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# Survey and Census Techniques for Canids

E.M. Gese

## 15.1 Introduction

We already know that the status and distribution of canid populations throughout the world is of growing concern for biologists and the public alike. Habitat loss, fragmentation and degradation, human persecution, decreases in prey, disease, poaching, and increased competition with other carnivores due to reduced space and habitat, have led to some canid species facing extinction, while others occupy only a fraction of their former range. While reintroductions of some species have been successful (e.g., grey wolves *Canis lupus* to the Northern Rockies of the U.S.), other species face an uncertain future (e.g., African wild dogs *Lycaon pictus*). Paramount to canid recovery, reintroduction, or management, is acquiring accurate information regarding the status of a species, or a particular population. Reliable methods that provide accurate data on the distribution, abundance, and population trend of a species are required. These parameters are also fundamental for helping to determine the conservation status of a species according to the IUCN Red List Categories and Criteria (for example, the B criterion relies on knowledge of geographic range size, where a species with a range of less than 20,000km<sup>2</sup> could qualify in one of the categories of threat). However, because many canids are secretive, nocturnal, wide ranging, in densely vegetated habitats or remote areas, or at extremely low densities, surveys of a canid species or population can be very difficult.

Abundance may be assessed in two ways: relative and absolute. Relative abundance uses indices of animal abundance (e.g., track counts, dens) that can be compared over time or between areas. Absolute abundance involves actually counting animals and estimating the number or density of animals in the population. With repeated sampling over time, both relative indices and absolute estimates can be used to monitor population trends. This chapter reviews techniques useful for censusing canids, and is adapted from Gese (2001). For techniques related to determining demographic parameters (birth, death, emigration, immigration), readers are referred to Caughley (1977), White and Garrott (1990), Royama (1992), and Thompson *et al.* (1998). Methods for censusing or surveying wild canids vary in accuracy, reliability and cost. Many of the techniques described herein require in-depth evaluation as to their accuracy and reliability in monitoring population trends (Gese 2001). As an example, a recent

study by Schauster *et al.* (2002a) compared six survey techniques for monitoring abundance of swift foxes (*Vulpes velox*) in Colorado, USA. This study found that mark-recapture estimates ( $r = 0.711$ ) were the best predictor of fox density, followed by scat deposition surveys ( $r = 0.697$ ), scent-post surveys ( $r = 0.608$ ), spotlight surveys ( $r = 0.420$ ), trapping surveys ( $r = 0.326$ ), and lastly, activity index surveys ( $r = 0.067$ ). Combinations of techniques increased prediction capabilities. Other studies that used, or attempted to use, the techniques described in this chapter have been included as examples.

### Some considerations before implementing a survey

Prior to surveying any canid population, the precision, accuracy, power, sample size, survey design, and statistical assumptions of each method should be considered (Skalski and Robson 1992). In addition, for each method the observer must address problems pertaining to “observability” or “catchability” of the species, the size of area to be sampled, costs, logistics, manpower, and time constraints (Lancia *et al.* 1994).

## 15.2 Methods employed to determine species distribution

Sometimes it may only be necessary to determine the presence and distribution of a species. Methods typically used to determine species distribution include habitat mapping, questionnaires, interviews, sighting reports, or confirmation of sign. Any survey method that provides an estimate of animal abundance provides distribution information as well.

### 15.2.1 Habitat mapping

Time can be saved by considering the type of habitat required for a species and examination of habitat maps or aerial photos. Habitat suitability models have been developed for many wildlife species (e.g., Boyle and Fendley 1987; Rogers and Allen 1987), but have not been developed for canids. With the continued development of satellite imagery, remote sensing, and Geographic Information Systems (GIS), areas containing suitable habitat for a species can be identified allowing for maximisation of survey efforts. Surveys can then be stratified by habitat types or land classes (Macdonald *et al.* 1998).

### 15.2.2 Questionnaires, interviews, and sighting reports

Many agencies compile status reports using questionnaires to assess the relative abundance and distribution of canid species. Sightings and general impressions from people in the field can determine species distribution, and gain a subjective estimate of animal abundance. More in-depth questionnaires or interviews of persons with knowledge of the area and who spend considerable time in the field provide not only a range report, but may also provide an estimate of abundance (e.g., Allen and Sargeant 1975; Harris 1981). Questionnaires, interviews, and sighting reports have been used to determine distribution, and sometimes abundance of several species (e.g., Allen and Sargeant 1975; Harris 1981; Fuller *et al.* 1992; Fanshawe *et al.* 1997). Problems with this method include misidentification of species, low response levels to the questionnaire, a bias for animal sightings concentrated along roads or near human habitation, and the reliability of the respondents.

