quantitative analysis, whereas observations from non-random transects are biased and cannot be used for drawing any sort of wider inference. We consider approaches in which transect surveys could be implemented in conjunction with other techniques. In general, limited conservation resources could be better spent on other techniques and other measures that can usefully inform conservation.

KEY WORDS. — transects, carnivores, Borneo, study design, distance sampling, occupancy

INTRODUCTION

Assessing the conservation status of mammalian carnivores is challenging as they are often cryptic and usually occur at naturally low densities (Linkie et al., 2007; Balme et al., 2009). In Borneo's forests, the challenge is even greater due to difficult terrain, dense vegetation, and poor accessibility (Mohd-Azlan, 2009). Nonetheless, as carnivores in Borneo are threatened by deforestation, degradation and fragmentation of natural habitats (Curran et al., 2004; Poffenberger, 2009; Mathai et al., 2010), and indiscriminate hunting, it is important to generate relevant and sound information on carnivore distribution, abundance, population trends, habitat use, and other ecological measures. The identification and application of appropriate data collection and analytical techniques is therefore crucial, as techniques vary in advantages and limitations (e.g., Wilson & Delahay, 2001; Davison et al., 2002).

One of the most commonly used approaches in the study of forest mammals, including Bornean carnivores, is to conduct transect surveys to address a variety of questions. Unfortunately, much time, effort, and resources are invested in such surveys, with little increase in our understanding of the distribution, status, and biology of these species. In this paper, we discuss the suitability of transects for the study of carnivores in Borneo. We describe different types of transect surveys as well as analytical techniques for data from these surveys. Assumptions to be met while collecting and analysing data are presented, as are the consequences of violating these assumptions. Since Bornean carnivores are essentially unstudied in this depth, the issues are discussed with reference to general survey principles with examples from a wide variety of mammals. It is hoped that this paper will help future researchers make informed decisions about what parameters to estimate, data collection and analytical techniques for transect data, and to avoid common pitfalls. While we focus on the study of carnivores in the rainforests of Borneo, many of the issues are relevant for studies of these animals, and of other taxa, in similar habitats elsewhere.

***What are transect surveys*?** — A transect, in its most general sense, is a predetermined line (though the term is often used even when the route is not predetermined), which may be a road, trail, river, or a line selected for some reason. A transect survey involves travelling along this line and recording qualitative or quantitative observations, depending on the objectives of the study. Whether or not a study employs a probability-based study design (i.e., all parts of the study area have a predetermined probability of being surveyed) has important implications for how the information can be used and what inferences can be drawn. When studies focus on estimating population parameters (or indices thereof), aspects of good study design such as replication and randomisation, as well as satisfying of assumptions of the analytical approach are so critical for robust and reliable inference that these parameters are not worth estimating if the assumptions are not at least almost met.

Transect surveys can be classified based on the mode by which they are conducted:

***Walks*.** — Transect walks are conducted by one or more observers walking slowly through the habitat, continuously searching all vegetation storeys relevant to the species being surveyed while remaining alert for the sounds of dropping fruit, vegetation displacement or calls (Duckworth, 1998). When conducted at night, observer(s) use head torches to scan for animals' body shapes or eye-shine, though not all species have a reflective tapetum (Duckworth, 1998; Table 1). Following a detection, observers may record pertinent data (e.g., time, group size, height, substrate; depending on the questions being addressed) and move on, or stop to observe behaviour for as long as possible (e.g., to record feeding); observing behaviour is especially important for poorly known species.

Encounter rates of Bornean carnivores during diurnal transect walks are typically very low (see Table 1 and Mathai et al., 2010). Because most species are nocturnal, encounter rates are usually much higher for night walks. In many unlogged areas, however, night walks are hindered by the lack of roads and trails, the uneven terrain which makes walking noisy and requires the focus of the surveyor to move from seeking animals down to the floor to prevent stumbling (Mathai et al., 2010), and the dense vegetation which hinders effective observation.

***Drives*.** — Transect drives are usually conducted at night from slow-moving vehicles with observers sitting in the back, equipped with high-powered torches (Mohamed et al., 2009) and recording detections of live animals and road-kills. Transect drives could also be conducted by day, though the range of species recordable and the number of species with frequent records would be much lower.

Typically, encounter rates per unit time are greater with night drives than with night walks, as more ground can be covered. However, encounter rates per unit distance may not be greater with night drives as increased speed and vehicle noise may cause animals to be missed. Also, drives are obviously restricted to accessible roads, whereas walks can be conducted both on and off roads.

***Boat rides*.** — There is little information from surveys done by boat in Borneo, perhaps due to the difficulty in negotiating rivers by night. By day, they are not useful as there are few incidental reports from surveyors or even from local hunters of carnivores being seen from boats during the daytime.

IMPORTANCE OF CLEAR STUDY OBJECTIVES

Regardless of the survey tool being used, it is essential to first clarify the objectives of the study or monitoring programme (Nichols, 2001; Pollock et al., 2002; Gotelli & Ellison, 2004; MacKenzie et al., 2006). Study design and subsequent analytical techniques should be question-driven: What is the point of the study? What kind of information is needed and what kind of inference is to be drawn? How will data obtained from the study provide this information (Pollock et al., 2002)? A key decision at this stage is to decide if population or higher-level parameters need to be estimated, and if so, which one(s): Distribution and occupancy? Relative abundance? Absolute abundance and density? This decision should be based on matching information requirements with available resources (e.g., person power, technical and field skills, budget, equipment, time), and constraints (e.g., availability and accessibility of sites, weather; Karanth et al., 2002).

