



Counting gibbons: The evolution of sample methods

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Abstract

Estimating the population sizes of endangered species in the natural environment is a major activity of conservationists. Different types of animals require different methods of population census and sampling. Statistical standards of sampling populations have increased and new analytical software has reduced the time needed for manual computation, but increased the need for standardized data collection methods. Here I discuss the methodology used in gibbon population sampling and current discussions regarding the best method of data analysis. Gibbons are most efficiently sampled by listening for their duetted songs given by mated reproductive pairs in small territorial groups. Several problems have to be overcome in field data collection and analysis: the decline in sound detection with distance, the possibility of groups singing more than once in a day, the probability of a group singing (or not singing) on a given day, and determination of the total area that the audible groups are occupying. The traditional way of dealing with these problems is by triangulating on singing groups from several simultaneous listening posts, and carefully mapping the locations of groups. There are biases present in most methods and ways overcoming bias using newer methods are discussed. Survey of gibbons and other animals is a constantly evolving process, and there is still no universally accepted methodology.

Keywords: Auditory survey, census methods, gibbons, population sampling, wildlife survey

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1. Introduction

Conservation of endangered species of plants and animals requires methods for estimating population sizes, and also the probability of survival of the species or continued decline [1]. Complete census of individuals is usually only possible for a few Critically Endangered species that have declined to very low numbers; other species require methods of sampling large populations often distributed patchily over the landscape. Cryptic or secretive habits, wide-ranging movements and difficulty of identification make statistical sampling very difficult for most species. Tracks, signs and vocal cues are important aids in sampling animals and studying population structure and movements [2].

The naturalists who initially observed, described and mapped animal populations were not concerned with estimating the sizes of populations, and did not have the methods for doing so. Modern conservation biologists now are concerned with studying population demographic and genetic structure and estimating population size for a variety of reasons, and have a growing statistical toolbox for doing so. The particular methods used for sampling gibbon populations

have gone through an evolution that is still continuing and improving; as a participant in this evolutionary development I wish to outline it and present my ideas on what is being done and what might still need to be improved.

Gibbons make loud noises, including duets performed by male-female pairs, with other members of the group sometimes participating [3, 4]. Ellefson (1974) [5] may have been the first person to describe a gibbon duet, consisting of the female's great-call and male's hoot series, as the loud songs signaling the presence of a mated pair on its territory. The adult pair are the central component of a small territorial group that occupies a permanent range, usually around 15 – 50 ha in area, depending on species. These characteristics make gibbons relatively easy animals to census through direct observation, but such census is time-consuming and cannot be applied to large populations. The availability of gibbon duets as auditory cues that indicate the presence of breeding pairs make auditory sampling the method of choice in gibbon surveys.

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2. Auditory Sampling

By listening for the loud calls or songs of gibbon groups we can estimate the density of groups in an area, and by replicating sample areas we can then estimate the density of the population within a large sampled area such as a national park. Before attempting to do this we must be familiar with all the call types that gibbons make, and the structure of the duet bout. The duet consists of repeated great-call sequences given by the pair at intervals of 1 to 2 min, and lasting as long as 10 to 20 min. The duet structure varies somewhat between the species of gibbons. Haimoff (1984) [6] has described these duet patterns and attempted to standardize their terminology. Distinctive solos are also given by the males of all species. These are easily recognizable but both mated and not-yet-mated males may give solo calls in most species. Special alarm hoots and inter-group conflict hoots are also given by gibbons which are important to behavioral researchers but not of much use in sampling a population.

2.1. Triangulation from listening posts and mapping

Auditory sampling of gibbons can enable us to determine the locations of singing groups by recording the compass direction of each group duet heard and estimating its distance away. Gibbon duetted songs can be heard from as far away as 2 km, but estimating the distance is very difficult, although accuracy improves with experience. In order to map the groups in an area, three or four “listening posts” (LPs) are established on nearby hilltops or ridges and the groups heard from each LP are noted down over a period of several days (usually four days). In order to map the locations of groups, listeners on different LPs several hundred meters apart take compass readings simultaneously which can be used to determine the location through “triangulation”, mapping the intersections of the compass directions from two or more LPs. (Fig. 1). The exact times of all the bouts heard from all LPs must be noted down so that it can be assured that calls that are triangulated from different LPs emanate from the same group. Songs that are too far away to be heard by listeners from at least two LPs are usually not included in population estimates.