### 15.2.3 Presence of sign

In the absence of visual confirmation of the species itself, surveys of animal sign may be used to determine presence. Several different methods of sign surveys have been used, including documentation of tracks, scats, scratches, burrows or dens, and hair samples (often obtained through the use of hair snares or hair tubes). The use of track plates to determine species presence has proven useful (e.g., Zielinski and Truex 1995). A full description is provided by Zielinski (1995), but track surfaces may generally be produced from smoked or carbon-sooted aluminum plates, contact paper, chalk, or ink. A visual and/or olfactory lure is used as an attractant and while investigating the attractant, the animal leaves tracks on the tracking surface. Identification of tracks, getting the animal to step on the plate, transportation of the plates, and protecting the track plates from weather are just a few of the common problems that require prior planning (Zielinski 1995; Zielinski and Truex 1995). This technique provides a reliable measure of species distribution or presence, but may be unreliable for determining relative animal abundance.

A common problem with using sign to determine canid distribution is the consistent identification of tracks, scats, burrows, and hair samples. Species identification from scats can be facilitated by using faecal bile acid patterns (e.g., Major *et al.* 1980). Examination of hair samples with a light microscope and comparison to a hair key or reference collection can aid species identification (e.g., Adorjan and Kolenosky 1969; Moore *et al.* 1974). DNA techniques allow for more accurate identification from scat or hair samples (Foran *et al.* 1997a,b; Paxinos *et al.* 1997), and

can also be used to identify individual animals allowing for estimation of population size (e.g., Kohn *et al.* 1999). When using scat surveys, the seasonal decay rate of the scats may need to be considered, as well as whether scats are being consumed by scavengers. Also, the amount of sign left behind by an animal does not always correlate with animal density, nor does failure to find sign necessarily indicate species absence.

In their most rudimentary form, sign surveys provide distribution information. When standardised, these sign surveys may be used as an index of animal abundance. If certain areas or habitats are repeatedly surveyed over time and the number of hours of searching (or some measure of effort) is recorded, then surveys may be standardised to allow for trends over time or comparisons between areas.

### 15.2.4 Remote cameras

The use of remote cameras set along trails, near bait stations, or nests has been used mainly to detect forest carnivores. The cameras, commercially available from several manufacturers (Kucera *et al.* 1995), can be triggered by an animal tripping a line, or activated remotely by pressure-sensitive plates, motion or heat detectors, or breaking of an infrared beam.

## 15.3 Methods for estimating animal abundance

After determining species distribution, data on animal abundance and population trends may be required. Animal abundance may be monitored indirectly by counting animal sign, or by direct methods of counting the animals themselves. Estimating animal abundance requires consistent and standardised application of a technique to be able to detect changes or differences with some degree of accuracy, precision, and power. Therefore, for the following techniques one must maintain a standardised protocol for the survey and consistently apply it to all future surveys. Whether sign surveys, indices of relative abundance, or measures of absolute animal abundance are used, caution should be exercised when examining population trends. Assessing rates of increase or decrease from trend data should take into account the precision and accuracy of the methods used. The influence of other variables on survey results should also be taken into consideration, such as characteristics of the animals themselves, topography and vegetation, temporal factors, observer experience, ability, and fatigue, and spatial distribution of the species. One should examine the assumptions and power of the technique to determine its ability to detect population changes (Gerrodette 1987; Eberhardt and Simmons 1992).

