

## RESEARCH ARTICLE

# Selection of Line-Transect Methods for Estimating the Density of Group-Living Animals: Lessons from the Primates

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We review the four major contemporary methods for estimating density of group-living animals from line-transect sampling: perpendicular modelling of group centers, perpendicular modelling of center of measurable individuals, strip transects and animal–observer distance. The efficacy of each method is evaluated to produce a simple selection guide. We review the literature and use field data from the Udzungwa Mountains, Tanzania. The review is relevant to all group-living animals; however, examples are drawn from the primates. Perpendicular methods have better mathematical justification than non-perpendicular methods. For perpendicular methods using detection function models, it is preferable to measure group location using center of measurable individuals, as group centers are hard to estimate. The assumptions of detection function models are often broken in poor visibility habitats or with unhabituated animals. Alternatively strip transects may be used where there are reliable data on group spread and/or visibility. Strip transects are also the most practical, along with the animal–observer method; however, the latter lacks mathematical justification. We conclude that there are arguments for continued use of all four methods. In certain situations the use of raw encounter rates may also be considered. The appropriate method is determined by minimizing bias and considering time, resources and field conditions. *Am. J. Primatol.* 70:452–462, 2008. © 2008 Wiley-Liss, Inc.

**Key words:** abundance; census; detectability; distance sampling; monitoring

## INTRODUCTION

Opinions remain deeply polarized on method selection for estimating the density of primate groups. Although no method is bias free, the most accurate density estimates are obtained from complete counts [Davenport et al., 2007; McNeilage et al., 2001] or focal group studies of home range [Chapman et al., 2000; Fashing & Cords, 2000; National Research Council, 1981]. However, these methods require sampling effort that is often impractical, especially over large areas. In most cases, line-transect distance sampling is the most practical method [Plumptre, 2000; Struhsaker, 1997]. However, there is extensive debate on how to obtain accurate and precise density estimates, particularly where the assumptions are violated by human disturbance.

## Rationale for Line-Transect Distance Sampling

The basic output from line-transects is the encounter rate, i.e. the number of observations per distance walked. Although this has been used to estimate relative density, it does not account for visibility or detectability. Visibility is limited and highly variable in complex habitats such as forest. Figure 1 shows that the distribution of sighting

distances varies among sites, not just the mean. Thus, the reliable sighting distance cannot simply be adjusted using correction factors. Furthermore, models accounting for visibility using inanimate objects [Robinette et al., 1974] cannot simulate animal behaviour, e.g. animals in disturbed or hunted areas may be more cryptic [Johns, 1985].

The problem of visibility and detectability along line-transects can be dealt with by measuring the distance from the transect or observer to each observation (distance sampling). The sample area is then estimated from the decreasing likelihood of seeing a group or individual with increasing distance from the transect. This involves modelling the decline in observations and estimating the number

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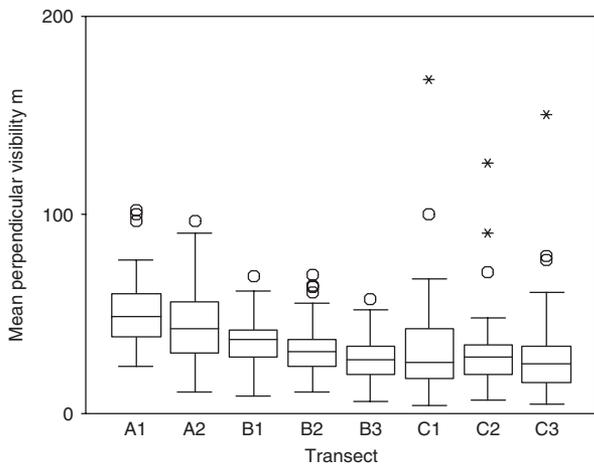


Fig. 1. Visibility along forest transects in the Udzungwa Mountains, Tanzania: (A) Magombera, closed canopy; (B) and (C) Matundu, semi-open and heavily logged; Kruskal–Wallis:  $\chi^2 = 21.42$ ,  $P = 0.003$ ). Visibility was the distance to the furthest visible point at 100 m intervals. Boxes show median and quartiles. Whiskers show maximum and minimum excluding outliers  $>1.5$  ( $\circ$ ) and  $>3$  ( $*$ ) times the interquartile range.

missed or estimating a reliable strip within which all individuals or groups have been seen with certainty [Fig. 2a and b; Buckland et al., 1993, 2001; Burnham et al., 1980; Whitesides et al., 1988].

We use the term “group” to refer to an aggregation of individuals at a given moment in time. To some, the term “group” may infer a complete aggregation of all individuals that usually associate together. However, during a census walk the point of measurement could also be a temporary foraging party or subgroup. This information can be hard to determine in the limited time during a census walk; hence, we only use one term.

