A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation

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Abstract. This paper reviews field methods for estimating and monitoring the abundance of terrestrial carnivores that do not involve capture. Effective methods of monitoring abundance are important tools for the management and conservation of many species. The development of methods for carnivores presents particular challenges, as they are often secretive and widely dispersed. Nevertheless, a variety of approaches based on direct observations and quantification of field signs have been employed. These techniques are described in relation to carnivore ecology and resource implications, and the advantages and deficiencies of each are discussed with reference to case studies.

Introduction

Monitoring the distribution and abundance of animals is fundamental to the conservation, research and management of wildlife populations. Estimates of abundance are particularly important in conservation programmes where the principal objectives are to assess, maintain and enhance the size of endangered target populations. In contrast, when the abundance of a species gives it 'pest' status the management objective may be to reduce population size. In both cases the progress and ultimate success or failure of the management programme will be measured in terms of population size. Furthermore, ecological field studies, such as those involving population dynamics, predator–prey relationships and the effects of disease, all rely on the ability to make reliable estimates of animal abundance.

Estimation of the size of wildlife populations can be problematic, and this is particularly true for carnivores as they are often cryptic, nocturnal and may have large home ranges. A further complicating factor is that patterns of spatial organisation in carnivore populations vary widely, from solitary individuals, a pattern common in felids and viverrids (e.g. mountain lion (*Felis concolor*), European genet (*Genetta genetta*)), or pairs defending exclusive territories, as in several canids (e.g. kit fox (*Vulpes macrotis*) and raccoon dog (*Nyctereutes procyonoides*)), to large social groups, as found in some viverrids, e.g. banded mongoose (*Mungos mungo*). There may also be intra-specific variation in patterns of social organisation, as in the Eurasian badger (*Meles meles*), which may live alone or in a wide range of social group sizes throughout its range (Neal and Cheeseman

1996). These factors have resulted in the development of a wide variety of methods to estimate carnivore abundance.

Some of the earliest, and most extensive, studies of carnivore abundance have used data arising from commercial exploitation and culling. For example, Elton and Nicholson (1942) examined cyclic population change in Canada lynx (*Lynx canadensis*) over a period of more than 200 years using the records of furs traded by the Hudson's Bay Company. In Britain, long-term population trends of some carnivores have been indirectly inferred from 'bag records' kept by gamekeepers in the course of predator control (Tapper 1992). However, as these methods of assessing abundance are possible only in the context of some form of exploitation or lethal control, they are obviously not widely applicable. Furthermore, data collected in this way are sensitive to variations in trapping effort (McDonald and Harris 1999).

Which method of abundance estimation to use will depend on the behavioural ecology of the target species, the size of the area of interest, the aims of the study and the available resources. Two main approaches are available to wildlife managers: the estimation of true abundance, or the calculation of indices that relate in some way to abundance.

When information on true abundance is the aim, population-estimation techniques fall into two classes: complete counts where all individuals are assumed to be observed (either over the entire area of interest, or on sample plots), or incomplete counts where only a proportion of the individuals are detected. In practice it is seldom possible to observe all carnivores in an area (but see Ogutu and Dublin 1998). More often, population estimates are calculated from incomplete counts where a fraction of the individuals present is detected

and a mathematically derived estimate of population size is calculated as a function of the probability of detection. Because the areas involved are often too large to survey completely, a representative sub-sample may be covered, and an estimate for the whole area produced by extrapolation. Thus, for both complete and incomplete counts, the two key elements in the design of the study are the probability of detection and sampling strategy (Bookhout 1996). The sampling strategy must take into account aspects of the ecology of the species of interest such as its distribution in space, movement patterns, and relationships with landscape and habitat, in order that the results can be reliably extrapolated. In-depth discussion of sampling design can be found in Krebs (1989), and Snedecor and Cochran (1967).

Statistically inferred estimates of population size from incomplete counts of carnivores are usually derived from catch–recapture (CR) surveys. Bookhout (1996) refered to these as formal estimation methods. A variety of mathematical models have been developed to estimate population size from such data, and there is an extensive literature covering these techniques (White *et al.* 1982; Krebs 1989; Pollock *et al.* 1990; Thompson *et al.* 1998), and a number of established analytical computer programs (e.g. CAPTURE: Rextad and Burnham 1991). Assuming that the underlying assumptions of any model are met for the population of interest, then these methods produce robust population estimates with known levels of precision and accuracy. Indeed, carnivore abundance has been estimated in this way in several studies, e.g. the Eurasian badger (Rogers *et al.* 1997), the small Indian mongoose (*Herpestes javanicus*) (Corn and Conroy 1998), the feral ferret (*Mustela furo*) (Cross *et al.* 1998), and the stoat (*Mustela erminea*) (Erlinge 1983).