### 15.3.1 Indirect methods

#### Scent-station surveys

One of the most common sign surveys used for indexing canid abundance is scent-post or scent-station surveys (Linhart and Knowlton 1975; Roughton and Sweeny 1982; Schauster *et al.* 2002a). Scent-station surveys involve placing a scented tablet or other attractant within a circular area of sifted dirt. Tracks left by an animal are identified and recorded. Typically, stations are spaced at predetermined intervals along roads or trails and then visited for 3–4 consecutive nights to record tracks; the sifted area is swept smooth after each night. The frequency of animal visitation to operable stations (i.e., those not disturbed by wind, rain, vehicles) is used as an index of abundance. Scent-post surveys have been used to estimate the relative abundance of many canid species (e.g., Linhart and Knowlton 1975; Travaini *et al.* 1996; Sargeant *et al.* 1998; Schauster *et al.* 2002a). Seasonal changes in habitat use and visits to multiple stations by a single animal can contribute to invalid correlations of animal density and visitation rates; see Smith *et al.* (1994) and Sargeant *et al.* (1998) for recommendations on how to use these methods appropriately. Misidentification of tracks, weather (wind, precipitation), wariness of animals, and manpower should also be considered with scent-station surveys.

#### Activity index

A variation of the scent-station survey that has been used to index dingo populations is the activity index (Allen and Engeman 1995; Allen *et al.* 1996). This index of animal visitation uses a sifted dirt area on a road without any scent or lure to attract animals (Schauster *et al.* 2002a). The number of track sets crossing the sifted area is used to assess relative abundance and calculate a variance estimate (Engeman *et al.* 1998).

#### Scat deposition transects

The rate at which scats are deposited along established roadways or trails has been used to estimate relative abundance of canids (e.g., Andelt and Andelt 1984; Crête and Messier 1987; Beltrán *et al.* 1991; Schauster *et al.* 2002a). This method involves designating transects or routes along a roadway or trail, clearing all scats from the road, then returning and collecting all scats encountered two weeks later. If transects vary in length, or the time between collections varies, then the index can be standardised to scats/km/day. A study by Knowlton (1984) found that scat deposition rates for coyotes were correlated with estimates of animal density derived from mark-recapture techniques using radio-isotope tagging of faeces. For long-term monitoring, scat transects should be conducted along the same routes at the same time of year to avoid introducing biases associated with differential prey digestibility and seasonal changes in food items

consumed (Andelt and Andelt 1984). Misidentification of scats and heavy vehicle traffic on roadways can be problematic when using scat counts. Use of DNA techniques for identifying species from scats may alleviate the problems of misidentification (Foran *et al.* 1997a,b) and identification of individual animals collected during scat deposition transects could be used to estimate population size (Paxinos *et al.* 1997; Kohn *et al.* 1999). A recent study by Harrison *et al.* (2002) compared survey techniques for estimating relative and absolute abundances of swift foxes in New Mexico. This study found that for relative abundance surveys, the most efficient technique was collection of scats followed by verification of species depositing scats with DNA analysis, while for absolute abundance surveys, trapping and re-sighting with remote cameras at bait stations was more accurate than counting unique microsatellite DNA genotypes from collected scats.

#### Track counts along a transect

Tracks left by canids along river beds, dry washes, sandy fire breaks or roads, or on snow-covered roads and trails have been used as a relatively simple, efficient, and inexpensive measure of relative abundance for canids (e.g., Crête and Messier 1987; Servin *et al.* 1987). Canids which occupy regions that receive snow can be monitored by counting tracks along established transects one to two days after fresh snowfall. Some pitfalls when attempting transect counts of tracks should be noted. Misidentification of tracks and low power to detect population changes can occur with track counts (Ballard *et al.* 1995). Precision can be increased by increasing sampling effort, or increasing the length of transects if censusing highly nomadic species. Much of the power of this estimator is dependent upon a high rate of encountering sign along the transects (Kendall *et al.* 1992). When working in areas with snowfall, one must also consider the condition, consistency and depth of the snow, ambient temperature, and the time of year. As is typical for any survey technique involving sign, observer experience at interpreting tracks is also crucial for consistent and reliable monitoring.

#### Den and burrow surveys

Ground and aerial surveys for active dens have been conducted along transects to index relative abundance of some canids, mainly foxes (e.g., Trautman *et al.* 1974; Garrott *et al.* 1983; Hersteinsson *et al.* 2000). The key to this survey technique is relatively open habitat with little vegetative cover and a species that makes conspicuous dens or burrows. These surveys can be relatively expensive (aerial searches) and/or labor intensive (ground searches). The presence of faeces or tracks at the burrow or den can assist in species identification. Ground surveys along transects can also be used to calculate the density of dens if the perpendicular distance from the transect to the den

is recorded. This technique does not work well for indexing canids with large social units. For animals that exist in packs, the number of active dens would more likely indicate the number of social units present across an area, but not the size of the social unit.