In light of the objectives, each possible method should be evaluated for its suitability. If the objective is to make inferences on natural history, are the necessary observations best recorded from transects? If density or occupancy are the state variables of interest, are transects the best way to obtain the required data? Unfortunately, in many past studies in Borneo (and elsewhere), investigators have collected data without foresight to the proper technique(s) necessary to draw the required inference(s). There is a critical need to shift from this to the more focused approach of determining the questions first, and then deciding on which tool/technique is best suited to answer these questions.

NATURAL HISTORY OBSERVATIONS

Natural history observations entail the detailed documentation of what is seen as it occurs in its natural setting and thinking about what it means then and afterwards. This could be done by any form of transect survey, and it is useful to apply 'purposive' transect selection (i.e., locating transects where the target species is suspected to be more likely to occur). Standardisation in recording natural history information to minimise subjectivity in observation, documentation, and interpretation should be advocated, when possible. At present, natural history records are subjective interpretations based on familiarity with the species or habitat concerned.

Table 1. Carnivores that may be detected by transect surveys in Borneo. The assessments are inferred from observations of the species, or related species, elsewhere (References: Giman et al., 2007, Hearn et al., 2010, Mathai et al., 2010, Wilting et al., 2010, Azlan Mohamed pers. comm., Jason Hon pers. comm., Joanna Ross pers. comm., Than Zaw and Saw Htun pers. comm., and personal experience of the authors).

	Walks		**Drives**		**Boat Rides**		**Reflective Tapetum**	**IUCN Red Listing**
	Day	**Night**	**Day**	**Night**	**Day**	**Night**		
Sun Bear *Helarctos malayanus*	O	O	O	O	O	O	Weak to moderate	VU
Yellow-throated Marten *Martes flavigula*	O	U	O	U	O	U	Weak to moderate	LC
Malay Weasel *Mustela nudipes*	O*	U	O*	U	O*	U	Unknown	LC
Bornean Ferret Badger *Melogale everetti*	U	O*	U	U	U	U	Unknown (probably moderate)	DD
Sunda Stink Badger *Mydaus javanensis*	U	O*	U	O*	U	U	Moderate to strong	LC
Otter (Lutrinae), not usually identifiable to species	O*	O*	U	U	O*	O*	Moderate/Strong	**
Banded Linsang *Prionodon linsang*	U	O*	U	U	U	U	Strong	LC
Malay Civet *Viverra tangalunga*	U	O	U	O	U	O*	Strong	LC
Common Palm Civet *Paradoxurus hermaphroditus*	U	O	U	O	U	O	Strong	LC
Masked Palm Civet *Paguma larvata*	U	O	U	O	U	O*	Strong	LC
Small-toothed Palm Civet *Arctogalidia trivirgata*	U	O	U	O	U	O	Strong	LC
Binturong *Arctictis binturong*	O	O	O	O	O	O	Strong	VU
Otter Civet *Cynogale bennettii*	U	O*	U	O*	U	U	Strong	EN
Banded Civet *Hemigalus derbyanus*	U	O	U	O*	U	U	Strong	VU
Hose's Civet *Diplogale hosei*	U	O*	U	U	U	U	Strong	VU
Short-tailed Mongoose *Herpestes brachyurus*	O	U	O	U	U	U	Unknown (probably weak)	LC
Collared Mongoose *Herpestes semitorquatus*	O	O*	O	O*	U	U	Unknown (probably weak)	DD
Sunda Clouded Leopard *Neofelis diardi*	O*	O*	U	O*	U	U	Strong	VU
Marbled Cat *Pardofelis marmorata*	O*	O*	U	O*	U	U	Strong	VU
Bay Cat *Pardofelis badia*	U	U	U	U	U	U	Strong	EN
Flat-headed Cat *Prionailurus planiceps*	U	O*	U	U	U	O*	Strong	EN
Leopard Cat *Prionailurus bengalensis*	U	O	U	O	U	U	Strong	LC

O = Occasionally detectable, under favourable conditions (usually those preventing meaningful quantitative analysis, such as using roads, rivers and good-visibility paths as survey lines), frequently; O* = Very occasionally detectable, but not often enough to allow any meaningful status assessment; U = Unlikely to be detected; ** = all possible species are at least Near Threatened

Such a need for opportunistic noting of natural history remains very high for many Bornean carnivores and such subjective interpretations may remain the best system for poorly understood species until they are the subject of specific research. However, given the opportunistic nature of such field work, recording data accurately, not influencing behaviour and, as far as possible, objective interpretation of observations are vital. Nonetheless, accurate identification of observed species is a rarely considered assumption that is often violated in natural history surveys (Than Zaw et al., 2008; Duckworth et al., 2009). Measures should be taken (e.g., viewing museum specimens, photographs, observations of captive animals) prior to conducting field observations to ensure accuracy in identification, and it must be recognised that some individuals encountered have to remain unidentified.

