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GENERAL GUIDELINES FOR STANDARDIZING LINE-TRANSECT SURVEYS OF TROPICAL FOREST PRIMATES

Carlos A. Peres

Line-transect surveys have been widely used over the last three decades to quantify primate population abundance in tropical forests. However, the details of the census methodology applied by different investigators remains highly variable despite a number of reports attempting to standardize primate census techniques (Wilson and Wilson, 1975; Janson and Terborgh, 1980; NRC, 1981; Brockelman and Ali, 1987; Defler and Pintor, 1985; Johns, 1985; Skorupa, 1987; Whitesides *et al.*, 1988). Many of the currently used field procedures, involving site selection, transect preparation, and the way the censuses are carried out across different studies, are therefore not strictly comparable. In addition, manipulation and analysis of census data, as reported in the formal and grey literature, can also diverge considerably. To a large extent, this hinders the level of confidence attributed to primate abundance estimates at a given forest site, and undermines the comparative power of surveys at different sites, whether these are reported in the form of linear detection indices (e.g., group sighting rates/10 km walked) or population density estimates (e.g., ind./km^2).

Here I prescribe a set of practical guidelines and recommendations for conducting line-transect surveys of tropical forest primates. Although readers of *Neotropical Primates* may be primarily interested in primates, the methodology outlined here could be equally applied to a number of large vertebrate taxa amenable to direct observations under similar conditions, provided that their intrinsic detectability and spatial behaviour do not violate some of the basic assumptions of line-transect census theory (see below). These guidelines focus on the practicalities of the actual field procedures of one choice method that is widely used, rather than on the accuracy and pros and cons of different census methods. They are thus intended to complement, rather than replace, a number of other useful discussions of line-transect census methodology (Janson and Terborgh, 1980; NRC, 1981; Brockelman and Ali, 1987; Whitesides *et al.*, 1988; Buckland *et al.*, 1993; Greenwood, 1996; Southwell, 1996), which may provide useful field tests of the accuracy of different techniques. The theoretical background of the most current modelling tools for analysing census data are described in detail elsewhere, and are largely beyond the scope of this paper. Buckland and collaborators (1993) provide a detailed treatment on the statistical analysis of distance sampling data used to estimate population densities, which largely supersedes its predecessor (Burnham *et al.*, 1980). However, I also provide some common-sense recommendations for enhancing field procedures in order to minimize or prevent some common sampling biases. This is critical because the robustness and accuracy of model estimators are highly dependent on the quality of field data, and no amount of sophistication in post-survey data analysis can correct for some basic flaws in sampling methods.

This set of guidelines results from first-hand experience obtained during a standardized program of 26 diurnal wildlife censuses conducted throughout Brazilian Amazonia over the last 15 years (1984-1998: Peres 1988, 1989a, 1990, 1993a, 1997a, 1997b, in press a, in press b, Peres and Dolman, in press; C. Peres and H. Nascimento, unpubl. data), each of which lasted approximately one month. Our field procedures have thus been repeatedly tested and "refined to a fine art" over the course of this long-term census program. This condensed set of guidelines is therefore intended to provide a straightforward and workable sampling protocol for both the novice and experienced field investigator who wishes to standardize a census methodology in order to improve its overall efficiency, accuracy, and comparability.

Sampling Site Selection

Once the general survey area has been selected, two reasonably long random transects (4-5 km) from the base-camp should be cut, preferably at angles of 135°-180° from one another. With the exception of drive-censuses where transects are laid parallel to one another, it is best if the nearest point along different transects in the same survey area are at least 1 km from one another. If the general census area is intersected by a river, then it may be more appropriate to set up transects on opposite banks of the river. Although transect placement is inherently dependent upon the objectives of the survey, establishing random transects may be preferable in areas of continuous forest. In practice, however, a blind policy of random transects may not be feasible or entirely appropriate because of irregularities in terrain topography, distribution of undesirable landscape features (e.g., river contours; proximity to active households) and, depending on survey objectives, the need to avoid sampling areas or vegetation types which could substantially bias detection probabilities in a habitat mosaic (e.g., forest edges when sampling core-habitat populations; secondary forest patches when sampling primary forest species). Moreover, it may be actually more appropriate to carry out some form of systematic sampling in a small forest fragment (<500 ha), such as through parallel transects which will provide a more even coverage of the survey area and prevent transect lines from crossing one another. Staunch advocates of strictly random sampling, who tend to inherently dislike systematic placement of transects, would compromise their ideal in such small survey area. Here the best policy is to use information gathered *in situ* and decide transect placement with a strong dose of common sense, for it is impossible to anticipate all circumstances under which a survey will be conducted. However, it is important to carefully consider the survey objectives and all sources of prior information available on the landscape in which the census will be done (e.g., maps; satellite photos; local interviews; reconnaissance walks) before the number, length and orientation of transects are decided.