### Points of Contention

Here we consider the contemporary line-transect methods for estimating density of group-living animals. Deciding on methods is complicated by mixed messages in the recent literature. In particular, the debate involves (a) the use of animal–observer distance [Chapman et al., 1988, 2000; Struhsaker, 1975, 2002] vs. perpendicular distance to the transect [Buckland et al., 1993, 2001; Burnham et al., 1980; Plumptre & Cox, 2006], (b) whether to determine individual densities by use of group sizes estimated during census walks [Plumptre, 2000; Plumptre & Reynolds, 1994], independent group counts [Defler & Pintor, 1985; Struhsaker, 1997] or counts of only those individuals seen during transect walks [Plumptre & Cox, 2006] and (c) whether or not to incorporate information on group spread [Plumptre & Cox, 2006; Whitesides et al., 1988].

### Aims and Objectives

We summarize the four major contemporary line-transect methods for estimating density and discuss the efficacy of each method using published sources, personal observations and data from the Udzungwa Mountains, Tanzania. We suggest a simple procedure for method selection. Focus is on the unresolved issues of group location, size and spread. We assume that only one or two observers are available, and animals can be detected from direct observations. The methods were developed for medium-to-large diurnal primates but are relevant to any group-living animals in poor visibility habitats.

### ASSUMPTIONS AND LIMITATIONS

The assumptions and limitations of line-transect density estimation are many [Buckland et al., 1993, 2001; Burnham et al., 1980]. The most problematic are (f) and (g) below:

(a) Objects should be measured from their initial location. Observers must tread carefully and wear inconspicuous clothing so that animals do not flee. This may be hard where animals are hunted or vegetation is tangled. Solitary individuals flee more quietly than groups, although they may not represent a high percentage of the population.

(b) Sightings should be independent. Groups are usually non-independently distributed, e.g. associations, fission–fusion and competition. However, the methods are generally robust to such violations of this assumption [Buckland et al., 2001]. Repeated transect walks should be spread across seasons and spaced by several days, e.g. 2 weeks.

(c) The observer must walk faster than the animals. This is so that animals do not pass into the area being searched. Violation of this would lead to overestimation of density owing to additional groups entering the study area and double counting. For the same reason, observers should not spend a long time with any given group (e.g. 10–15 min).

(d) Transects should be placed at random with respect to the distribution of the animals. This assumption applies where population estimates are extrapolated to a larger area, to avoid bias from clumping. Density estimation may be affected where paths or ridges are used [e.g. duikers; Struhsaker, 1997]. Stratified random sampling may allow for habitat variation if the distribution of habitats is known. The assumption is irrelevant where extrapolation is not required [Ross & Reeve, 2003; Rovero et al., 2006].

(e) Sufficient sightings are required for the estimation of a detection function or strip. Typically at least 40 sightings are required; however, 60–80 observations are preferable to accurately model detection functions [Buckland et al., 1993, 2001]. Estimating density from line-transects is therefore