How useful are transect surveys for carnivores in Borneo for this purpose? Diurnal or nocturnal walks conducted from random (as defined below in the sub-section *Spatial sampling: survey design*) transects in the forest result in very few observations even after huge effort. If night walks are conducted along non-random transects such as roads or established paths, encounter rates of nocturnal species may be much higher due to superior viewing conditions. However, species encountered frequently are relatively well known in terms of natural history and it needs to be seriously considered whether the huge investment of time, labour, and funds are well spent to elicit further information about the natural histories of species mainly (except Binturong *Arctictis binturong*; Table 1) classified as Least Concerned on *The IUCN Red List of Threatened Species*.

A more pragmatic approach may be to document such observations while conducting transect walks or other fieldwork for other taxa such as primates, which are more appropriately studied using transects (Johnson et al., 2005; Marshall et al., 2008). Many such incidental records of small carnivores may not be documented by those whose interests are with other animals, and—such people being less likely to have undertaken pre-observation investigation into identification—reliability requires particular consideration; record photographs are of great value. There is also a need for mechanisms whereby such incidental records can be collected and shared with those who require the data, such as ‘wiki’ platforms and citizen science websites.

QUANTITATIVE OBSERVATIONS FOR STATISTICAL ANALYSIS

Sampling designs are important for estimating various population- or higher-level (e.g., landscape-scale) parameters. Whatever the question, the use of quantitative observations for statistical analysis requires good study design. Wildlife studies using transects (and most other tools) need to consider two issues that confound the relationship between observations (data) and reality—spatial sampling and detection probability (also referred to as detectability, detection bias, or partial observability; Thompson et al., 1998; MacKenzie et al., 2002; Pollock et al., 2002; Williams et al., 2002; MacKenzie et al., 2006).

Spatial sampling: survey design. — The first step in designing a study is to identify the target population clearly and to ensure that the sampled population coincides with this (Williams et al., 2002). Typically, the entire area over which inference needs to be drawn cannot be surveyed. Hence, sample units need to be carefully defined, selected probabilistically, and surveyed. The results of these surveys are then used to draw inferences over the entire area (Thompson, 1998; MacKenzie et al., 2002; Pollock et al., 2002; Williams et al., 2002; MacKenzie et al., 2006). Thus, it is important that what was observed (sampled) is representative of what was not observed. This is ensured by randomisation and replication of sample units while designing the study, as detailed in the following paragraph.

In terms of transect surveys, randomisation refers to the random positioning of transects with respect to the spatial distribution of animals within the survey region (Buckland et al., 2010b). Practices such as sampling along roads, rivers or contours, or establishing transects based on convenience, all violate randomisation, thus precluding extrapolation of inferences from the surveyed area to the study area (Buckland et al., 2010b). Haphazard sampling (e.g., ambling about opportunistically in the forest) does not constitute randomisation and very likely violates assumptions of sampling theory. Replication refers to the need for multiple sample units (e.g., transects) within a study area. High replication is important as few replicates, though randomly located, may all pass through atypical (e.g., high density) areas just by chance (Buckland et al., 2010b). Replication is also required for estimating the variance of encounter rate across transects, one of the three components of the variance of density in distance sampling (Buckland et al., 2001, 2010b).

Probabilistic sampling schemes include simple random sampling (i.e., each sample unit in the study area has equal probability of selection for surveys), stratified random sampling (with effort allocated optimally across strata given stratum-specific sizes, variances and per-unit costs), systematic sampling with a random start (i.e., the first transect is located randomly, subsequent transects are spaced at even intervals), cluster sampling and various kinds of adaptive sampling; all use randomisation and replication as foundational elements of the sampling design (Cochran, 1977; Thompson, 1998; Williams et al., 2002). Program DISTANCE (Thomas et al., 2009) has a useful survey design module that enables most of these sampling schemes to be implemented, if geographical information systems (GIS) layers of the study area are available.

Detection probability: modelling the detection process. — The need for estimating detection probability stems from the typical inability to detect every individual animal of the survey species in the sampled area (Nichols & Karanth, 2002; Pollock et al., 2002; Williams et al., 2002; MacKenzie et al., 2006). Typically, a count statistic is obtained representing some unknown proportion of true abundance, and ancillary data (e.g., distance from transect line) and various other methods are used to estimate the probability of detecting an individual that is present within the surveyed area within a specified period. The count can then be divided by the estimated detection probability (and the proportion of area surveyed) as per the canonical estimator of abundance (Nichols & Karanth, 2002; Williams et al., 2002; Pollock et al., 2002; MacKenzie et al., 2006) so that true abundance or density may then be estimated. Studies that do not consider detection probability (i.e., those that rely on indices of abundance) implicitly or explicitly assume that detectability is perfect (i.e., equal to one) or, at least, constant. These assumptions rarely hold (Anderson, 2001; Williams et al., 2002; Rota et al., 2011), because detectability is almost always less than one, and, more importantly, varies unpredictably over time and between sites, strata, species, and individuals of the same species. When detection probability is not estimated, then estimated differences in the count statistic may simply reflect differences in detectability rather than genuine differences in the state variable (Anderson, 2001; Williams et al., 2002). Depending on the relationships between detectability, abundance, and features such as habitat, patterns in detectability may induce spurious patterns or obscure true patterns in abundance over space or time (Jathanna et al., 2008). This is especially true where individuals are difficult to detect (i.e., they are shy or elusive) or survey effort is limited (Gu & Swihart, 2004)—issues very relevant to Bornean carnivores. Detectability also needs to be considered in occupancy estimation because the species may be present but undetected in sites, possibly as a function of site or time-varying attributes such as habitat or weather (MacKenzie et al., 2002; Gu & Swihart, 2004; MacKenzie et al., 2006). Similarly, estimation of species richness may be biased because some (variable) proportion of species is not detected during surveys. The only rigorous approach to estimating population or higher-level parameters is to incorporate estimation of detection probability for both spatial and temporal comparisons (Anderson, 2001; Pollock et al., 2002). Various approaches exist to estimate detectability: in capture-recapture modelling, detectability (capture probability) is estimated from the frequencies of recaptures of different individuals across multiple occasions (Amstrup et al., 2005), while in distance sampling, detectability is estimated from the spatial distribution of detections away from the transect line or point (Buckland et al., 2001).