### **Vocalisation response surveys**

For canids that utilise howls to communicate, the response rate to simulated vocalisations has been used as an index of relative abundance (e.g., Wenger and Cringan 1978; Okoniewski and Chambers 1984; Fuller and Sampson 1988; Robbins and McCreery 2003). Howling surveys typically employ recorded vocalisations, although human imitation can be used. Travelling along roads or trails and stopping at predetermined intervals, howls are produced and then observers listen for a specified amount of time for a response from the target species. A recent study using both playbacks and human simulations of long distance calls of African wild dogs recorded that dogs would approach from distances of as much as 2km, and found that playbacks are an effective conservation tool particularly where road networks are limited and/or thick vegetation restrict off-road driving (Robbins and McCreery 2003). Surveys may be conducted over several nights using the vocalisation response to estimate relative abundance. Standardisation and consistency of this method is needed for reliable and comparable results for trend analyses. The seasonal, social, temporal, and spatial factors that influence vocalisation rates also need to be noted (Harrington and Mech 1982; Walsh and Inglis 1989; Gese and Ruff 1998). For an accurate population census, the area of interest needs to be intensively surveyed to obtain adequate coverage (Fuller and Sampson 1988).

### **Frequency of depredation complaints**

The frequency of livestock depredation complaints may be useful as an indicator of relative abundance under the general belief that animal abundance is correlated with rates of livestock predation. Because this relationship has not been explicitly tested, caution should be exercised when using this technique as depredation rates are subject to changes in livestock stocking rates, habitat type, size of area used, husbandry practices, and environmental variables (Knowlton *et al.* 1999).

### **Some considerations when using indirect methods**

Indirect methods provide only relative abundance and must be applied consistently for any reliable comparisons between areas, habitats, or time. Whenever indices of relative abundance are used, it should be determined whether relative indices and absolute abundance are positively and linearly related. Comparison of an inexpensive indirect method to a more expensive direct method could prove worthwhile for calibration of the less expensive technique. During calibration, the techniques

should be performed concurrently and conducted on a species-specific, habitat-specific, and seasonal basis. Unfortunately, few indices of relative abundance have been tested with a known population estimate.

## **15.3.2 Direct counts**

Direct counts involve actually counting the animals themselves, in contrast to counting sign. These counts may use either dead animals (e.g., harvest reports, mortality samples) or live animals (e.g., trapping, sightings). The assumptions of direct counts and the estimators used to determine population size should be reviewed (Caughley 1977; Burnham *et al.* 1980; Skalski and Robson 1992). Counts may involve total counts of the area, or a subsample of the area with extrapolation to the rest of the area of concern. Stratification of subsamples by habitat type can increase the validity, usefulness, and precision of the survey (Macdonald *et al.* 1998).

### **Harvest reports and pelt registration**

One method of estimating abundance (and distribution) of a species is using historical and current harvest or trapping records (e.g., Clark and Andrews 1982). In the Canadian provinces, mandatory pelt sealing reports have been used to estimate furbearer population trends (Novak 1987). While information from harvested animals can be used to construct models for population estimation (Clark and Andrews 1982), harvest data alone is generally not a reliable estimate of population trends. Pelt prices, trapper behaviour and memory recall, differential harvest methods, and environmental and social factors all influence harvest rates (Clark and Andrews 1982). For rare species, harvest reports are generally unreliable for population trends, while harvest reports for abundant furbearers may be reliable measures of population trend. However, little in-depth testing has been conducted to confirm the relationship between population density and harvest statistics.

### **Road mortality samples**

The frequency of carcasses found on roads has been proposed as a measure of population trend, usually as an index of relative abundance (e.g., Clark and Andrews 1982). However, differences in animal behavior and movements, habitat, traffic density, road surface, and road density likely influence kill rates of some canids. The relationship between population density and road kill rate also has not been adequately examined. Road mortality samples can confirm species presence.

### **Drive counts**

In certain habitats, animals may be driven into an area and counted as they cross the observer's line (e.g., Beltrán *et al.* 1991). This technique is labour intensive, due to the use of



counters, beaters, and possibly hounds, and sample sizes may be difficult for statistical analyses and comparison.