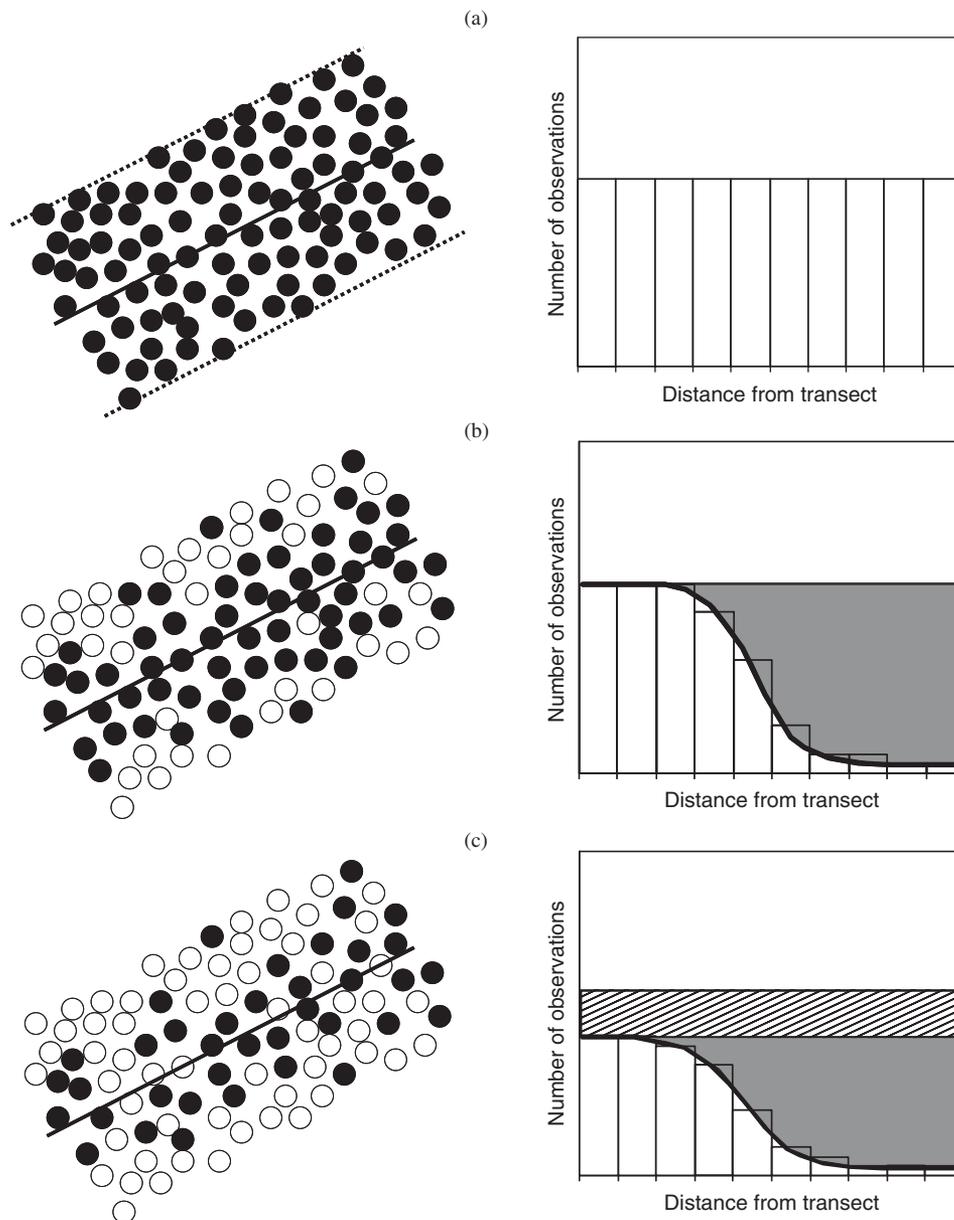


Fig. 2. Diagram of the effect of visibility on density estimation: (a) 100% visibility (i.e. strip transect, dashed lines); (b) visibility declining with distance from transect; (c) poor visibility with individuals missed on the transect. Left: locations of groups seen (○) or missed (●). Right: effect of missed groups on histograms and detection functions. Shaded areas: (b) and (c), number of groups estimated to be missed; hatched area: (c), underestimation caused by individuals missed on the transect.

impractical for low densities. For example, in Mkungusi (lowland Udzungwa), only one group of red colobus, *Procolobus gordonorum*, was seen in 40 km of walking [Marshall, 2007; Marshall et al., submitted]. This would require 1,600 km to reach 40 observations. Fewer sightings may, however, be used based on common sense and experience [e.g. 15–30 observations; Peres, 1999].

(f) Objects on or near the transect should be detected with certainty. Where visibility is 100%, observations do not decrease with distance (Fig. 2a).

More typically, visibility and the number of observations decline with distance (Fig. 2b). If visibility/detectability is reduced such that groups are missed on the transect line, the histogram bars and curve decrease, thus underestimating density (Fig. 2c). In dense habitats, such as tropical forests, there is a high chance that individuals are missed on the transect. Groups are therefore the more popular sample unit as they are less likely to be missed.

(g) Measurements should be exact. Estimating distances visually may lead to overestimates in

density [Brugière & Fleury, 2000]. A compass is essential and an accurate measuring device (e.g. laser rangefinder) is desirable. Observers should be trained and inter-observer reliability checked [Mitani et al., 2000; Rovero et al., 2006]. It is impractical to measure the location of every individual, e.g. Udzungwa red colobus have groups up to 83 individuals and mean 27.2 [Marshall et al., 2008; Struhsaker et al., 2004]. This again emphasizes that the group is the appropriate sample unit; however, choosing the point for measurement is contentious, as we now discuss.

## GROUP PARAMETERS

### Group Size

Group density is converted into individual density by weighting by mean group size. Where possible, group size should be estimated during transect walks, so that distance data correspond to group size data [Plumptre, 2000]. Including a second or third observer may help; however, time is a limitation. In fact it is rare that reliable counts of group size can be made during transect walks [Brugière & Fleury, 2000; Defler & Pintor, 1985]. Group counts of *Procolobus tephrosceles* required 10–60 hr and redtail monkeys *Cercopithecus ascanius schmidtii* hundreds of hours [Struhsaker, 1997]. Selection of groups for counting independently from line-transect walks should be a representative sample and should not concentrate on the largest or most habituated [Plumptre, 2000]. Low sample size will result in low-precision density estimates. Therefore, sufficient sample size is required, e.g. using precision or power analysis.

### Group Center/Spread

For traditional line-transect sampling, the point of measurement is the group center [Buckland et al., 1993, 2001; Burnham et al., 1980]. Measurement to the group center during transect walks is preferable [Plumptre, 2000]. However, this requires good visibility and tight, habituated groups. These situations are rare owing to undulating terrain, dense vegetation and animal behavior. Group spread should therefore be assessed independently of transect walks and should be measured from several angles across the group [e.g. every 30 min; Plumptre, 2000]. Group spread calculation assumes that the average group shape is approximately circular [diagram, Marshall, 2007; Whitesides et al., 1988] and thus sampling must be sufficient to account for deviation from this. Spread should also be measured before human influence, which may be impossible for unhabituated animals. Plumptre [2000] advises against measuring group spread owing to daily variation. It can also be unreliable, prone to subjectivity and time consuming.