However, trapping carnivores at the intensity required to produce such estimates is not always possible, as it can be practically difficult, labour intensive and prohibitively expensive. As field signs such as droppings, footprints and den sites may often provide the only practical means by which to monitor carnivore activity, a number of methods have been developed to estimate abundance from index scores. These methods assume that the intensity or frequency of field signs is related in some way to the number of animals present (i.e. it provides an index of abundance). Indices are most widely used to provide relative estimates of abundance, where the intention is not to estimate population size but to compare abundance between areas in space or to monitor trends in one location over time. However, index values can also be used to estimate population size when it is possible to calibrate them with estimates derived from a formal estimation method carried out in parallel. Recent developments in techniques such as remote photography and molecular ecology have further increased the options available to researchers, providing alternative methods to assess or monitor population size when a trapping program is not possible.

Although the theory and principles of mammal population monitoring are well documented in the scientific literature (e.g. Krebs 1989; Bookhout 1996; Thompson *et al.* 1998), few publications have reviewed the various methods available in any detail, with the exception of CR. This is particularly true for carnivores. The current paper reviews field techniques for assessing the abundance of terrestrial carnivores that do not rely on capture, and discusses the advantages and deficiencies of each.

Definitions

In the present paper absolute abundance refers to the total number of animals present in a population. Population density is the number of animals present expressed per unit area. Estimates of relative abundance are often used where it is not possible to calculate absolute numbers. Relative abundance is therefore a measure of the number of animals present on one sampling occasion in relation to others, which may be separated in space or time. Relative abundance is usually expressed as an index value calculated from the frequency of signs or observations per standardised unit of sampling effort.

Methods based on detection of field signs

Carnivores often leave signs of characteristic appearance that indicate their presence. In some species excretory products are used as territorial marks, and may regularly be deposited at specific or predictable sites (e.g. Eurasian badgers (Neal and Cheeseman 1996), European otters (*Lutra lutra*) (Chanin 1985) and raccoon dogs (Yamamoto and Hidaka 1984)). Footprints can also be diagnostic and habitual behaviour may result in the creation of recognisable paths and trails (Sutherland 1996). Further evidence can be obtained from the number, magnitude and status of the characteristic structures occupied by some carnivores (e.g. fox dens, meerkat (*Suricata suricatta*), burrow systems and badger setts). Such methods rely upon the systematic identification of field signs and consequently results are potentially variable depending on the abilities of fieldworkers. The skills of experienced fieldworkers are a valuable resource in wildlife research and management, but are often overlooked in the face of financial constraints. Recent work has demonstrated the objective value of 'field craft' in wildlife research (Stander *et al.* 1997) and such skills are likely to increase the power of surveys by enhancing rates of detection and interpretation.

A number of extrinsic factors may influence index scores independently of abundance, and should be considered when designing a monitoring program. Patterns of movement and hence the distribution of signs, may vary according to season, and differences in habitat and landscape types between study sites. Similarly, sex and age-related differences in behaviour (e.g. wider-ranging behaviour of male mountain li-

ons (*Felis concolor californica*) (Van Dyke *et al.* 1986)) can also affect movement patterns (e.g. Stanley and Bart 1991). Also, the probability of finding signs may vary between areas of different habitat composition (e.g. Kutilek *et al.* 1983; Stanley and Bart 1991), and as a result of the effects of local weather conditions on the persistence of field signs (Bider 1968).

Bias owing to seasonal and habitat effects can be minimised by attention to survey design, or by including them as covariates in any comparisons (Smallwood and Fitzhugh 1995). It is usually more difficult to control for differences in habitat types between locations than to minimise seasonal or weather effects in longitudinal studies. Therefore, in general, index scores based on field signs are likely to be more reliable when used to approximate population trends over time in one location than when used to compare between areas.