Transect Preparation

Each of our transects at different Amazonian forest sites are usually prepared from scratch within the same day (0630-1630 h) by three trail cutters aided by a fourth person guarding the rear who measures and marks the transect. For a field survey lasting no more than 30 days, including site selection and transect preparation, we find it most cost-effective to cut two transects of 4.5 km each. In many cases, this extended transect length allows us to get away from portions of the study area more accessible to hunters (e.g., riparian forests) which may be an advantage in hunted areas. Given our time and personnel limitations, a greater effort allocated to transect preparation would be simply ineffective, as it is important to optimize the amount of time cutting transects and carrying out the actual census. Given the average speed at which observers should walk the transects (approx. 1,250 m/h), this line length allows each census walk to be completed within about 3 h 36 min, but in practice this often takes about 4 h because of normal delays following detection events, particularly where the abundance of target species is high. This is compatible with the peak activity periods of most diurnal animals whether census walks are conducted only early in the morning, or repeated in the afternoon from 1400 h onwards.

In order to minimize disturbance of the sampling area, however, we always retain a buffer zone around our base-camp by cutting an additional access trail of 300-500 m before beginning to cut the actual transect. Our transects within undisturbed primary forest are thus cut at a rate of some 500 m/h, depending on manpower and undergrowth conditions, but these are never wider than 1 m, and do not always appear to be meticulously "clean" and well-trodden at the beginning of the survey. Although our transects remain rigorously faithful to the same pre-established compass bearing, which is double-checked by the leading trail-cutter at approximately every 50 m using a Suunto® precision compass, we do not attempt to cut through and overcome every natural obstacle (e.g. a large fallen tree trunk) in order to maintain absolute transect linearity. Slight detours immediately around small patches of dense undergrowth, say around a regenerating tree-fall gap, do not change the overall objectives of the survey, but considerably speed up the process of transect preparation. It is important however that the leading trail-cutter can make sensible decisions about slight deviations in transect orientation, and resume the original compass bearing immediately on the other side of such obstacles.

Transects should be measured (with the aid of a Hip-Chain® or a 50-m forester's tape) and marked every 50m, which will facilitate accurate mapping of detection events. Brightly colored vinyl plastic flagging and permanent pens are usually good enough for these purposes, and tape marks are expected to last for at least 12 months provided they are not removed by sciurids or destroyed by ants. In the interest of efficiency, this is usually done by a single person walking well behind the last trail-cutter, and using a piece of low-elasticity nylon rope of c. 51 m in length (with knots tied 50 cm from both ends), which can be reversed at every 50-m section along the transect. In the absence of a Hip-Chain, this will prevent the rear person's need to frequently backtrack along the trail to release the ends of the rope (or tape), which will effectively halve the total distance walked in the process of measuring the entire transect.

Freshly prepared transects should be "laid to rest" (left alone by observers) for at least one whole day, which will allow the disruption created by the trail preparation personnel to normalise, and animals to redistribute themselves in space along the transect area in the total absence of observer disturbance. This is critical because trail cutters may often shout to one another along the transect, and loud human voices can be heard for hundreds of meters and potentially repel a number of game vertebrates, particularly in persistently hunted areas. In our experience, however, transect preparation over a single day's work is insufficient to condition animals to avoid the transect area, provided that transects are left alone for at least a whole day before census walks are initiated. This routine is also perfectly compatible with surveys based on multiple transects because this will require the field crew to rotate among different survey areas during the initial stage of transect preparation.

Getting Started

Line-transect census theory relies on five basic assumptions (in decreasing order of importance) which must be met for accurate density estimation (Burnham *et al.*, 1980; Buckland *et al.*, 1993): (1) all animals on the transect line must be detected; (2) animals are detected at their initial location, prior to any movement in response to the observer, and are not counted twice; (3) animals of target species move slowly relative to the speed of the observer; (4) distances from the transect are measured accurately; and (5) detections are independent events. It is therefore important to reduce or eliminate systematic observer biases which compromise these assumptions and standardize sampling protocols such as group counts, and estimates of perpendicular distances (see below) and spread of social groups. This should be done even among previously trained observers by jointly carrying out some census walks on the first days of a survey, and attempting to standardize data collection on the basis of non-independent detection events. Observers should practice rapid counts of individuals in a group of the target species before undertaking the survey, and become previously familiar with their behaviour and escape responses.