## “ACCEPTED” METHODS

The procedure for line-transect sampling is reasonably consistent between methods [Buckland et al., 1993, 2001; National Research Council, 1981]. Data suitable for the alternative methods can even be collected simultaneously [Fashing & Cords, 2000]. Typically the observer walks at a pace of 1–2 kmh<sup>-1</sup> [Ross & Reeve, 2003] for 2–5 km, usually starting early in the morning. Horizontal distance and bearing to all observations are taken and if possible perpendicular distance to the transect. If horizontal distance is not measurable, the distance and slope to the observation can be taken for conversion using trigonometry. The methods differ in the point of measurement, calculation of area and conversion to individual density. Four methods (a–d) are compared here for bias, accuracy, violation of assumptions, correction factors and practicalities.

### Perpendicular Distance to Group Methods

#### (a) *Perpendicular modelling of group centers (traditional detection function modelling)*

The traditional modelling method uses a detection function of perpendicular distances from group center to transect [Buckland et al., 1993, 2001; Burnham et al., 1980]. The program *Distance* is popular for this and is free to download [Buckland et al., 1993, 2001; <http://www.mbr.nbs.gov/software.html>]. Various models are fitted on histograms of perpendicular distance vs. frequency. The best model is then used to estimate density by allowing for missed individuals (Fig. 2b). The hazard-rate model has had the best fit for primates [Plumptre & Reynolds, 1994] except for small samples [ $<30$ , Whitesides et al., 1988]. An advantage of detection functions over cut-off distances is that all data are used. Comparisons of density estimates from such models to focal groups show good accuracy [Fashing & Cords, 2000; Whitesides et al., 1988].

This method requires group size and spread estimates and is therefore prone to error. Estimating group location is the major concern [Chapman et al., 1988; Plumptre, 2000; Plumptre & Cox, 2006; Struhsaker, 1997]. If group center is unknown, it is estimated by summing the observer to group edge distance and the mean radius [Whitesides et al., 1988]. Using this and the bearing to group edge, the perpendicular distance is estimated (Fig. 3a). Defining the point of measurement to group edge is also not simple. Using the first individual seen assumes that it is on the side of the group nearest to the observer and in line from observer to group center (Fig. 3a). Therefore, the result is often only a minimum estimate. Using the nearest individual to the observer is inappropriate as it would place many groups at 0 m from the transect (pers. obs.). As for

