The difficulty of estimating population densities of nocturnal forest mammals from transect counts of animals

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INTRODUCTION

Many nocturnal small- to medium-sized forest mammals can be surveyed only by directly sighting or hearing each individual. This is particularly so in tropical regions. Signs (footprints, dung scratch-marks, etc.) are often not identifiable to species (similar species frequently occur together); villagers' identifications are rarely clear enough for research purposes, and the provenance of specimens in markets can rarely be established to satisfactory precision. Assessments of animal status from brief surveys are becoming increasingly important for many conservation purposes. A repeatable methodology for field assessment of the status of nocturnal mammals is needed to allow comparisons, particularly between sites.

Nocturnal forest mammals are commonly surveyed by an observer walking slowly through the area, continuously searching all vegetation storeys with a head-torch for animals' reflecting eyes or body shapes whilst remaining alert for the sounds of dropping fruit, vegetation displacement and calls. Results may be expressed by dividing the survey time by the total number of contacts (e.g. Duckworth, 1992*a*); population densities are sometimes calculated (e.g. Walker & Cant, 1977; Charles-Dominique, 1978; Glanz, 1982). A contact frequency has no intrinsic meaning, but an accurate population density is a feature of biological value; therefore it is clearly desirable to calculate the latter if it is possible to do so. The use of line transect surveys to estimate animal population densities has greatly advanced recently and this paper discusses the possibilities of performing these calculations for nocturnal mammals by assessing whether the assumptions made explicit by Buckland *et al.* (1993) for DISTANCE sampling theory are upheld.

THE DIFFICULTY OF DETECTING ALL INDIVIDUALS ON THE TRANSECT MIDLINE

If detection of mammals on the transect midline falls below 100%, the detectability function starts at an unknown point and densities are underestimated. Many individual nocturnal forest mammals of many species are missed for reasons other than their distance from the transect midline, and so this assumption is not met. Animals can be detected by eye-shine only if they have a reflective tapetum to the eye, are unobscured and look towards the torch. Sighting of the body shape rarely reveals animals unless they are in the open, close to the observer, silhouetted, large or gliding. Detection by ear (of calls, rustles or dropping fruit) is only usual for noisy species, which are calling, moving or feeding when the observer passes. Mammal species vary in their ease of detection. Four classes of mammals linked by their detectability reveal that these three methods do not allow a complete census of mammals on the transect midline.

1. Partially nocturnal primates with weak eye-shine who alarm call at the observer, e.g. baboons *Papio* spp., colobus monkeys *Colobus* spp. and brown lemur *Eulemur fulvus*. The calling animals are extremely difficult to see, even from directly underneath because they are obscured by the vegetation and their eye-shine is so weak. Detection depends almost entirely on their calling. Although these mammals would not be surveyed by night, they are an instructive group for comparing with fully nocturnal species.

2. Mammals with bright eye-shine that move quietly and call rarely (at least seasonally), e.g. lorises *Nycticebus* spp., lemurs *Cheirogaleus* spp. and *Avahi* spp., common palm civet *Paradoxurus hermaphroditus* and colugo *Cynocephalus variegatus*. Even though their bright eye-shine aids detection, many animals are missed as they are obscured by vegetation: this is demonstrated as some escape detection until the observer has passed and looks behind; at a pause, animals are found several minutes (and scans) after stopping; and the second of two adjacent observers invariably finds animals the first observer has overlooked. Animals can be missed even in the open: a slow loris *Nycticebus coucang* observed in a leafless tree for 55 min was invisible for many periods of several minutes simply because it was not looking at the torch. A passing observer could easily have overlooked it.

3. Noisy mammals with bright eye-shine, e.g. kinkajou *Potos flavus*, small-toothed palm civet *Arctogalidia trivirgata* and bushbabies *Galago* spp. The two carnivores are usually detected by sound rather than eye-shine; when in the canopy they are easily overlooked visually (see category 1). At one site in Ethiopia, bushbabies in low bushland acacias were usually found by eye-shine, but those in adjacent dense forest were heard first (Duckworth, 1992*b*). Small-toothed palm civet and pygmy loris *Nycticebus pygmaeus* were two common

arboreal mammals at one site in Laos (Duckworth, 1994). Lorises, detected only by eye-shine, were never heard calling or rustling; civets called loudly and crashed through the canopy. Four pygmy lorises were found and nine civets; only one of the latter was detected by eye-shine, suggesting that a large number of pygmy lorises were passed over.

4. Quiet mammals with no eye-shine, e.g. sloths *Choloepus* spp. and neotropical porcupines *Coendou* spp. As there is no easy way of detecting the animals, sightings are disproportionately rare, although dung counts reveal that sloths are among the commonest forest mammals (Glanz, 1982). The proportion of animals on the midline that are overlooked defies easy estimation. The development of methodology to allow population estimation where many midline animals are missed is experimental (Buckland *et al.*, 1993) and has not addressed the specific problems with nocturnal forest mammals. Distance sampling techniques override problems of variation in cue production, observer ability and environment effects (Buckland *et al.*, 1993), but only when detection on the transect midline is not reduced. Detection of nocturnal mammals, including on the midline, is affected by patterns in activity or vocalization during the night or with season (e.g. Duckworth, 1992*b*), lunar cycles (e.g. Emmons, 1982), plant phenology (notably in deciduous forests; e.g. Laurance, 1990) and hunting pressure (leading to torch-shyness) in the area.