Needless to say, it is critical that all single observers censusing independently know their animals and are equally proficient at their detection and identification skills. In practice, this often relies on the accurate identification of rather subtle search images and acoustic cues such as alarm-calls, patterns of branch crashes, and other escape maneuvers in diurnal surveys, as well as patterns of eye shine in nocturnal surveys. This becomes a greater challenge in community-wide vertebrate surveys that can include as many as 45 reptile, bird, and mammal species[1]. In western Amazonian primate communities, this requires considerable background training as species-specific detection cues cannot be learnt overnight by a novice observer unfamiliar with the local fauna. Over the years we have found that teaching census protocols to (mostly uneducated but proficient) local hunters is far easier than doing the same to the even the brightest, but inexperienced, student of urban background. In addition, using illiterate but otherwise skilled local field assistants is not generally a problem provided that they can record their data into a handheld micro-cassette recorder, which can be easily operated in the field.

Walking the Transects

Censusing should be avoided during rainy days, particularly from early in the morning, because this affects the ability of observers to detect different animal species (e.g. unfavourable acoustic background dominated by raindrops on the foliage), as well as their intrinsic detectability (e.g. animals often become less active, and "freeze" rather than flee as a behavioural response to the presence of observers). In practice, however, more ephemeral rainshowers tend to occur later in the day, and should not entirely compromise the quality of at least some of the census data, provided that observers discontinue census walks during rain and subsequent periods of heavy raindrops trickling down from the canopy, and resume censusing immediately thereafter. This is particularly appropriate in time-limited surveys in many regions of tropical forests where rainstorms are more likely to occur in the afternoon, thus allowing uninterrupted census walks to be carried out in the morning, which in any event is the best time of day for conduct-

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[1] Our vertebrate surveys in Amazonia (Peres, in press a), for example, include the following taxa: callitrichid primates (e.g. *Callithrix*, *Saguinus*), all larger primates (*Callicebus*, *Saimiri*, *Pithecia*, *Chiropotes*, *Cacajao*, *Cebus*, *Alouatta*, *Lagothrix*, and *Ateles*), squirrels (*Microsciurus* and *Sciurus* spp.), acouchis (*Myoprocta*), agoutis (*Dasyprocta*), five species of forest ungulates (collared peccary *Tayassu tajacu*, white-lipped peccary *T. pecari*, red brocket deer *Mazama americana*, gray brocket deer *M. gouazoubira*, and lowland tapir *Tapirus terrestris*), woodquails (*Odontophorus* spp.), small tinamous (*Crypturellus*), large tinamous (*Tinamus*), trumpeters (*Psophia*), common guans *Penelope* and piping guans *Aburria pipile*, curassows (*Crax* spp. and *Mitu mitu*), and tortoises (*Geochelone*).

ing censuses.

Transects should be walked by single observers at average speeds of approximately 1,250 m/h, from 0630-0645 h to 1030-1045 h in the morning, and 1400 to 1800h in the afternoon. Brief stops every 100 m are advisable for even the most sensitive observers in order to minimize background noise, particularly where detection cues are primarily acoustic and the leaf litter is dry. A period of 4 h is therefore usually quite sufficient to conduct each one-way census replicate, including the time allocated to observations and data collection. Return walks in the afternoons should be done after 1400 h, following a midday period of approximately 3 h, when observers should remain relatively quiet at the end of the transects. This allows sufficient time for animals to redistribute themselves and overcomes the midday period of reduced activity for a number of target species. However, analysing data from return (afternoon) census walks is problematic for diurnal species retiring to their sleeping sites (or becoming less detectable) before 1700 h, as is often the case with callitrichids (Peres 1989b; 1993b). In these terms, return census walks may not overlap the entire activity period of different marmoset, tamarin, and lion tamarin species thus potentially underestimating their densities. The trick here is to use those data selectively, and stratify density estimates by time of day, as group counts and PD estimates during return census walks may be perfectly valid data, whereas the overall detection rate may not.

In our surveys, observers are rotated on a daily basis between different transects in order to minimize or cancel out potential observer-dependent biases. This system has worked very well at our survey sites where groups of two and three transect lines have been used simultaneously (by observers with synchronized watches). This also allows observers operating alone to establish a better overall team effort over the course of the survey, and double-check one another's previous efforts by inspecting daily marks left on a plastic tape at the end of the transect.