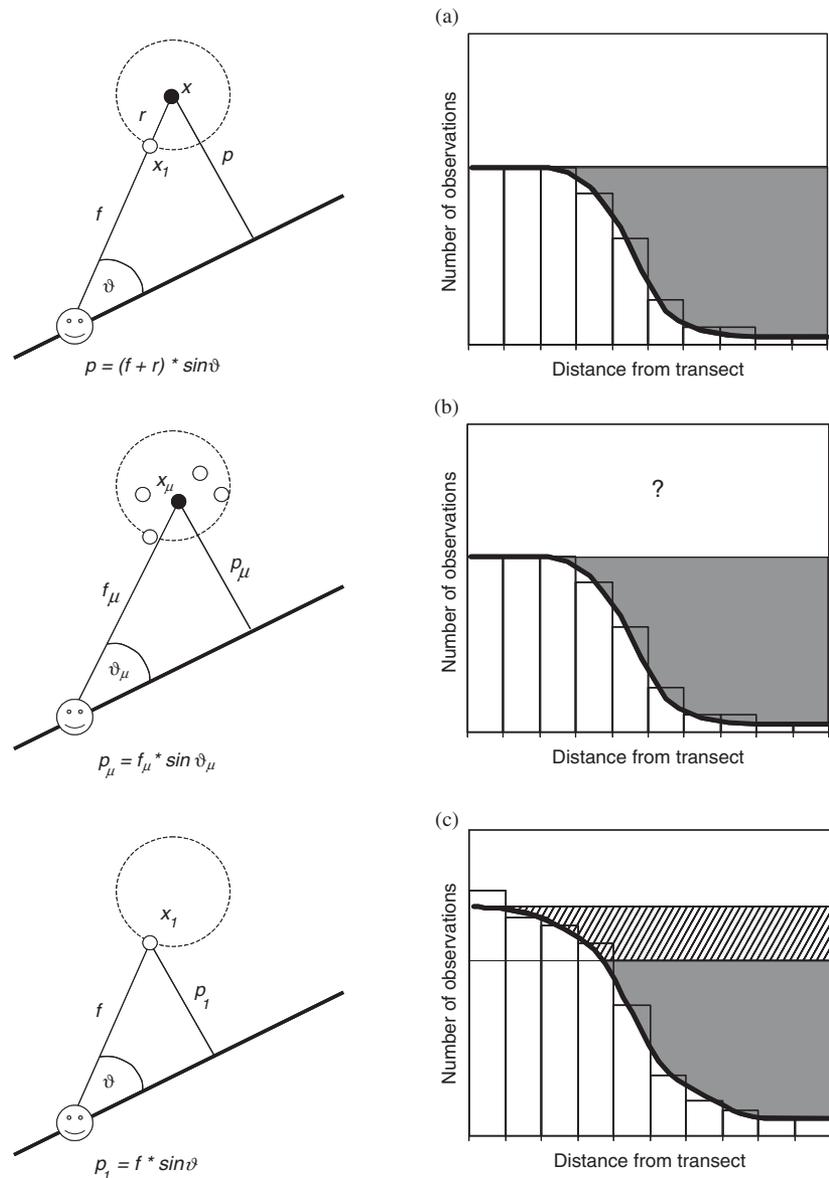


Fig. 3. Models expected from estimating perpendicular distance as (a) group center  $x$ , (b) geometric center of measurable individuals  $x_\mu$ , and (c) first individual seen  $x_1$ . Left: schematic diagrams and calculations. Right: effect on the detection functions. Shaded areas: estimated number of groups missed. Hatched area: (c), overestimation using first individual. The question mark indicates that method (b) remains untested.

group center and spread, determining group edge requires good visibility and tight, habituated groups.

*(b) Perpendicular modelling of center of measurable individuals*

Plumptre and Cox [2006] use the center of only those individuals whose initial location can be measured during a transect walk (Fig. 3b). Consequently, only a proportion of each group is used to make density estimates. This method is a recent development and remains to be tested against known

densities; however, it removes the error associated with estimating group size and spread. It also allows density estimates to be made from line-transect walks alone, without the need for independent assessment of groups.

Methods for density estimation should keep correction factors to a minimum [Plumptre, 2000]. However, additional correction factors are required for dealing with bias in this method. One correction is made for the higher detectability of large groups vs. small groups, particularly with increasing distance [Plumptre & Cox, 2006]. Secondly, because

individuals are often missed on the transect, two observers are required, with one recording only those individuals on or near the transect. The probability of missing individuals on the transect is calculated from the difference in the number of individuals seen [Buckland et al., 1993, 2001; Plumptre & Cox, 2006]. This is dependent on the second observer seeing more individuals on the transect than the first. It is therefore impractical in low visibility habitats or for unhabituated animals. In fact only one or two individuals are seen at their initial location in most groups in the Udzungwa Mountains (pers. obs.), giving poor-quality data for assessing group size and density.

(c) *Strip transects (truncated distance method or Kelker method)*

Early methods estimated densities by determining a cut-off distance and excluding all observations beyond [Robinette et al., 1974]. Despite development of mathematical models for estimating detection functions, many studies still employ modified versions of strip transects [see the list in Marshall, 2007; Whitesides et al., 1988]. The general principle is that of the Kelker method, where the cut-off is defined as the perpendicular distance beyond which observations decrease [Robinette et al., 1974].

There is a range of methods for determining an appropriate cut-off distance [National Research Council, 1981; Robinette et al., 1974]. Although rather arbitrary, the most popular method for primates is the 50% rule [Chapman et al., 1988; Marsh & Wilson, 1981; Whitesides et al., 1988]. Data are arranged in 10 m distance intervals and are then excluded beyond the interval where observations decrease by half or more in the next one (or sometimes two) interval. The 50% rule can be adapted by using the “effective distance” or “effective strip width” [Buckland et al., 1993, 2001; Whitesides et al., 1988] so that observations are not excluded.

This method assumes that groups are detected with 100% certainty within the cut-off distance (Fig. 2a). In fulfilling this assumption, some subjectivity is required. This has been a source of criticism [Brockelman & Ali, 1987]: however, subjectivity is preferable to an arbitrary cut-off that is sometimes wrong (e.g. Fig. 4 for animal-observer method). Also experimenting with a range of histogram bin widths (e.g. 5–10 m) may help to better detect a cut-off, rather than the arbitrary 10 m [Marshall, 2007]. This is built into the *Distance* program or easily calculated using standard spreadsheet/graphics packages.

As for perpendicular distance modelling, group locations must be measured to the group center. Where centers cannot be determined, the cut-off distance is obtained by adding a group radius

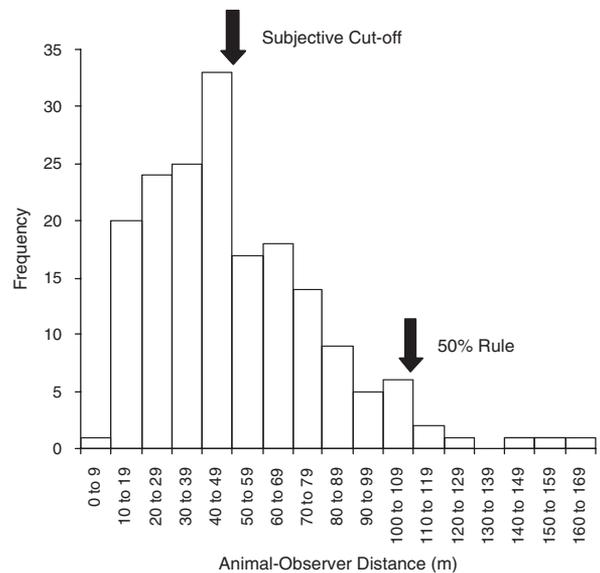


Fig. 4. Subjective vs. 50% rule for determining cut-off, using animal-observer distances of Sykes monkey groups in Matundu forest. The clear drop in observations at 50 m (33–17 observations) is only 48%, and therefore not detected by the 50% rule.