SAMPLE SIZES

For population to be derived meaningfully from distance surveys, a minimum of 60–80 contacts is needed (Buckland *et al.*, 1993). Over much of South East Asia, it is rare to find mammals (as a whole) more frequently than once per hour. Even frequently seen species are rarely found more often than once per 6–9 h (Duckworth, Timmins *et al.*, 1994). Thousands of hours would thus be needed per site to achieve adequate samples for a representative selection of species.

OTHER POINTS OF SURVEY DESIGN

The use of roads and paths

For unbiased results, survey lines should be placed randomly with respect to object distribution (Buckland *et al.*, 1993); this is most unlikely to be so if roads are walked (e.g. Duckworth, 1992). In practice, for rapid assessment surveys (as distinct from detailed study), roads offer excellent opportunities for high visibility and quiet passage. Walking within forest gives low sighting rates; being surrounded by vegetation, the observer cannot see much, and anyway has flushed many of the animals by making so much noise. In faunal surveys is usually imperative to maximize the number of encounters with respect to time, because many surveys are done under great time constraint.

Multiple use of trails

An important point often not discussed is the extent to which observations were made repeatedly along the same line. Roads are often scarce, so each may be used many times (Walker & Cant, 1977; Emmons, 1982; Glanz, 1982; Laurance, 1990; Duckworth, 1992*a,b*). Ideally, for any measure of the relative abundance of each mammal species, each route would be walked only once. Multiple counts require careful statistical testing as the independence of data may be compromised; Glanz (1982) discussed this problem for red spider monkeys *Ateles geoffroyi* on Barro Colorado Island and similar principles would apply to nocturnal species. This is often not too serious a problem, however, as a line walked 3 nights in a row often yields largely different species each time, with, furthermore, different individuals of a given species on different nights (Duckworth, 1992*a*), because encounters so depend on chance that one detects a different subset of the population every night. Logically, therefore, unstructured multiple trail use is incompatible with estimating population densities: such trail use is acceptable if only a small proportion of the animals available are in fact detected, while the calculation assumes much more complete coverage. In theory, because even the crudest contact frequencies assume the principle of statistical independence (the sampled subsection should represent the whole area), the survey area should be divided up into sections of line. Within each section, the entire length should be walked the same number of times. For each section, a separate encounter rate should be calculated, and these rates combined, weighted according to the length of section, to produce an overall rate representing the whole area. Laurance (1990) did this. This low proportion of species where individual animals are seen repeatedly includes indolent sub-canopy species such as common palm civet and sportive lemurs *Lepilemur* spp. and crepuscular species with regular resting sites (e.g. canids and deer). The observer is likely to notice in the field any error strong enough to be of biological importance, and make allowance.

RECOMMENDATIONS

For most nocturnal forest mammals it is not possible to use direct contact transect data to calculate population densities because major assumptions of distance theory are not met. However, for many purposes, the most pressing need is a rough estimate of the status of a species in an area. Population estimates may not be the best use of available time: comparable data from further areas are often more useful in assessing conservation priorities for species and areas. Laurance (1990) presented many conclusions of high relevance to forest mammal conservation based entirely on sighting frequencies: no population densities were estimated. Brockelman & Ali (1987) deplored the presentation of population density estimates for diurnal primates with little indication of

how they were derived (making it impossible for others to try alternative calculations), in place of raw data.

Until theory and technique for calculating populations has addressed the problems of low detectability of animals on the midline, information from nocturnal transect surveys is best presented as contact frequencies accompanied by some contextual information:

1. Contacts are more usefully related to time than to distance because a paused observer detects new animals after several stationary minutes: no new distance is traversed, but time has elapsed. An observer cannot double the number of contacts per hour simply by covering twice as much ground, because less conspicuous animals are then overlooked. However, the balance of species recorded may change with speed: preliminary results from Borneo showed that walking faster produced more mouse-deer and fewer canopy flying squirrels (Duckworth, in press).

2. Calculations, including statistical tests, should use the number of contacts rather than the number of individuals (each group of more than one animal being a single contact) since the animals within a group are not statistically independent. Information showing the total number of animals must also be presented.

3. Visibility in the habitat should be indicated, since animals are detected at greater distances in more open habitats; results should indicate the typical sighting distance of animals.

4. Main methods of detection should be given for each species; contacts of those detected by ear are relatively unaffected by vegetation thickness.

5. Hunting pressure in the area should be indicated as this may affect both the population and its detectability.

6. Whether observations were made from roads, paths, or across the habitat at random should be stated; results should be presented separately for each category.

Acknowledgements

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Cached fungi in non-native conifer forests and their importance for red squirrels (*Sciurus vulgaris* L.)

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Abstract

The caching of fungi by red squirrels *Sciurus vulgaris* was investigated in commercial conifer plantations by walking transects in Kielder Forest, Cumbria and Wauchope Forest, Scotland. In 11 transects, a total of 58 fungal fruiting bodies were observed on branches in trees, consisting of four different species (49