Recording Data

Observers should record date, transect identity, weather conditions, and personnel at the beginning of a census walk, as well as the start and end time of each walk. Upon a detection event, the time, species identity, group size, group spread, sighting location along the transect, and detection cue should be recorded, preferably in the same sequence onto a standardized datasheet which facilitates their entry into an electronic data file. The opportunity to record subsidiary information such as activity, diet, height, age and sex of animals sighted, mixed-species associations, and vegetation features are also important and should not be wasted. As a general policy, observers should remain on the transect line, but in some cases it may be necessary to move away from the transect (for no more than 10 min) and approach the animals to make further observations possible.

If sighting distances (SD) and angles are taken, they should be transformed to perpendicular distances (PD) for analysis because density estimators based on SD (i) require unrealistic assumptions about the detection process that are not required by PD methods (Burnham *et al.*, 1980; Buckland *et al.*, 1993), and (ii) perform poorly relative to those based on PD (Hayes and Buckland, 1983). In practice, it is actually easier to restrict distance estimates to PD by memorizing the exact location where an animal (or a group of animals) was first detected, and then walking to the nearest point along the transect from this location.

Distances to each independent subject should be measured or estimated accurately (these data are referred to as "ungrouped"). If an observer cannot reliably estimate distances accurately, than an optical range finder (c. US$50) or a more expensive pair of survey laser binoculars (US$ 290-500) should be used. We have recently begun using the latter because of the additional accuracy afforded, despite the added cost. As a general rule, however, it is best if all observers calibrate the accuracy of their distance estimates prior to the actual census by either learning how to pace distances according to their stride length or practicing PD estimates based on repeated trials aided by a range finder or 50-m tape. Distance measurements are particularly critical close to the trackline because the behaviour of model estimators is highly dependent on the frequency distribution of short distances from the line. On the other hand, distance measurement errors for subjects away from the line matter comparatively little from a statistical standpoint because they have lesser consequences on the detection probability function. Extreme departures in PD values are also tolerated by most detection functions, either because (i) the data distribution is often truncated and outliers are eliminated, and (ii) estimates are robust to such departures provided that some 40 animal clusters (spatially independent groups or subgroups) or more are available.

In addition, pay close attention to animals possibly moving away (being flushed) from the trackline before the animal is detected by the observer, but after the observer is detected by the animal (assumptions 1 and 2). The same problem could happen with animals moving towards the observer just prior to detection but this is counter-intuitive for most tropical forest vertebrates and unlikely to happen. Statisticians who frequently handle line-transect data will refer to this as a "g(0) problem". The mathematical term g(0) refers to the probability of detection on the line, which is usually assumed to be greater than at increasing distances from the line. This is critical because most model estimates rest on the assumption that all animals on the trackline are detected (assumption 1), and that the detection probability is independent of the observer's presence (assumption 2). The probability of detecting an animal, given that it happens to be at the line, should therefore be one. Moreover, rounding errors of distance estimates, particularly at short distances from the transect, can be problematic if not repaired during data analysis by regrouping the PD class intervals or other "smearing" techniques. This is often common because of the observers' natural tendency to round distance estimates to the nearest multiple of five. It is therefore crucial that enough time (1-2 days) is allowed to practice and standardize distances measurements by independent observers prior to the onset of a survey.

In social species such as primates, the groups (or subgroups) must be considered to be the relevant spatial unit of the population and distances should be measured to the center of the group. Population density then becomes a product of group density times the average group size based on reliable group counts. In practice, however, animals nearest the observer are intrinsically more visible and the point defining the geometric center of the group cannot be easily assessed, particularly in species living in large groups (e.g., in Amazonian primates, *Saimiri* spp. *Cebus albifrons*, *Cacajao* spp. *Lagothrix* spp.: Peres, 1993; Peres, 1997a). It thus becomes essential to add a correction factor based on group spread or group diameter estimates for every independent sighting, or else the densities of species in large-groups, which are intrinsically more detectable, could be severely overestimated (see Janson and Terborgh, 1980; Brockelman and Ali, 1987; Peres 1997a). One other option for species forming extremely large and uncohesive groups, or with a strong tendency to split up into subgroups, is to treat each small party of animals independently and record party size and a PD estimate for every reasonably discrete animal cluster even if they are obviously part of a larger group (and therefore not moving independently). In these cases, sightings of adjacent subgroups may violate the theoretical condition that detection events should be independent (assumption 5), but this is not as serious as cluster-size dependent biases in species forming large, uncohesive groups. Because of the larger sample size, this approach should also result in more robust estimates of overall population density (S. Buckland and K. Burnham, pers. comm.), but which should be similar to those derived from methods based on larger cluster sizes, although cluster density estimates could diverge substantially.