Line transects for the estimation of density. — In terms of carnivores in Borneo, reliable estimates of abundance or density (number of animals per unit area) are helpful as they can indicate key conservation areas, population trends over time, responses to land-use change (particularly logging and conversion to monoculture plantations) and other threats, assessment of extinction risk, and assessment of the effectiveness of conservation measures and management strategies (Pollock et al., 2002).

When estimating densities, the goal is to reduce sources of bias through standardised survey design and protocols, and by reliably estimating detection probabilities (Kissling & Garton, 2006). Detection probability may vary across species, space (or habitat type), time (or environmental conditions), and observers (MacKenzie et al., 2002; Pollock et al., 2002; Kissling & Garton, 2006). The Kelker strip, an early approach to ensure that detection probability, p, is equal to one, used a fixed-width strip, narrow enough that all animals inside the strip were believed to be detected (determined by examining a histogram of detections at different distances), whereas animals outside the strip were ignored. For carnivores, where sample sizes are small to begin with, discarding observations outside narrow strips wastes valuable data. Strip-width choice was also subjective and ambiguous (Buckland et al., 2001, 2010a; Marshall et al., 2008). The alternative to fixed-width sampling is to choose a very wide strip so that not all animals are detected, and estimate the detection probability within a specified distance from the line (Buckland et al., 2001). Methods based on animal-observer distance such as modifications of Kelker's Method, and on estimating effective strip width based on mean perpendicular distance (King's Method) have no solid mathematical basis (Buckland et al., 2010a), but continue to be used even when better alternatives exist. Reliable density estimates are possible by combining good survey design with improved field and analytical methods (Buckland et al., 2010b).

Distance sampling. — The two most commonly used forms of distance sampling are line transect and point transect sampling, though we focus here on line transect distance sampling, because carnivore encounters are unlikely to be high enough to make point counts viable. Distance sampling is based on the idea that probability of detecting an animal depends on its distance from the transect line or point (Buckland et al., 2001). The term "line transects" should be reserved for this approach based on distance sampling though it is widely and inappropriately used for other things including ambling about in the general area without any predetermined route.

For each encounter along the transect, perpendicular distance (or radial distance and angle of detection) from the transect to the animal is recorded, and detection probability (up to a specified distance) is then estimated by modelling the decline in observations (i.e., the process of how detectability changes) with increasing distance from the transect centre line (Buckland et al., 2001). One or several models (detection functions) are fitted to the observed distances and information criteria (e.g., Akaike's Information Criteria [Akaike, 1973]) may be used to select an appropriate model (Buckland et al., 2001). Under the best approximating model of the detection process, the number of groups seen n, the estimated proportion of groups detected $\hat{p}$, the estimated group size $\hat{s}$, total length covered l and maximum distance surveyed w, are then used to calculate density $\hat{D}$, as

$$\hat{D} = \frac{n\hat{s}}{2wl\hat{p}}$$

along with standard errors and confidence intervals (Buckland et al., 2001). Program DISTANCE is software widely used to analyse data from distance sampling surveys and standard distance sampling methods are detailed by Buckland et al. (2001).

Robust density estimates from distance sampling require several assumptions to be met. Meeting most of these assumptions when surveying carnivores in Bornean forests is challenging. The assumptions are:

1. **Transects are located randomly with respect to animal distribution**: Often incorrectly interpreted as animals being randomly distributed in space, this assumption is necessary for two distinct reasons. The first is the general spatial sampling requirement of randomisation, enabling density estimated along transects to represent density in the study area. The second reason, particular to distance sampling, is that the probability of the true location of animal (clusters) at different distances from the transect line is assumed to be uniform (note that this is not the same as saying that animals are randomly distributed in space, but that, since transects are positioned randomly with respect to animal distribution, there is no reason for animal distribution to be more [or less] at particular distances from the line), allowing estimation of the proportion missed, using the fitted detection functions. If animals redistribute themselves in response to the transect line (e.g., linear increase, decrease, peaks at certain distances, asymptotes) it is not possible to estimate detectability.

   Encounter rates are typically low when surveying carnivores in the Bornean rainforest, particularly when random transects are walked across the habitat. It may therefore be tempting to use established paths, ridges, roads and rivers as transect lines to maximise numbers of encounters. This violates both issues mentioned above: roads, rivers, trails, and ridges are never randomly placed with respect to animal distribution (roads and trails, for example, often tend to follow valley bottoms or ridgelines) and carnivores may show strong responses to roads and rivers.

2. **Animals directly on the line are always detected**: When this assumption is violated, some individuals or clusters on or close to the transect line are not found. Thus the detection function is overestimated and population densities are underestimated, as more animals are missed than is thought (Duckworth, 1998).