Track counts – general

Carnivore footprints can often be easy to identify and consequently the occurrence of tracks has received much attention from wildlife managers as a relatively inexpensive means of monitoring population trends. Where the target species is rare and wide ranging, then it may be sufficient to simply count sets of tracks to determine presence or absence and derive a crude estimate of population size (e.g. survey for snow leopards (*Panthera uncia*) in the Himalayas (Schaller 1977)). The two main systematic approaches to the collection of track data have been to survey transects for evidence of footprints, or to use lines of track stations of deliberately prepared footprint plots (sometimes with scented attractants). An index of abundance is calculated based on counts of tracks detected per unit of sampling effort. An ideal index is one in which the number of visits to track plots, transects or scent stations varies consistently with changes in abundance of the target species.

Absolute abundance of a species in an area can be estimated from track data where the footprints of individual animals can be recognised. This is sometimes possible with the aid of highly skilled fieldworkers (e.g. Stander *et al.* 1997) or by using objective techniques involving measurements from photographs of tracks (Smallwood and Fitzhugh 1993; Grigione *et al.* 1999).

When monitoring track counts over time at a location the ability to detect real changes in abundance depends on differences in the probability of finding tracks between sampling visits due to factors that are not related to population size (as listed above) and the relationship between track counts and population size. Some standardisation can be achieved by restricting sampling to certain weather conditions or selected seasons. Surveys are likely to become more statistically sensitive to trends in index scores as the proportion of sample units that contain tracks increases (i.e. the potential to detect smaller differences in index scores increases (Clevenger and Purroy 1996)). Allen *et al.* (1996) stated that

the method recording the highest number of visits to track stations was the most sensitive in terms of ability to detect the presence of animals. However, Engeman *et al.* (1998) described sensitivity as the ability to detect change. The authors produced variance estimates for their track station index (see below) for dingoes (*Canis familiaris dingo*) in Australia, which resulted in high sensitivity to change despite low index scores.

Track counts along transects

Continuous transects based along dirt roads with dusty surfaces that register animal footprints have been used to monitor carnivore populations in many studies (e.g. Van Dyke *et al.* 1986; Smallwood and Fitzhugh 1995; Edwards *et al.* 2000). Using vehicles, extensive lengths of transect can be surveyed rapidly. Transects are usually divided into shorter segments, such as kilometres, which form the units of survey. An index score of tracks counted per survey unit can then be calculated, and used for comparisons between locations in space or time. For example, indices have been calculated from the total number of sets of tracks per transect per day, or the presence or absence of footprints in each length of transect, or the length of interval between sets of footprints (e.g. O'Donoghue *et al.*1997; Stander *et al.*1998). In predator–prey studies, counts of carnivore tracks intercepting transect lines have been used as an index of 'predation pressure', where actual density is less important than predator activity levels in the area of interest (e.g. Kurki *et al.* 1998). Overton (1971) described a method of driving animals over sand transects to register their tracks and calculate numbers. However, drives are labour intensive and the consequent disruption to the population may be unacceptable.

Careful consideration must be given to the factors that may influence index values. Substrate quality is obviously important; for example, Van Dyke *et al.* (1986) found that the effort required to detect mountain lion tracks in Arizona, USA, varied according to the condition of the road surface. Trapping and radio-tracking data showed that transects on road surfaces with good dirt/dust cover produced results that were significantly more sensitive to changes in abundance than did other road types. In such cases an objective assessment of tracking conditions may be necessary when selecting transects. Where counts of tracks left in fresh snow along transects are used to provide indices of abundance, they should be carried out soon after snowfall to minimise the effects of freezing, thawing and windy conditions. Reid *et al.* (1987) estimated absolute abundance of the river otter (*Lutra canadensis*) from snow tracks, by counting the total number of individual track sets in a random sample of 500 m of lakeside transects and extrapolating the results to the entire study area. This was possible only in a brief early winter period when the lakes were frozen, and although otters were still active, they were restricted to riverbanks.

In studies where multiple transects are used to generate an abundance index for a given area, transects should be separated by sufficient distance such that the probability of a single animal being recorded on more than one line in any single survey period is minimised (Smallwood and Fitzhugh 1995; Edwards *et al.* 2000). This ensures the validity of certain statistical treatments that are commonly carried out on index scores based on means from more than one transect (Edwards *et al.* 2000).

Edwards *et al.* (2000) compared two track indices for assessing feral cat (*Felis catus*) and dingo populations in central Australia. One method used the total number of sets of tracks per kilometre surveyed (a measure of the maximum number of individuals recorded), and the other used counts of minimum number of individuals leaving tracks by assuming that tracks separated by less than 500 m were made by the same animal. The latter was considered more likely to show a linear relationship with true abundance at low densities, while the former would continue to reflect change in numbers up to higher levels of density.