adjustment to a cut-off determined from first individual distances. This adjustment is usually half the mean group spread (diagram, Marshall, 2007; “transect-width estimation,” Whitesides et al., 1988) or even a quarter or a third [Brockelman & Ali, 1987 (Janson & Terborgh, unpublished data)]. The half-mean group spread method has shown good concordance with known primate densities [Brugière & Fleury, 2000; Lawes, 1992; Oates et al., 1990; White, 1994; Whitesides et al., 1988]. One study found this method to overestimate density; however, distances were only estimated and the authors considered them potentially inaccurate [Brugière & Fleury, 2000].

The continued use of strip transects over detection function modelling may be owing to their simplicity and lack of expertise or software. Moreover they avoid the complication of measuring or estimating group centers or the center of individuals. Some studies have also rejected perpendicular modelling in favor of strip transects owing to insufficient sample size for modelling [Brugière & Fleury, 2000; McConkey & Chivers, 2004]. However, strip transects and the animal-observer method also require sufficient sample size for the estimation of cut-off distance. In fact, Burnham et al. [1985] reject the use of strip transects, for the very reason that they perform worse than perpendicular distance modelling under low sample size. It may be possible to make a conservative estimate of cut-off distance independently from the sample data. This “fixed-width” method requires intimate knowledge of the species and habitat.

As with perpendicular modelling of group centers, strip transect sampling is susceptible to bias in estimating group size and spread. Unlike detection function modelling, it can also be inefficient, as a lot of data beyond the cut-off are discarded. This leads to low precision where the sample size is low [Burnham et al., 1985]. Perpendicular distance modelling is therefore preferred by many when the assumptions are met [Brockelman & Ali, 1987; Buckland et al., 1993, 2001; Burnham et al., 1985; Whitesides et al., 1988].

### Perpendicular Distance to First Individual Methods

Some have criticized strip transects using a group radius adjustment, because they can be twice the width of strips using perpendicular distance to the first individual seen [Struhsaker, 1997]. Although this may seem extreme, it simply emphasizes the large error of using perpendicular distance to the first individual. Many studies have estimated density using strips or models based on the first individual rather than group center [Brugière & Fleury, 2000; Chapman et al., 1988; Chiarello, 2000; de Thoisy, 2000; Fashing & Cords, 2000; Palacios & Peres, 2004; Struhsaker, 1975]. This method avoids estimating group center; however, it is seriously flawed [Fashing & Cords, 2000; National Research Council, 1981; Whitesides et al., 1988], and we do not include this as an “accepted” method.

The major fault in this method is that the first individual is likely to be located nearer to the transect [National Research Council, 1981; pers. obs.] or the observer [Whitesides et al., 1988; pers. obs.] than group center. This has the effect of underestimating the perpendicular distance of each group and therefore increasing the number of groups in the lowest distance bands [National Research Council, 1981; Fig. 3c] and may explain previous overestimates [Fashing & Cords, 2000; Whitesides et al., 1988]. Therefore, for perpendicular distance methods, even an inexact measure incorporating group spread is preferable to using the first individual seen. Subsequently the transect width is increased, thus avoiding overestimation of density [Fashing & Cords, 2000].

### Non-Perpendicular Distance Method

#### (d) Animal–observer distance method (King’s method)

Although perpendicular distance methods based on the first or nearest individual seen have been rejected, a method based on the animal–observer distance to the first individual (“sighting distance”), is still used [Chapman et al., 1988, 2000; Defler & Pintor, 1985; McGraw, 1994; National Research Council, 1981; Robinette et al., 1974; Rovero et al.,

2006; Struhsaker, 1997]. Histograms of distance vs. frequency are plotted similar to other methods. As for strip transects, the observer can select a cut-off distance beyond which there is a large and sustained fall in observations (Fig. 4).

Because sighting distance is used rather than distance to transect, the pattern of decline with distance is a true detection function. However, problems arise when animals can be seen from a long way ahead. We have many examples from the Udzungwa mountains, e.g. one *P. gordonorum* group was recorded 160 m from the observer, whereas the group was only 22 m from the transect. The animal–observer method therefore does not define a physical survey area from which groups are selected for density estimation. It is a means of data reduction with no mathematical basis [Plumptre & Cox, 2006]. For these reasons the methods and assumptions have been developed for use with perpendicular distances [Brockelman & Ali, 1987; Burnham et al., 1980].