There are additional problems in mapping and identifying groups for density estimation. The major problem is that gibbon pairs may duet more than once during a day, or not at all. There are several procedures and rules-of-thumb that allow the reasonable determination of the number of groups singing. Sometimes particular features of the duet pattern such as sound frequency allow us to identify individual groups [7, 8]. Otherwise, it is usually assumed that if song locations map within 500 m of each other, they are from the same group unless proven otherwise. The most important condition that determines that singing locations are from different groups is their singing at the same time, or in bouts that are too close in time to be

from the same group. During a 4-day period of listening, it is possible to separate most groups that occupy adjacent territories and map the approximate location of the boundary that separates them (Fig. 2). At the end of the listening period, there are still likely to be a few groups that cannot be diagnosed as separate from other nearby groups, which will result in some underestimation of population density. With four days of listening, this is not likely to be more than about ten percent of the population (see Equation 2 below). Increasing the number of days of listening from each array of points would help reduce this problem, but this would demand more time and manpower and might reduce the number of arrays or sample areas that can be surveyed; this involves a trade-off between quality of data and quantity of data.

2.2. Listening area

The density (D) of groups within an area is calculated from

$$D = N/Ap \quad (1)$$

where N is the number of groups heard and mapped, A is the “listening area” and p represents a correction factor to compensate for groups that were present but did not happen to duet during the period of survey. The estimation of p will be described in the next section.

There are several ways of determining the listening area (LA), and most have the potential for introducing bias. Two ways were proposed by Brockelman and Ali (1977) [7]: the fixed radius method which assumes that all groups can be heard a fixed distance from the LP, and the terrain-limited method which uses a map of the terrain to determine how far groups can be heard around an array of carefully placed LPs. The fixed radius method has been used where there are no terrain features that limit the listening area, or where suitable topographic maps (preferably 1:50,000 UTM maps that also show forest cover) are not available. The fixed radius method has been used by many surveyors, usually assuming reliable detection within a radius of 1 km [8 – 13]. An example of a manual plot of gibbon singing data from four listening posts is shown in Fig. 1. In this survey, five days of listening were conducted per array of LPs. At the end of the survey, the mapped groups’ singing locations for all five days are all plotted on a single map, color coded by day. The challenge is then to determine the number of groups from this map (Fig. 2). The main device is to determine the locations that must be from different groups by identifying those that were heard during overlapping times; territorial boundaries must exist between these locations.

The fixed radius method always underestimates gibbon density unless the radius is made so small (< ca. 600 m) that most groups heard lie outside the listening area, which wastes much of the data. Several surveys have shown that a fixed radius of 600 m generally gives a significantly higher density than use of a

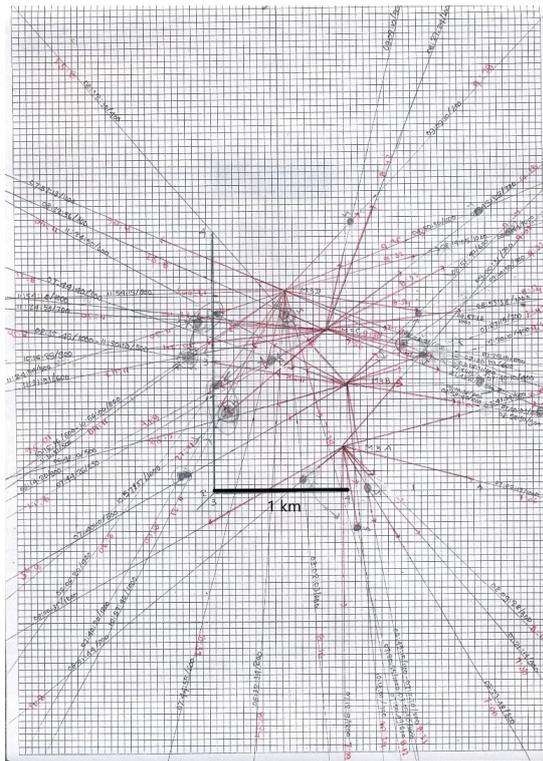


Figure 1: Map showing how groups are triangulated from 4 listening posts on a single day of listening. Singing times are written on the sighting lines to facilitate identification of groups, which here are marked by penciled points at the intersections of the lines. The red segments of the lines represent the crude estimates of distance from the listening posts. (Data from the Mahamyaing survey in Myanmar [8]).

radius of 1000 m [8, 13, and unpublished data], which indicates that many groups between 600 and 1000 m were not heard. These groups were located behind unseen hills or in valleys where sound transmission was blocked by the terrain.