When comparing track index scores between areas, an evaluation of topography and habitat is necessary. Some larger carnivores are known to walk on man-made tracks more often when they live in steep terrain and thick cover, therefore variations in track detection may be due to the character of the habitat rather than differences in abundance (Kutilek *et al.* 1983). Stanley and Bart (1991) showed that habitat type adjacent to their survey transects affected track index scores for red fox (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*) independently of density. This illustrates the potential for temporal changes in habitat in one location to produce misleading variations in relative abundance estimates. Smallwood and Fitzhugh (1995) found that the likelihood of encountering tracks could be increased by over 100% by selecting transects to reflect these ecological considerations. They recommended that transect selection based on such knowledge would maximise detection of the animals and the available manpower resources.

In some studies track count indices have been validated against populations of known size. Stander (1998) showed that road-transect track counts for lion (*Panthera leo*), leopard (*Panthera pardus*) and hunting dog (*Lycaon pictus*) in homogeneous landscape in Namibia were a function of true density (established from complete census using radio-tracking and marking of individuals). Servin *et al.* (1987) successfully produced a conversion factor to relate red fox tracks per kilometre of transect to density estimates based on radio-tracking data. O'Donoghue *et al.* (1997) surveyed a 25-km transect through their study area in south-west Yukon by snowmobile, recording the number of coyote, *Canis latrans*, and lynx tracks. For each species an index score was calculated for the number of sets of tracks per night per 100 km of transect surveyed. The raw counts were converted to least-squares mean values, which controlled for the covariates of time, year, weather and location. Trends in the track count index for both species closely mirrored those suggested by population estimates derived from other methods including radio-tracking. An earlier evaluation of this method for lynx (Stephenson and Karczmarczyk 1989) reported a poor correlation between the snow-track count index and absolute numbers, but this involved a far smaller number of surveys, and did not control for any covariates. This highlights the potential importance of sufficient survey effort and the collection of appropriate complementary data on environmental factors that could confound index scores.

Track stations

As tracks are visible only on certain substrates that may be absent or unsuitably distributed, their persistence is strongly influenced by environmental conditions. These problems can be minimised by the use of track stations, consisting of artificial substrates that preserve footprints and can be positioned where required (e.g. Allen *et al.* 1996; Mahon *et al.* 1998). Track stations can be completely artificial, such as a sooted plate, or can be as simple as a smoothed area across an unsurfaced road. The index of usage can be expressed as the mean number of tracks crossing the stations per night, the mean number of positive stations per night or the proportion of positive stations per line.

The precise pattern of deployment of track stations will vary according to the target species. To reduce the likelihood of visits to multiple stations by an individual in one sampling period, the distance between stations should take into account the ranging abilities of the species (Roughton and Sweeny 1982). Visits to multiple stations by individuals can lead to disproportionately high index scores, which may invalidate comparisons with other areas or periods. Sargeant *et al.* (1998) countered this by using presence or absence of visits to lines of stations as the raw data, which was robust to multiple visits to points on any given line irrespective of the spacing of the stations. However, this is possible only in large-scale surveys where many lines are used.

Allen *et al.* (1996) used track stations to monitor the size of a dingo population before and after lethal control. They prepared track stations by smoothing a 1-m-wide swathe across unpaved roads. Two 50-km transects were established with track stations at 1-km intervals. For four consecutive days the presence of dingo tracks was recorded at track stations and the surface of each station was re-smoothed. The mean number of tracks per transect per day provided the index of usage, which declined after the control operation on both transects. The variance estimate produced by Engeman *et al.* (1998) for this index provides a measure of precision and allows spatial and temporal comparisons.

Track stations have also been used in association with scented attractants to lure individuals to the site. Scent-station surveys have been used for decades to monitor the distribution and abundance of carnivores, including red and

gray foxes, lynx, bobcats (*Felis rufus*), raccoons (*Procyon lotor*), fishers (*Martes pennanti*), American martens (*Martes americana*), black bears (*Ursus americanus*) and coyote (e.g. Wood 1959; Linhart and Knowlton 1975; Lindzey and Thompson 1977; Linscombe *et al.* 1983; Leberg and Kennedy 1987; Smith *et al.* 1994; Travaini *et al.* 1996). Species-specific urine, commercially produced fermented egg, fish oil and synthetic fatty acid tablets have been used as attractants. Preliminary field comparisons may be required to determine the best attractant for the species in question (e.g. Allen *et al.* 1989; Trewhella *et al.* 1991).