   In Borneo, vegetation is dense, thus allowing many animals, particularly carnivores, to avoid detection, even when on the line. Several layers of forest canopy vegetation directly above the transect centre line may increase difficulty in detecting individuals in upper canopy layers. Animals with eye-shine may be detected on the line with night transects when not obscured by these vegetation layers; however, species that lack reflective tapetums or individuals that do not look in the direction of the light may be missed.

   Another problem with using distance sampling for carnivores in Borneo is estimating the proportion of animals available for detection. Given that many carnivores in Borneo sleep in enclosed places (such as hollow trees, rock cavities, and burrows), unless activity of the species is known in some detail, it is not possible to calculate true population density in the area. What is calculated is the density of animals available for detection (i.e., not sleeping in a hollow tree or burrow, or not in any other way having a zero probability of detection even if on the midline). Correcting for 'availability' would require an estimate of the proportion available for detection, perhaps from telemetry studies. This information may be difficult to obtain, especially if this proportion changes during the duration of the walk, as is likely during walks lasting several hours.

3. **Animals are detected at their initial location, prior to any movement in response to the observer**:
   Most carnivores (equipped with superlative hearing, sight, and smell) detect observers before observers detect them, and exhibit responsive movement, most commonly away from the observer and the transect centre line. Where hunting is common, many animals flee at the first detection of human beings, again violating this assumption. Depending on the scale, speed, and stealth of these evasive movements, one of two problems in the estimation of density may occur. First, if the animal is detected, but only after it has moved a certain distance, then the encounter rate estimate remains unaffected but detectability will be underestimated (because measured distances would be greater than they should have been). Second, if an animal on or very close to the transect centreline moves away and is not detected at all, then the detection function remains unaffected but the encounter rate will be biased downward. In either case, the resulting estimate of density will be biased negative.

4. **Distances are measured accurately**: In the Bornean rainforest, poor visibility (particularly in disturbed forest) and difficult terrain often impede the accurate measurement of distances. This is especially so when there are two or more individuals, as in the case of Yellow-throated Marten *Martes flavigula* (see Mathai et al., 2010) and otters (Wilting et al., 2010), in which case measurements need to be made to the group centre (Buckland et al., 2010b). In such cases, dense vegetation may cause some of the group members to be overlooked, thus causing group centres to be incorrectly chosen (see Marshall et al., 2008). When distances are estimated visually, it often leads to rounding-off and heaping on the line and at certain distances (e.g., 50 m, 100 m). Depending on the observers and habitat, visual estimates of distance may either underestimate or overestimate true distance, thus causing positive or negative biases in estimated density, respectively. It is therefore essential that surveyors are well trained in the use of, and equipped with, equipment such as laser range finders and compasses.

Additional considerations (though not assumptions) for reliable density estimation include:

1. **Sufficient encounters are required for the estimation of a detection function**: At minimum, 40 encounters are required to estimate parameters reliably from distance sampling, though 60–80 observations give much better precision (Buckland et al., 2001). This is usually impractical for carnivores in Borneo. In most situations, substantial effort is required to obtain 40 observations of one species.

   Investigators often pool data to increase observations to enable modelling of the detection function. Data are pooled over time (e.g., years), sites or species to model the detection function. Yearly, site-wise or species-specific encounter rates are then used with this global detection function to generate corresponding year-wise, site-wise or species-specific density estimates. Pooling assumes that detectability does not vary appreciably between the components pooled, and possibly, compared. Thus density estimates derived from the use of pooled detections functions are equivalent to using encounter rate as an index of density, and therefore need to be treated with just the same caution. Even in rare cases where pooling is justified, these methods will not help if even the total of pooled detections is still too low to model detection functions, as is often the case with Bornean carnivores.

2. **Minimising variance of detectability: sample size, stratification, covariate modelling:** A density estimate derived from distance sampling combines three different estimates, each with its own uncertainty: the estimate of encounter rate, the estimate of detectability, and the estimate of cluster size. Thus the uncertainty (expressed as variance and related quantities such as standard error, coefficient of variation, confidence interval) around the point estimate of density combines these three sources of uncertainty (Buckland et al., 2001).

   The uncertainty or variance associated with detectability (also referred to as variance of the detection function or variance of effective strip width) can be minimised by increased number of detections (Plumptre, 2000), which enhances confidence in the estimated detection function. One way of increasing detections is by lengthening transects. However, due to the difficult terrain in the Bornean rainforest, long transects will tire observers, and may compromise their ability to detect animals. Thus there is a trade-off between minimising transect length in difficult terrain and maximising numbers of detections. Based on our experience, in mountainous terrain, transects longer than 2–3 km are not recommended.

   Stopping and searching every 25 m or so along the transect, and at locations such as fruiting trees or waterholes, to look/listen carefully for animals, is an efficient way to detect carnivores and increase number of encounters in mountainous Bornean rainforests. However, stopping and searching for detections may artificially inflate detections as animals move in (from outside the range of visibility from the transect line) to within the distance where they will be detected. This natural movement (i.e., not influenced by the presence of the surveyor) of animals towards the transect line is not balanced by animals that move away from the transect line (and hence are not detected). Stopping and searching for detections may thus weaken the validity of quantitative results. However, observers may still go 'off effort' to stop and confirm observations provided that additional detections during this time are not included in the analysis.