The terrain-limited method of listening area estimation involves selecting a large valley from the map where sound transmission is not likely to be obstructed by terrain features. The method requires that four LPs be carefully selected so that all parts of the valley are within hearing range of at least two LPs. Often it can be assumed that any group heard from any LP must be in the valley. Often most parts of the valley are visible from the LPs so that it can be seen that sound transmission passes through open space over the forest canopy: this makes it possible to hear groups from distances of 2 km or so, provided that the air is still and not breezy. In the terrain-limited method, it is assumed that the all the groups heard represent a complete census of those that sang in the listening area.

One criticism sometimes heard of this method is that the habitat within the listening area may not be representative of the entire range of slope and elevation in the total area sampled. Usually the listening area encompasses all terrain types and elevations, although it is difficult to demonstrate this or convince

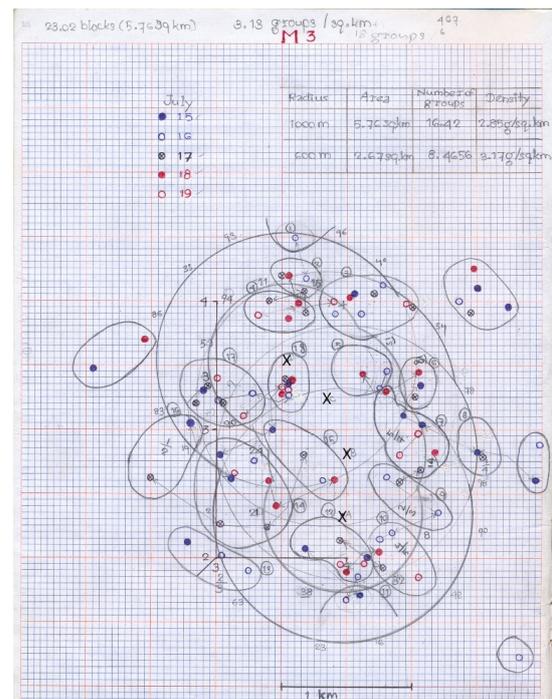


Figure 2: A plot of all singing locations triangulated on the 1-day singing data maps, color-coded by day (same array as in Fig. 1). Listening posts are marked by X. Groups heard singing at overlapping times are connected with lines (most too faint to see). Locations assumed to be of the same group are circled. The circles represent fixed radii of 1.0 and 0.6 km around each LP.

a statistician that there is no possible bias. Nevertheless, this method yields the highest estimates of gibbon density of all methods commonly in use [14 – 16].

The solution to the problem of eliminating bias in the determination of the listening area lies in the use of the Distance method for the analysis of line transect and point transect data [17]. Distance methods are now widely used in wildlife sampling and software is readily available on the R platform. The Distance program does not require estimation of a listening area, but determines the density of groups as the area under a detection function extending from the line or point, outward to some truncation distance. The main assumption of the Distance program is that the probability of detection is 1 if the group is directly over the transect line or point.

In the case of gibbons, auditory sampling uses the *point transect method* where distances of all singing groups are measured to a single sample point. However, distances all must be determined as accurately as possible using triangulation from multiple LPs. I believe that the best method of achieving this is to initially select the sample points for Distance on a map, and then arrange arrays of LPs around the sample points such that there is no possibility of missing any group singing near the sample point. Each array will consist of four LPs in a 4-sided polygon around the point, each LP approximately 300-500 m from the

point. It is not necessary that the LPs are in a regular polygon or square, as long as their locations are precisely known and mapped. The LPs are placed on elevated points of terrain selected from a topographic map, and explored on foot before the survey so that no unseen obstructions to sound are present. Prior to analysis, all distances of gibbon groups are remeasured on a map to the sample point. It is not necessary, or even desirable, to place an LP on or even near the sample point; doing so might spook or scare any groups that might be in the area.

A final requirement of Distance methods is that the sample points (or transects) are randomly selected within the whole sample area, or superimposed on a regular grid over the area. Most early surveys of gibbon populations have not properly randomized the sample procedure, but have rather carried out what may be considered to be representative area surveys. Proper means with confidence intervals cannot be placed around most such estimates.

A survey of white-handed gibbons in Huai Kha Khaeng Wildlife Sanctuary in western Thailand is now being completed by Wildlife Conservation Society–Thailand using triangulation from LPs and the point-transect Distance program described above. Preliminary (unpublished) results show that estimated densities of gibbon groups around the randomly selected sample points average >4 groups km^{-2} , rather higher than expected, which is a tribute to the quality of protection of the sanctuary by the Dept. of Parks, Wildlife and Plant Conservation, as well as to the efficacy of the survey methods used.