The relationship between scent-station index scores and absolute density has been validated against known populations for only a few species, and with ambiguous results (e.g. Diefenbach *et al.* 1994; Sargeant *et al.* 1998). In an experimental manipulation of raccoon numbers in a closed population, scent-station index scores were inconsistent with abundance estimates from live trapping (Smith *et al.* 1994). Conversely, Conner *et al.* (1983) found that indices based on visits to scent stations accurately reflected changes in numbers of raccoons, bobcats and gray foxes, as determined by trapping, radio-isotope tagging and radio-tracking. Diefenbach *et al.* (1994) found that the proportion of scent stations visited by bobcats was positively correlated with actual population size (known from a collateral study), but only large changes in abundance were detectable. The use of scented attractants may be particularly susceptible to seasonal and density-dependent variations in activity (Allen *et al.* 1996; Edwards *et al.* 2000). Potential bias may also result if the probability of attraction varies with the age, sex or social status of individuals (Allen *et al.* 1996). Allen *et al.* (1996) concluded that track plots without scented attractants provided a more reliable index of relative abundance for dingoes in their study.

Track-based surveys are a relatively inexpensive method for the identification of trends in carnivore populations and can allow several different species to be monitored simultaneously. The method is best suited to providing a relative index of abundance when monitoring temporal changes in fixed locations over several years. Relating the trend in index values to actual abundance may be difficult. The biological relevance of changes in index scores after, for example, a control treatment must be viewed carefully in light of knowledge of the ecology of the target animal, e.g. did ranging behaviour of the remaining animals increase, giving higher index scores unrelated to population size? The survey design must take these factors into account, in addition to the availability of suitable transects and manpower requirements.

Faecal counts – general

Where droppings can be accurately attributed to the target species they may be used to estimate animal abundance (see Putman 1984). Faecal counts can provide relative abundance estimates over time or between locations, and in some cir-

cumstances estimates of absolute density. There are two main approaches to abundance estimation from faecal counts: (i) quantify the standing crop, i.e. the total amount of faecal material in a given area or transect, and (ii) quantify the accumulation rate, i.e. the rate of defaecation in fixed sample plots monitored in such a way that fresh additions can be accurately counted (e.g. by clearing or marking droppings between counts). As with counts of tracks, several factors can potentially affect counts of droppings independently of population size. In addition to the factors already described, faecal counts will also be affected by rate of decay of faecal matter, which is largely determined by weather. Also, carnivores may show marked seasonal variations in scent-marking behaviour, reflected in changes in the distribution and accumulation of droppings. Comparison of survey results over time or between sites of differing habitat types may be particularly susceptible to such influences. Where possible, it is highly desirable to design faecal surveys so as to minimise or control for these confounding effects. For example, when monitoring abundance on an annual basis, surveys should be standardised according to location and time of year. Where possible, comparisons between sites should pair areas of similar habitat types. However, this may be unrealistic if the purpose of the study is to acquire information on the relative density of animals in different habitat types. Surveys should be carried out under standard weather conditions to reduce variations related to differential dung-decay rates and searching efficiency. Where such controls are not practical, it is advisable to investigate how correction factors might be calculated by re-examination of data or experimentation.

Measuring the standing crop of faeces

Indices of faecal abundance can be produced by counting the number of droppings found on transects or within plots. Cavallini (1994) reported that counts of red fox droppings found on transects provided cheap and reliable indices of relative abundance. However, as the frequency of droppings found correlated negatively with rainfall over the previous 20 days, it was recommended that comparisons should be conducted only between areas and periods of similar rainfall. Lockie (1964) made repeat visits to transects and used the number of droppings found on each (corrected for faecal decay rate to standardise seasonal variation) as an index of abundance for pine martens (*Martes martes*) in Scottish woodlands.

At a national level, the otter population of England was monitored using repeated surveys at seven-year intervals (Lenton *et al.* 1980; Strachan *et al.* 1990; Strachan and Jefferies 1996), during which the presence of spraints was recorded on several hundred 200-m stretches of riverbank throughout the country. The results provided a relative abundance index (number of positive sites per region) which reflected both spatial and temporal trends in the status of the population. Surveys by Mason and Macdonald (1987) and

Strachan and Jefferies (1996) suggested that information on the status of regional otter populations could be inferred from the collection of such data from a sub-sample of sites. However, the relationship between 'otter-time' spent in an area and spraint density is unclear. During periods of relative stability in Scottish otter populations, wide fluctuations in spraint numbers occurred, probably resulting from seasonal and habitat-related variations in scent-marking behaviour (H. Kruuk, personal communication).