   Numbers of detections can also be increased by repeatedly surveying the same lines; however, investigators must be careful to ensure that during analysis, the effort invested in each transect reflects the multiple temporal replicates, and that each walk is not treated as an independent transect, which would constitute pseudo-replication (Hurlbert, 1984). For example, if a study used 20 transects, each 2-km long and each walked 4 times, the effort expended should be 20 transects × 8 km per transect = 160 km. What is (incorrectly) done very often is to specify 20 × 4 = 80 transects, each with 2 km to give a total effort of 160 km. Moreover, if temporal replicates are used, investigators should ensure that the number of walks is balanced across all transects, so that variation in detectability and encounter rates across space is not confounded with effort.

   When an overall detection function is estimated without considering detectability conditions, what is obtained is a weighted mean detection function (mean of all the detection conditions, weighted by the numbers of detections in different conditions). The detection functions used in program DISTANCE are known to be 'pooling robust', that is, the fact that each is actually composed of different functions, will not cause a bias in estimated overall detectability and density (Buckland et al., 2001), as long as this global detection function is not subsequently used with finer-scale (e.g., habitat or period-specific) encounter rates to obtain fine-scale densities which are then used to examine patterns across space or time, as discussed above. However, the uncertainty associated with the pooled detection function will be higher if the data were collected under different detectability conditions. If detectability is expected to vary significantly between discrete strata (such as vegetation types) stratification may be employed to estimate stratum-specific detection functions, and these can then be combined to generate a more precise estimate of overall density. Similarly, if detectability varies as function of a covariate measurable at each detection (e.g., misty or clear; time of day; canopy closure), detectability can be modelled as a function of the covariate using the multiple covariate distance sampling engine available in program DISTANCE (Buckland et al., 2004).

3. **Minimising variance of encounter rate: number of transects, stratification**: Reliable estimation of variance of encounter rate (over space) requires survey of at least 20 transects (Buckland et al., 2001); even more transects reduce the variance of encounter rate, which is usually the biggest contributor to variance of density (Fewster et al., 2009). Transects should be far enough apart to achieve independence from each other: the requisite distance depends on the species. Stratification can also be used to account for variance in encounter rates across transects situated in different habitats by using stratum-specific encounter rates to estimate overall mean density, thus increasing precision of the estimate. If there are known gradients in density within the study area, cluster sampling (orienting transects parallel to the gradient) can help minimise variance of encounter rate.

4. **Speed of walking, noise, number of observers, line clearing**: An often underappreciated issue when carrying out transect surveys is the speed of movement: because observers are moving points detecting other moving points in space, walking too slowly or stopping for appreciable lengths of time will cause detections to accumulate closer to the line, causing a positive bias. Conversely, walking too fast compromises the ability to detect animals, even if they are on the transect line, and causes too much noise, leading to evasive movements (and animals either being undetected or assigned a distance from the line larger than they should have), leading to negative biases. Observers should walk at a comfortable pace so as to make as little noise as possible, yet be able to scan the area for animal movements. Brief one minute stops, every 25 m or so to scan may be necessary, particularly in mountainous rainforests, but must be avoided where possible or minimised, as discussed earlier.

   Additional observers increase noise, so surveys should be conducted alone except where this is too risky, such as in remote areas. Having observers conduct the survey separately also reduces many people's psychological tendency to be careless about making noise when in a group. During survey programmes using multiple observers, the individuals may vary in their detection abilities. If the variation between observers is considerable, this information (i.e., observer identity for each detection, given sufficient data per observer) can be used in the modelling to provide more precise estimates.

   Although clearing transect lines to some extent may be required to allow observers to pass noiselessly through vegetation, such clearing may attract or repel animals from the line, changing their natural distribution (and thus observed perpendicular distances). In addition, excessive clearing will artificially inflate detectability on the line so that animals on the line but far ahead of the observer are detected when they would not normally be. Hence, clearing of transects is not recommended.

5. **Estimating densities from signs**: When signs such as tracks or faeces can be accurately attributed to target species, they may, in theory, be used to estimate densities of animals via line transect surveys (Plumptre, 2000; Wilson & Delahey, 2001). This, however, requires a high proportion of contacts identifiable to species with very few errors. At present, this is impractical for Bornean carnivores, with the exception of Sun Bear (*Helarctos malayanus*). For terrestrial carnivores other than Sun Bear, sign-based surveys from random transects in the forest will first require careful pilot testing on the ability to identify signs, and defining where areas of overlap occur between ecologically and behaviourally similar species where their signs can be confused (see Steinmetz & Garshelis, 2008). Moreover, biases owing to seasonal and habitat effects (such as weather and substrate type) need to be minimised by careful study design or be dealt with through covariates for comparisons. While distance sampling can provide accurate estimates of the density of the sign, estimation of animal density remains problematic and unreliable. Given the difficulty in reliably estimating (species, site, habitat, and season-specific) deposition and decay rates of signs (Plumptre, 2000; Wilson & Delahey, 2001), as well as the uncertainty associated with these estimates, the use of signs to estimate carnivore density is impossible at the present time. In addition, using tracks to identify carnivores in Borneo other than Sun Bear may not be practical as it is difficult to identify so many potentially co-occurring carnivores to species from tracks (Mathai et al., 2010). Finally, carnivore faeces are seldom encountered during transect walks through the forest with the exception of, apparently, Malay Civet (*Viverra tangalunga*) latrines (Mathai et al., 2010).