2.3. Singing probability

The final challenge to accurate estimation of gibbon groups is the estimation of the probability that an average group will duet on any particular day of the survey, defined as $p(1)$. From this can be estimated the probability that a group will duet at least once over a period of n days, $p(n)$, which will become the correction factor in the above Equation (1). The sequence of singing or not singing over a period of n days is treated as a binomial process where p and $(1 - p)$ are the probabilities of the two alternatives. The model assumes that p on successive days is independent. The probability of singing at least once in n days is predictable from $p(1)$, as

$$p(n) = 1 - [1 - p(1)]^n \quad (2)$$

This formula was devised, or reinvented and applied to gibbon calling, by Brockelman and Srikosamatara (1993) [14]. While it allowed us to determine the probability of missing groups that did not sing after n days knowing the value of $p(1)$, it did not allow accurate estimation of $p(1)$. That is, there was no simple way of estimating the number of silent groups—the groups that did not sing at least once during the survey. Members of the Gibbon Subgroup of the IUCN Primate Specialist Group, assigned with preparing “Best

practice guidelines for surveying and monitoring gibbons”, have recently figured out how to estimate $p(1)$ from data on the frequencies of groups singing on n numbers of days out of the total number of days of survey per array of LPs (usually 4 days). A maximum likelihood estimator has been developed by David Borchers (personal communication) for estimation of $p(1)$ and $p(n)$ with confidence limits. The basic data for this estimation consist of the numbers of groups that sang on increasing numbers of days out of n . First, we need to tabulate the singing record of each group over the n days. For example, if $n = 4$, we need the number that sang on only one day out of four, on any two days out of four, any three days out of four, and on all four days. This is simply the frequency distribution of the total number of days on which each group sang.

For most gibbon species and sites, the probability of singing on a single day $p(1)$ varies from about 0.20 (for some western hoolock populations) to about 0.70 (for some *Hylobates lar* populations). For a $p(1)$ well below 0.5, the correction factor in equation (1) will make a sizable difference to the estimation of density.

2.4. Capture-recapture method for density estimation

A number of statistical methods have been developed for sampling wildlife populations that can be applied to the use of data consisting of cues such as songs and calls detected by listeners. Some methods require the ability to identify individual callers or groups (such as capture–recapture methods) and others do not. A method that is now receiving much attention is the Spatially Explicit Capture-Recapture (SECR) method that uses auditory data [18, 19]. It involves analysis of the probability that a group is heard calling from two LPs (as opposed to just one LP) a known distance apart. Data on joint detection frequency of groups at various distances from the listeners allow determination of a detection function and also group density. The method is touted to require no mapping of groups and, potentially, require less time and manpower than more traditional methods that involve detailed mapping. The claim that no mapping is required, however, is suspect.

An issue that “remains to be resolved” for the SECR method is how to deal with uncertain recapture identification [18]. Ascertaining that the same group has been detected from two LPs on a single occasion depends primarily on matching the times of the bouts heard, and verifying that the listening angles intersect at a plausible distance away. Greater difficulty is encountered in determining if another duet heard later in the day is given by a group heard earlier, or represents a new group, because groups can duet more than once during a morning, and usually move between singing locations. Matching bouts heard on successive days presents further challenges. The SECR software requires users to input the “capture histories” of all groups, but no instructions are provided for how to

determine group histories. In relatively dense populations (> 2 groups km^{-2}), where group ranges often border one another or even overlap slightly, allocating singing events to different groups requires detailed mapping of singing locations from data collected over at least 4 days, as explained in the above sections. Such determination and mapping of groups is required for estimation of singing probability as well as for verifying recapture identifications. Borchers et al. [18] state that “we expect that methods that use location data to quantify the probability that detections are recaptures will be useful.” I agree with this admission and am hopeful that such a process, which we now carry out on paper maps or with the help of GIS, can be automated.

2.5. *N-mixture models*

Among the methods that do not require identifying or marking individuals is a class called *N-mixture models* for estimating populations using call count data [20]. Spatially replicated point counts are made for calling or singing species without identifying individuals, or measuring distances to all groups heard. Estimation of density involves a maximum likelihood procedure that makes assumptions about the spatial distribution of the callers (Poisson) and calling probability (modeled as a binomial process). The method has been tested on bird data and can produce population size estimates from simple and easy-to-collect field data. However, the method has been criticized for reliance on assumptions (random distribution of groups and binomial singing frequencies) which may be inappropriate in some cases, resulting in poor estimation of detection probability [21]. The method needs to be tested further against other more data-intensive methods.