Sampling Effort

Our Amazonian surveys usually consist of a cumulative one-way distance on each transect line of at least 75 km. This corresponds to a one-way distance of at least 150 km along two forest transects, or a two-way distance of 300 km for both transects. This usually requires 17 days of census if two independent observers are available to walk both transects simultaneously. In practice, however, even this relatively large census effort may not be sufficient to detect a pre-specified number of objects compatible with a robust density estimate for some rare species. Although the recommended number of independent detection events per species per census should exceed 40, smaller sample sizes can derive robust density estimates if treated carefully. In general, there is no fixed rule about a sufficient sample size, because strip-width estimates are highly dependent on the nature of the distribution of detection distances, and as few as 20 sightings may suffice to derive good density estimates provided that the data distribution is highly favourable (S. Buckland, pers. comm.). In neotropical primate communities, however, even a small sample size of 20 sighting/species may be unrealistic for species occurring in low group densities (e.g., *Callimico*, *Pithecia* spp., *Lagothrix* spp.), even if relatively labour-intensive surveys involving a cumulative distance >300 km are considered. One possibility for strengthening such small sample sizes is to pool the data from different surveys conducted in the same forest type and then stratify the analysis according to survey location (e.g., Peres 1997a). However, I recommend that initially the PD distribution at different sites should be examined through analysis of variance, because of possible differences in the understory structure (and detectability) of different forests. An independent measure of understory density at different survey sites would also offer further support for data-pooling procedures. If additional data from independent surveys are simply unavailable then I recommend that data on sample sizes (number of sightings), sampling effort (distance walked), and confidence intervals (CI) of density estimates should be presented in the final report to extent that dangerously large CIs can be tolerated.

Data Analysis

In the 1980s, TRANSECT (Laake *et al.*, 1979) became the most popular comprehensive computer software for analysis of line-transect data from surveys of tropical forest vertebrates. More recently this program has been superseded by DISTANCE (Laake *et al.*, 1991; Buckland *et al.*, 1993), which has become well-established and is relatively easy to use, as it is now available for a Windows platform (version 3.5). DISTANCE provides several estimators for computing group (and population) density from either PD or SD and sighting-angle data, and is currently the best available comprehensive software package dedicated for density estimates based on distance data. DISTANCE models the probability density function of the PD data by first selecting a key function and then a series expansion (Buckland *et al.*, 1993), and handles all the necessary computations. An information criterion built into the software facilitates model selection for each grouped or ungrouped PD distribution. The Hazard-rate model with one of a number of mathematical adjustments is often the best density estimator for g(x) "shoulders" resulting from forest primate censuses (Peres 1997a), and performs reasonably well for most other non-primate species.

I hope this rather brief set of guidelines will prove useful in the planning and execution stages of future line-transect surveys of tropical forest vertebrates, which have become important biodiversity conservation assessment tools. This may also serve to stimulate the adoption of a standardized census protocol for further fieldwork in tropical wilderness frontiers, as previously remote primate populations become increasingly accessible to those wielding a pair of binoculars and notebook, rather than a shotgun.

Carlos A. Peres, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK. E-mail: <C.Peres@uea.ac.uk>.

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TAIL-USE IN CAPUCHIN MONKEYS

Dionisios Youlatos

Introduction

Capuchin monkeys, *Cebus*, are among the most widespread of the platyrrhines (Emmons, 1990). The brown capuchin, *C. apella*, has the largest geographic range, found east of the Andes from Colombia and Venezuela, south to Paraguay and northern Argentina (Emmons 1990). The white-fronted capuchin, *C. albifrons*, occurs in the upper Amazon and central Colombia, the white-faced capuchin, *C. capucinus*, occurs in northern Colombia and Central America, and the weeper capuchin, *C. olivaceus* ranges from Venezuela east to the Guianas and the north-eastern Brazilian Amazon. *C. apella* and *C. olivaceus* are sympatric in French Guiana.

Capuchins, like the large-bodied atelines, have a prehensile tail. Anatomical studies have shown, however, some morphological differences between the tails of *Cebus* and the atelines, suggesting that this feature has evolved twice in platyrrhines, and also that they may use their tails in different ways (Ankel, 1972; Grand, 1977; German, 1982; Rosenberger, 1983; Lemelin, 1995). There has been only limited quantitative study in tail use in the prehensile-tailed