However, the criticisms do not mean that the animal–observer method is obsolete. It has made good approximations to known densities of primates and other animals [Chapman et al., 1988; Defler & Pintor, 1985; Fashing & Cords, 2000; National Research Council, 1981; Robinette et al., 1974; Struhsaker, 1997]. Only one published study has compared known primate density with both animal–observer and “accepted” perpendicular methods [Fashing & Cords, 2000]. They found that strip transects weighted by group radius produced only narrowly better estimates for *Colobus guereza* than the animal–observer method. The strip transect method, however, performed better than the animal–observer method for *Cercopithecus mitis*. They concluded that, “if mean spread cannot be determined... the [animal–observer] method provides a reasonable alternative [but is] prone to providing overestimates of density for species whose groups spread out over large areas.” Given the error associated with group spread, the animal–observer method may therefore be widely applicable. The recent assertion that Fashing and Cords [2000] “advise against” using this method [Plumptre & Cox, 2006] is misleading.

### COMPARISON OF METHODS

A summary of the above discussion is given in Table I. Six selection criteria are used (number of correction factors, survey components, whether the physical survey area can be defined [mathematical justification], empirical support, sample-size limitations and whether software or training is required). From this, perpendicular modelling followed by strip transects, have the best mathematical justification (as they have a definable physical sample area); however, the animal–observer method is more practical (as it is simple and requires few correction factors). Method selection will be strongly dependent

**TABLE I. Comparison of Limitations of the Four Major Contemporary Methods for Estimating Density of Group-Living Animals from Line-Transects**

Selection criteria	Method				
	Perpendicular distance		Strip transect	Animal-observer distance	Encounter rates
	Detection function models (group center)	Detection function models (center measurable individuals)	Cut-off point; mean group size; mean group radius	Cut-off point; mean group size	Cut-off point; <sup>b</sup> mean group size
Correction factors required	Detection function; mean group size; mean group radius; group center; (map location; perpendicular distance <sup>a</sup> )	Detection function; individuals missed; group size versus detection error; (map location; perpendicular distance <sup>a</sup> )	Cut-off point; mean group size; mean group radius	Cut-off point; mean group size	Cut-off point; <sup>b</sup> mean group size
Survey components	3 (Transects; group size and radius)	1 (Transects)	3 (Transects; group size and radius)	2 (Transects; group size)	2 (Transects; group size)
Physical survey area definable	Yes	Yes	Yes	No	No
Empirical support	Yes	No	Yes	Yes	Yes
Dependent on sample size	Yes	Yes	Yes <sup>c</sup>	Yes	Yes/No <sup>b</sup>
Software/training required	Yes	Yes	No	No	No

Encounter rates (i.e. number of individuals per kilometre transect) are also presented for comparison.

<sup>a</sup>Additional correction factors required for non-straight transects.

<sup>b</sup>Depends on study aims and visibility.

<sup>c</sup>Unless a reliable 'fixed-width' can be estimated from earlier knowledge.

on field conditions, and the choices required are considered in the general discussion below.

Table I also includes encounter rates, i.e. the number of individuals seen per distance walked. The use of raw encounter rates is inappropriate where visibility is variable [Buckland et al., 1993, 2001]. We have already reasoned that this is rare, particularly where disturbance is high (Fig. 1). However, where there are several confounding variables and where the study aims do not require density estimates, they may have the least bias and have been widely employed [Butynski & Koster, 1994; Mitani et al., 2000; Marshall et al., 2005; Rovero et al., 2006; Seber, 1982]. A cut-off distance should be calculated or estimated to reduce the effect of visibility [Rovero et al., 2006]. Where the aim is simply to monitor change over time, the visibility issue may be reduced;

however, this makes the unlikely assumption that temporal habitat changes do not affect visibility.

## GENERAL DISCUSSION

### Method Selection

The many assumptions and correction factors required by perpendicular methods (Table I) mean that they have unknown error. The lack of mathematical basis for the animal-observer method means that the assumptions and error of this method are also unknown. Method selection is therefore a compromise that should minimize bias by consideration of the field conditions, available resources and personnel. To assist with method selection, a choice chart is presented including the key decisions for method selection (Fig. 5). This chart is designed as