### **Spotlight surveys**

Spotlight surveys are a cost effective method typically used for assessing the relative abundance of nocturnal canids (e.g., Ralls and Eberhardt 1997; Schauster *et al.* 2002a). These surveys involve two observers standing in the back of a truck driven slowly along roadways, scanning the road and sides using spotlights. When an animal is detected, usually by eye shine, the driver stops and the observers identify the animal (sometimes using binoculars or a spotting scope). The mileage and time of detection is recorded for each sighting. An index of animals/km is then calculated. Spotlight counts can be used to estimate population size with line-transect methodology if the perpendicular distance to the sighted animal is recorded (Thompson *et al.* 1998). Transects need to be fairly lengthy, and because vegetative cover and topography influences visibility, these variables should be considered in survey design (Ralls and Eberhardt 1997). Surveys can be conducted over several nights (repeated counts) to obtain a measure of sampling error. Large samples with replication are needed to detect changes in population size with any statistical power (Ralls and Eberhardt 1997). Surveys can be conducted seasonally and annually for population trend analysis (Schauster *et al.* 2002a). Spotlight counts do not work well in areas with low densities of canids. A recent study by Ruelle *et al.* (2003) has noted that a number of methodological improvements are necessary before spotlight distance sampling can become a routine monitoring tool for fox species.

### **Remote camera traps**

While camera systems have been used to detect species presence and identify animals at bait stations or nests, they can also be used to determine abundance if individuals can be identified by artificial tags (e.g., ear tags, radio collars) or natural features (pelage, etc.) and then apply mark-recapture estimators. Harrison *et al.* (2002) found that re-sighting with cameras at bait stations was more accurate for estimating swift fox abundance than counting unique microsatellite DNA genotypes from collected scats. Remote cameras also provide a permanent photographic record. Disadvantages of remote cameras include their expense (although the technology is becoming increasingly affordable), getting animals to trigger the camera, non-target species activating the camera, and the delay between photo acquisition and development (although digital cameras may negate this concern).

### **Catch-per-unit-effort**

Live-trapping gives a positive confirmation of species presence (distribution) and the number of animals captured per trap night can also be used as an index of

relative abundance (e.g., Knowlton 1984; Crooks 1994; Schauster *et al.* 2002a). Trapping is expensive and labour intensive, and can be ineffective in areas with low density. In addition, standardisation of capture procedures and variation among individual trappers can cause problems.

### **Capture-mark-recapture**

While mark-recapture is fairly time consuming, labour intensive, and costly, it has proved useful for estimating population size in canids (e.g., Roemer *et al.* 1994; Hein and Andelt 1995; Schauster *et al.* 2002a). Mark-recapture can provide relatively accurate estimates of population size if sample sizes are adequate, collection techniques are unbiased, and the basic assumptions for the population estimator are not violated (see Caughley 1977; Thompson *et al.* 1998, and references therein). This method involves capturing and marking individuals, then recapturing a number of the marked individuals again and estimating population size based upon the ratio of marked to unmarked animals recaptured using one of several models (e.g., Pollock 1981; Seber 1982). Marks employed to tag the animal include ear tags, radio collars, dyes, and physiological markers such as radioactive isotopes (Kruuk *et al.* 1980), iophenoxic acid (Knowlton *et al.* 1988), or chlorinated benzenes (Johnston *et al.* 1998). Recapture may involve physical recapture, re-sighting or photographs, returns from trappers or hunters, recapture via fecal analysis for a physiological marker, faecal DNA analysis, or a combination of these. If the extent of the area of interest is known, density estimates can be derived. Several models for population estimation (e.g., the Petersen, Jolly-Seber, and Schnabel asymptotic methods) can be used to calculate population size (Caughley 1977; Jolly 1982; Seber 1982; Thompson *et al.* 1998). Many of these models are available on computer software, such as CAPTURE (White *et al.* 1982), NOREMARK (White 1996), and EAGLES (Arnason *et al.* 1991).

### **Direct counts by removal**

For some species that are considered pests, the removal method has been used to estimate animal abundance (e.g., Skalski *et al.* 1984). Disadvantages of this technique is the lack of knowledge of what proportion of the population was missed or not captured, and how large an area was affected by the removal. Due to the economic importance of the species, intrinsic values, and/or the social and ethical ramifications, the removal method is rarely employed.