OTHER POSSIBLE USES OF TRANSECTS

Given the aforementioned limitations, line transects are unlikely ever to be useful to estimate densities of Bornean forest carnivores. Could transects have any other uses in recording quantitative data for statistical analysis? In the following sections, we discuss the use of transects as a stand-alone technique for the estimation of encounter rates, and as a tool used in combination with other tools for the estimation of occupancy. We then discuss transects when used in combination with other techniques for estimating diversity indices and species distribution modelling.

Transects for the estimation of encounter rates. — When detection functions cannot be estimated using distance sampling, a frequently used approach is to assume that detectability is constant (over time, space or species) and then estimate encounter rates over unit length covered or unit time spent (Wilson & Delahey, 2001) as surrogates of abundance or density. Both direct observations and signs (e.g., tracks or faeces) are used. Encounter rates can either be count-based (e.g., number of Sun Bear faeces km^{-1} walked) or frequency-based (e.g., proportion of 1-km segments with Sun Bear faeces; Karanth & Kumar, 2002). Alternatively, the inverse can be used, where survey time (or distance) is divided by total number of contacts (e.g., Duckworth et al., 1992).

The underlying assumptions when using encounter rate (or any other relative abundance index) to indicate abundance is that there is a linear relationship between the estimated measure and population density, and that detectability is constant across the units being compared (e.g., different years, places, and/ or species). As discussed earlier, this assumption rarely holds: detectability clearly varies across space and species, and even over time within the same area. Hence, so-called 'relative abundance indices' should not be used, as they have no direct biological meaning (Duckworth, 1998; Anderson, 2001; Williams et al., 2002). If these measures must be used, they must be referred to as encounter rates or something similar, to avert any possible suggestion of proportionality to abundance. Such rates may sometimes be used because badly estimated densities (when one or more of the key assumptions are seriously violated) are arguably more misleading than simple encounter rates. With the former, it is often difficult for readers to assess whether assumptions have been reasonably met and how reliable the estimates are, while with indices of encounter frequency, readers are explicitly alerted that variable detectability may have induced spurious patterns or obscured true patterns. Thus, where density estimation using distance sampling or some other approach is not feasible for one or more reasons (as is likely for Bornean carnivores in most cases), encounter rates may be reported with the necessary caveats, especially if provided with adequate contextual detail such as locations of transects, habitat attributes, season, time of day and duration of surveys, speed of movement, among others, and where possible, split by factors that appear to influence the index value.

Occupancy estimation from transect data. — Estimation of occupancy (the proportion of area occupied by a species, also the probability that a 'site' is occupied by the species), has gained enormous popularity in recent years, as it requires less effort and is cheaper to implement than density estimation (MacKenzie et al., 2002, 2006). The approach can be used in initial surveys of poorly known or rare species to generate rigorous baseline estimates of occupancy, while also allowing investigators to answer ecological and conservation questions on what determines the probability of occurrence. Occupancy is most relevant when abundance straddles the zero individuals—some individuals boundary (at approximately the home range scale), and thus is very relevant to carnivore studies in Borneo. Another advantage of occupancy modelling is the explicit focus on estimating detectability (p, here defined as the probability of detecting a species in a site, given that it is present), and the ability to model occupancy and/ or detection probabilities varying as functions of habitat or disturbance covariates.

The basic sampling scenario in occupancy surveys involves looking for the presence of target species (from sightings or signs) in a number of sites for a distinct number of occasions in time at each. Such detection/non-detection data can be derived from many sources such as transect surveys (direct observation or sign), live trapping, camera trapping (MacKenzie et al., 2006, Nichols et al., 2008) and even local markets and, in theory, informants (if issues of the reliability of second-hand information can be addressed). Detectability is estimated from the frequencies of detections at each site over multiple occasions, similar to capture–recapture modelling. As with other statistically rigorous approaches, occupancy estimation comes with its set of assumptions, and these apply to any technique used to obtain the data, including transect surveys.

Issues related to design of occupancy surveys such as selection of sampling units, timing of repeat surveys and allocation of survey effort, are discussed by MacKenzie & Royle (2005). When detections comprise direct sightings during transect surveys, frequency of detection tends to be extremely low for carnivores in rainforests. For a given level of precision, the required effort is inversely proportional to detection probability, so that when detectability is very low (as for Bornean carnivores based on direct sightings), the required effort will usually be far too high to be practically achievable. Detectability might in principle be higher when detections are based on encounters of species' signs (e.g., scats, tracks) during transect surveys, but this requires reliable species identification from signs, which is unlikely for most carnivores in Borneo (except Sun Bear; see Mathai et al., 2010). DNA-based species identification from faeces or hair could be used (Wilson & Delahay, 2001; Heinemeyer et al., 2008), should sufficiently fresh samples be obtained, and funds and technical skills available for laboratory genetic methods, but is likely to prove too expensive for most projects. Since such samples are seldom encountered during transect walks through the forest, roads and trails are more often used due to convenient access, ease of travel and sightability of signs (Heinemeyer et al., 2008). Using roads and trails, however, violate assumptions required for addressing other questions, as discussed in previous sections of this paper. Thus, transect-based occupancy surveys may have limited use as a stand-alone tool for studying Bornean forest carnivores.