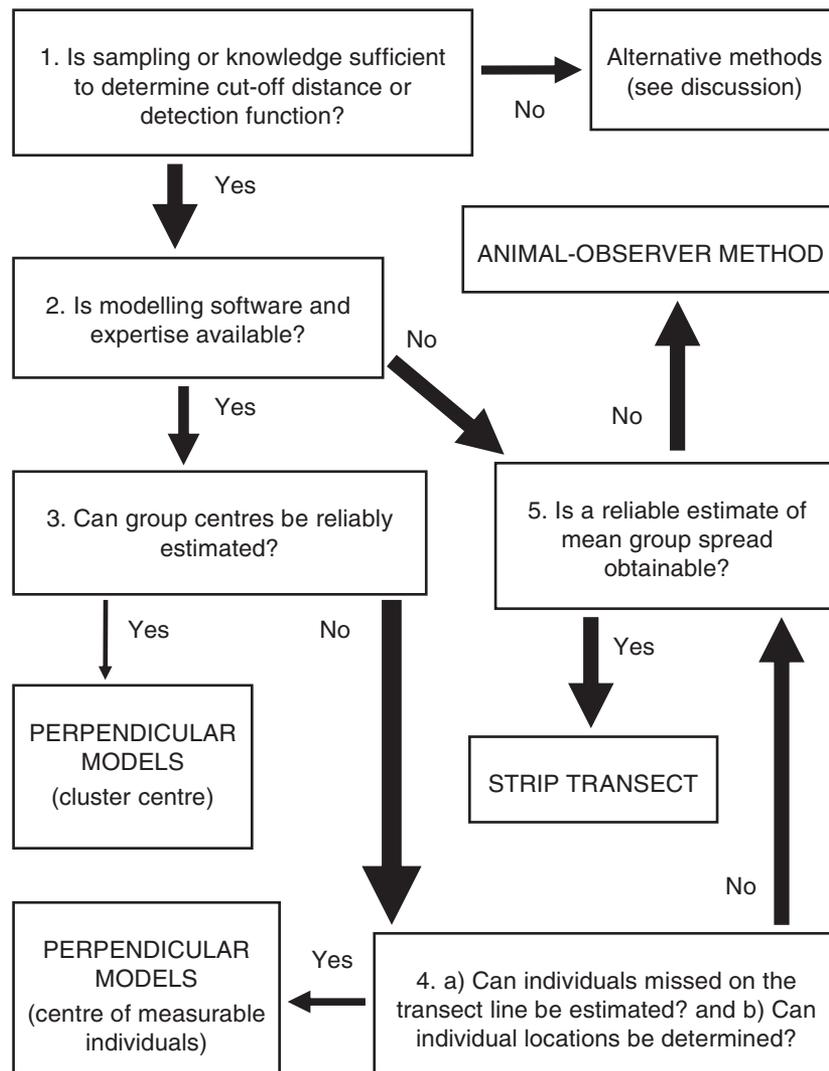


Fig. 5. Choices for deciding between line-transect density estimation methods. Arrow width suggests relative likelihood from our experience in tropical forests.

an extension to that of Ross and Reeve [2003], who give guidance on where line-transects are applicable. To assist decision-making we speculate on the likelihood of the various conditions of each method being met.

Given strong mathematical justification for perpendicular modelling methods and the many useful features of the *Distance* program, these methods are very attractive. This is providing the assumptions are met, correction factors can be measured with certainty and technical expertise is available (Fig. 5, choices 2–4). The many assumptions and correction factors, however, mean that these methods require caution.

If perpendicular modelling is feasible, a researcher must then determine which of the two alternative methods is most appropriate (group center vs. center of measurable individuals; Fig. 5, choices 3 and 4). It is difficult to determine which of these two alternatives is the most desirable. Using only the measurable individuals avoids error associated with group spread. However, without information on the relative bias of the several correction factors required for the two methods, this is inconclusive [Plumptre & Cox, 2006]. In particular, the error in estimating the number of individuals missed on the transect line is unknown and cannot be tested without independent counts of group size.

In rare situations of undisturbed forest with good visibility and habituated animals, group centers can sometimes be estimated, and there is no advantage in using the center of measurable individuals (Fig. 5, choice 3). In disturbed forests, and where group centers have to be estimated by mapping owing to non-straight transects, we suggest that the potential errors preclude perpendicular modelling of group centers. Finally, where a second observer is unavailable, where the second observer is unable to detect more individuals than the first, or where only one or two individuals can be measured per group, alternatives to perpendicular modelling should be considered (Fig. 5, choice 4).

For these reasons, many species require alternatives to perpendicular modelling. We have highlighted that the strip transect method is simple and accurate (Table I). Furthermore, correction factors are not applied to every single observation. Estimation of a strip width using knowledge of the habitat may also reduce the number of samples required. The main criticism is the error in measuring group spread (Fig. 5, choice 5). However, with common sense, a deliberately high estimate of group spread can be used to give a minimum density estimate. Hence, we suggest that strip transects are at least as employable as the animal–observer method; yet, they have greater mathematical justification.

After the rejection of other methods, we are left with the animal–observer method. Although critics of this method are resolute [Plumptre & Cox, 2006;

S. Buckland, pers. comm.], we have presented arguments for its continued use. It may be particularly useful for rapid surveys where time and resources prevent consideration of assumptions or correction factors (Table I). The lack of mathematical justification for the animal–observer method is of concern. However, in the absence of alternatives, empirical evidence suggests that the method is adequate. Given that poor visibility, unhabituated animals and difficult terrain, are common, it may be widely applicable.

We do not wish to dismiss any of the four methods as they all have strong arguments. Encounter rates can also be useful to indicate broad trends and to allow the reader to see the raw data, although visibility should be considered. Where there is uncertainty in cut-off distance for any method, we stress on the importance of presenting a range of densities [National Research Council, 1981]. Uncertainty in group spread and group size could be dealt with in the same way. Where group size is unknown, group density can be used rather than individual density [Buckland et al., 1993, 2001; National Research Council, 1981]. Where population density is low and information on visibility is unavailable, alternative methods are needed [Fig. 5, choice 1; see Marshall, 2007 for options]. Owing to continuing habitat loss, degradation and hunting, this is a perpetual problem. Also some populations are simply not appropriate for density estimation [Marshall, 2007].

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