### **Transect, strip, or area sampling**

In certain circumstances, it may be possible to count the number of animals along transects, strips, in quadrants, or within a defined area and estimate animal population size or density (e.g., Burnham *et al.* 1980). Trends in

relative abundance can be compared from direct counts; absolute abundance may be estimated if correction factors can account for problems with 'sightability'. Population estimates can also be calculated by distance methods along line-transects (Burnham *et al.* 1980). Software programs that estimate population size using distance data along transects include DISTANCE (Buckland *et al.* 1993, Laake *et al.* 1993) and TRANSECT (Burnham *et al.* 1980). Aerial surveys typically require a large species occupying sparsely vegetated habitat allowing for maximum 'sightability'. The number of animals sighted can be affected by animal behaviour, weather, vegetation, visibility, and observer experience and fatigue. The use of ultraviolet, infrared, or thermal imagery photography may enhance "sightability" (e.g., Havens and Sharp 1998). Ground surveys are practical for animals readily viewed in open habitats. In certain situations, the entire area of interest may be surveyed, and through repeated sampling, the entire population may be counted. However, the ability to count all individuals in an area is rare, but correction factors from a radio-marked sample allow determination of a more accurate estimate of population size. For transect and sighting surveys, it is important that the different habitats within the area be sampled, not just the areas with good visibility.

### Identification of individual animals

While the opportunity to directly observe canids may be considered rare, there are certain species living in national parks or reserves with open habitats that allow for direct observation and identification of all individuals in the study area. Maddock and Mills (1993) censused African wild dogs by collecting photographs from tourists and other field personnel. They were able to identify 357 wild dogs from 26 packs by examining more than 5,000 photographs. Studies using identification of individuals are usually conducted in relatively open habitat and with a species that is observable and tolerant of human presence. Also, the animals do not necessarily need to be marked for individual identification, as individuals may be re-sighted and identified indirectly. Track characteristics have been used in which tracks of individual animals were separated on the basis of characteristics and location. The main advantage of using characteristics of individual tracks for identification is that it entails less effort than a large-scale trapping programme, although the accuracy of this method in relation to changes in population size remains untested. While individual identification allows for a relatively complete count, the time and effort necessary means that this method is useful only in particular situations and is often conducted in conjunction with behaviour studies (e.g., Gese *et al.* 1996c). Again, the use of hair snares to acquire hair samples can be used with DNA sequencing to identify individuals in the population.

### Radio-telemetry

The advent of radiotelemetry increased the ability to monitor secretive canids. Using this method, one can estimate the home range or territory size of an animal. It is now widely accepted that combining territory size (and overlap) with the number of members of the social unit, plus the percentage of radio-collared transients sampled from the population, density estimates can be derived for the population (e.g., Mech 1973; Fuller 1989). For more solitary species, estimates of home-range size, the extent of inter- and intrasexual home-range overlap, and the proportion of transients in the population are used to estimate population density. While radiotelemetry is labour intensive and costly, this technique provides one of the best and most reliable estimates of population density for many species. With the advent of satellite and GPS technology, more intensive monitoring of large and medium-sized canids will be possible (e.g., Ballard *et al.* 1998; Merrill *et al.* 1998), but the technology is still somewhat expensive and systems for smaller species will require further technological development.

Águas Emendadas Ecological Station is one of the most important regions to conservation in Distrito Federal, Brazil, but is threatened by urban expansion. It is a protected area, devoted solely for preservation purposes, and is home to many ecologically important native species being monitored, including the maned wolf (*Chrysocyon brachyurus*), crab-eating fox (*Cerdocyon thous*) and hoary fox (*Pseudalopex vetulus*). This radio-collared adult female maned wolf vocalises when a researcher approaches her cub. Águas Emendadas Ecological Station, Distrito Federal, Brazil, 1997.



Flávio Rodrigues



## 15.4 Conclusions

The methods and techniques available for determining the presence and abundance of canid species are varied, and this chapter has attempted to illustrate by means of examples some of the instances where these techniques have been applied to studies on canid populations (or other similar large predators) and the advantages and disadvantages of each. While a combination of methods

is always likely to provide the best results (see, for example, Schauster *et al.* 2002a), the feasibility and application of the appropriate methodology will always depend on factors such as the species, habitat, costs, manpower, time constraints (Lancia *et al.* 1994), and also on the kind of questions that are being addressed and the consequent accuracy and power of the statistical assumptions of each method (Skalski and Robson 1992).