Estimation of diversity indices. — Species richness and diversity indices (e.g., Shannon-Weiner and Simpson's indices) are often measured in mammal studies in Borneo (sometimes using sightings from transect walks) and used as a surrogate for the health of habitats and assemblages. Typically, these measures do not consider detectability (here, the proportion of species present in an area that are actually detected, or the average probability that a species is detected by a survey). Because detectability can vary over space and time in systematic but unpredictable ways, it is crucial to estimate the proportion of species missed and its precision. There are estimators of true species richness, based on either capture recapture-type modelling (Williams et al., 2002) or rarefaction (Magurran, 2004). In the case of diversity indices, observed counts of each species in a sample are clearly determined both by the true abundance of each species as well as differences in individual-level detectability across species. While detectability can be estimated and included in estimates of species richness, diversity indices cannot be corrected as the abundance of unobserved species is not known.

Even if detectability could be accounted for, diversity indices are often not useful in conservation terms and can even be very misleading. First, species richness and diversity may be informative when species richness of the group is reasonably large, as in the case of plants, birds, and invertebrates, but is unlikely to be useful in the case of carnivore assemblages, which consist of maximum two dozen species. Second, species richness and diversity may not be useful for monitoring biodiversity over time as changes in true species richness are likely to occur less frequently than major changes in abundance. Finally, diversity indices and species richness treat individuals of common species and rare species as equals. Thus, when an area is disturbed, many generalist species may move in at the expense of a few, rarer, forest-obligate species. This results in higher species richness and diversity, even though the habitat and wildlife community has a reduced conservation value. Species differ markedly in their inherent value and in their conservation urgency. Species may be localised but not threatened, widespread but seriously threatened, localised and seriously threatened, widespread and not threatened, or anywhere on this two-dimensional continuum. The lumping together of all this heterogeneity to provide one 'soundbite' figure is widespread, and continues to be one of the biggest pieces of intellectual fraudulence in conservation (please see Hurlbert, 1971 and Devictor & Robert, 2009 for more discussion on this issue).

Species distribution modelling. — Models of species distribution are used to describe the geographic distribution of plants and animals by quantifying and extrapolating species-environment relationships (Guisan & Thuiller, 2005). Species distribution models fall into three main categories: those that use presence-only data (e.g., maximum entropy; Philips et al., 2006), those that use purported presence-'absence' data but do not consider imperfect detection (e.g., logistic regression), and those that use detection/non-detection data and account for imperfect detection (e.g., occupancy modelling). For difficult-to-detect species such as carnivores in Borneo, preferred approaches may be either models using detection/non-detection data while accounting for imperfect detection or those that use presence-only data (see Rota et al., 2011 for details), though as with all presence-only ecological data (see e.g. Yackulic et al., 2013), great care is needed with the spurious patterns readily induced. Whichever approach is used, transects might sometimes warrant use as one of a number of techniques in the sampling process, though—given the inherent low detection rate—definitely not a stand-alone method for Bornean forest carnivore community studies.

CONCLUSIONS

Transect surveys, though an important tool in the study of species such as primates and ungulates in many parts of the world, are of very little use as a stand-alone technique for the study of carnivores in Borneo. The elusive and secretive nature of carnivores, coupled with the difficult terrain and poor visibility within the Bornean forest, leads to very few encounters after huge expenditure of time, money, and labour. These resources could be better spent on other methods such as (well-designed) camera trapping, live trapping or radio telemetry studies, which yield better and more reliable data.

For obtaining information on the natural history of carnivores, transects do not prove very useful in the Bornean context. Most species encountered with any regularity during transect walks are relatively well understood and are not of high conservation priority. Observations on natural history could be taken when conducting transects for other species, or as incidental observations when setting up cameras or live traps. However, it may be useful to conduct some transects from roads or rivers as there may be opportunities for documenting species of high conservation value. The costs of this as a planned survey method need to be weighed carefully, as opportunities to observe such species are rare and the expenditure for conducting these surveys is high.

At best, transect surveys give estimates of parameters which have little or no conservation value such as encounter rates (though these can aid in understanding conservation concerns, provided there is a reasonable understanding of species natural history and sources of bias in the method), species richness (not very useful for carnivores, in conservation terms) or diversity indices (both flawed and useless, in this context). Should sufficient encounters be obtained (which is generally unlikely), then biased estimates of densities may be estimated by distance sampling along roads, ridges and established paths. These estimates cannot be extrapolated to the larger study area. Should the same 'transects' be sampled over time, then these estimates may be used as an index of abundance along these 'transects' only for comparisons over time.

For low-density and cryptic species such as carnivores in Borneo, occupancy methods using detection/non-detection data may be the most pragmatic approach. Data for occupancy estimation can be derived from a number of sources including transects (focused on non-carnivores). Also, transects can provide presence data for species distribution modelling (although opportunistic/purposive walks are likely to be much better at doing this) and being an "on ground" approach, can aid in the collection of faeces and hair for molecular studies. However, transects should not be the method of choice for any of these sorts of carnivore studies in Borneo, considering the time and resources required for their application, as well as the very limited usefulness of the resulting data. Conservation and research organisations working in Borneo would do well to better direct their limited resources by articulating their objectives clearly and by asking questions that can be reasonably and reliably answered using the best available field and analytical approaches that are affordable within the resources available.

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