3. Methods Using Visual Detection

3.1. *Population census*

Seeing gibbons is much more difficult than hearing them. Because gibbon pairs of nearly all species duet on most days of good weather, and no groups have been found that do not duet (even after many years of research on well-known study populations), auditory location is the standard in gibbon survey and study. Observation of groups, however, is necessary when we wish to conduct a *census*, which is an inventory of *all* groups and individuals residing in a defined area. A census involves approaching each group and observing its size, age composition, color morphs and any other features that distinguish it from other groups in the neighborhood. Approaching wild groups for close observation requires skill and practice. One technique that is useful is to approach while the group is duetting, when its attention to what is on the ground is relaxed. When duetting stops, one must take cover and move extremely quietly. Census is best done in

wet weather; when the leaves and sticks are dry and crackle underfoot, approaching wild gibbons is almost impossible. A thorough census requires at least one day per group in the area, and hence only relatively small areas (a few square km) can realistically be censused.

An auditory/visual census is required in several situations, including (1) site preparation for a long term study, (2) preparation of an educational or tourism area featuring gibbons, (3) replicated, long term monitoring of the demography or density of a population, and (4) monitoring of a critically endangered species such as the Hainan black-crested gibbon.

3.2. *Line transect method*

Line transect methods in the standard Distance software package have a relatively long history of development [17] and require little explanation here. They use visual detection of social groups or individuals, and have been widely employed in primate surveys [7, 22 – 24]. The Distance line transect method evolved from the older “strip transect” methods of Kelker, Hayne, and others [22]. Debate has continued regarding which is the least biased method [25, 26]. Such methods seldom give very accurate estimates of primate density because of frequent failure to satisfy the required assumptions: probability of detecting animals over the transect line = 1, detection of animals before significant movement away, failure to determine group center, lack of sufficient observations, etc. Lack of sufficient replicated transects is almost always a problem because of the heavy work involved. For gibbons, the problem of groups fleeing before detection can be very serious. In areas where gibbons have been habituated to humans, however, overestimation of density rather than underestimation may result due to differences caused in the detection function [25].

4. Discussion

The estimation of the population sizes of gibbons in the natural environment depends on accurate methods for estimation of density of breeding groups in the forest. The behavioral and ecological characteristics of gibbons make population survey of gibbons easier than for other types of primates: relatively stable, sedentary groups, and loud singing by mated pairs. The genetic effective population size of gibbon populations is roughly twice the number of groups.

The two major issues in the estimation of gibbon group density have been the estimation of the number of groups in a given area from the songs or duets heard, and the estimation of the area that they occupy. Interpreting the auditory data requires information on the singing frequency of groups (probability of singing per day), the number of songs given per day. Estimation of the area requires knowing how detectability (chance of hearing a group that sings) decreases

with distance from listeners. This will depend very much on selection of listening posts and the terrain roughness, as well as factors such as weather and season. Distance software analysis is now the preferred method for modeling detectability, and does not require prior determination of the “listening area”. But it does require careful selection of listening posts using a topographic map, and careful mapping of groups.

The newer SECR method models detectability using auditory data from two or more listening posts and does not require measurement of distances to groups. However, there appear to be a few issues that have not been fully dealt with in the SECR method. The software does not contain methods for verifying recapture identification from multiple calls (songs) within days and between days. This is left to the users’ ingenuity, and normally such verification requires detailed mapping exercises. The software also does not estimate the probability of calling. Because of these problems the SECR method may require further development, or specification of how these problems are to be solved. In spite of these problems, the SECR method is ingenious and promises to become a useful method for density estimation. It is still being improved and testing it against other methods such as the point transect is highly desirable. This has not progressed very far because the point transect Distance method itself is also still in the process of being refined and tested for use in gibbon survey.

Auditory methods probably give more reliable estimates of gibbon density than visual line transect methods, partly because they allow for coverage of much more sample area than is normally the case in line transect surveys. The preparation of transects in dense tropical forests, especially over difficult terrain, is laborious (in some areas impossible) and hence under-sampling usually results. Gibbons can be heard singing from distances greater than 1 km away, but can be seen reliably only 20–30 meters away in evergreen forest (provided they don’t see you first).

5. Conclusions

The methods of survey and sampling of wildlife populations have evolved in spurts of research activity and they continue their transition into the modern age of improved statistical estimation and computer modeling. The development of better methods of gibbon sampling must continue as there is at present no unanimous agreement as to the best or most promising method. The most modern methods will employ more advanced detection technology such as acoustical analysis and recording equipment, as well as field data input methods. But as better methodology is being developed, gibbon populations are becoming more fragmented and are declining in numbers. As populations decline in numbers it becomes more critical that we know how many there are left.

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