In order to use counts of faeces to estimate absolute abundance, information on defaecation and decay rates are required. Absolute abundance estimates can be calculated by dividing the number of droppings found by the number produced per day (the defaecation rate), for the number of days it is expected that they will remain visible (the decay rate). Perhaps the most important potential sources of error associated with such calculations are the possibility of not detecting all faecal deposits, and the inaccurate estimation of decay or defaecation rates. Faecal decay rates can be obtained relatively easily by observation and experiment (e.g. Kohn *et al.* 1999), but calculating defaecation rates of wild animals is likely to be more problematic. Studies using captive animals can be used, although the results should be treated with caution as defaecation rates in captivity may be influenced by artificial diet (Rau 1988) and activity patterns. Estimation of absolute abundance from counts of the standing crop of faeces is an impractical goal for most carnivores.

Measuring rates of faecal accumulation

The effect of variations in weather and diet on decay rate, and therefore on the probability that droppings will be detected, may be reduced by observing the rate of faecal accumulation during frequent revisits to an area. If the average individual defaecation rate and the probability of detection are known, then population size can be calcuated from the faecal accumulation rate per unit area monitored. Alternatively, if an area of known population density is available then it may be possible to observe the accumulation rates of dung on plots or transects and use this relationship to calculate abundance in new locations (e.g. Putman 1984). In both cases it is important that the conditions for surveys in new areas are standardised with those prevailing during calibration. Ideally, this should be carried out at a range of densities, because accumulation rates per unit survey effort may not vary consistently with population density.

The red fox survey of Great Britain is an example of the application of this technique at a national level (P. Baker, personal communication). The method involves surveying for fox scats along transects within a sample of 1-km squares stratified according to habitat type. Scats are removed from the site as they are encountered, and a repeat search of all transects is conducted after a given time. This provides an estimate of the number of scats produced along the transects per unit time. Independently obtained estimates of defaeca-

tion rates and detection probability can then be used to calculate the number of resident foxes in each square.

One issue that should be addressed when considering such techniques is the potential influence of the removal of droppings on subsequent defaecation behaviour. An alternative approach would be to mark droppings on first encounter and search for additions on subsequent visits. Furthermore, given the heavy reliance on conversion factors for estimating density, several authors have recommended that counts of droppings should be used only as indices of relative abundance (Kolb 1982; Rau 1988; Beltran *et al.* 1991).

DNA analysis

Recent advances in molecular biology have given rise to techniques that allow the recovery of genetic material from faeces and hair, and the possibility of providing a method for the estimation of animal abundance (reviewed by Kohn and Wayne 1997).

Molecular scatology

Faeces contain a variety of cells originating from the gut of the excretor. Within species certain regions of repetative DNA are associated with a high degree of variation between individuals. These are known as polymorphic mini- or micro-satellite loci. Genetic fingerprinting is based on determination of the number of repeats at each locus by measuring the size of DNA fragments. Screening a number of polymorphic loci in several DNA samples makes it possible to distinguish individuals. The principal stages of the process are (i) systematic collection of faeces in the area of study, (ii) extraction of DNA from each sample, (iii) amplification of DNA from diagnostic microsatellite loci (using the polymerase chain reaction (PCR)), (iv) analysis of the size of amplified fragments, and (v) allocation of genotype.

Once a large sample of faeces has been examined in this way, the cumulative number of unique microsatellites can be expressed as a proportion of the number of faeces sampled. The asymptote of this curve can be determined analytically and gives an estimate of local population size (rarefaction analysis), although this may require a large number of droppings (see Kohn *et al.* 1999). Alternatively, CR models can be used to analyse this type of data, where faeces with the same multilocus genotypes in multiple sampling visits are treated as 'recaptures'.

Molecular primers for amplifying specific marker sequences are published for a number of species (see Kohn and Wayne 1997). The greater the genetic variation in the population the fewer different microsatellite profiles are required to positively identify individuals (Mowat and Strobeck 2000).

A number of technical challenges associated with this approach must be addressed. Collection of fresh faecal samples and their appropriate storage are critical to minimise degradation of DNA (Taberlet *et al.* 1999); storage in dessicating

silica beads is a particularly effective approach (Frantzen 1998; Seutin *et al.* 1991; Wasser *et al.* 1997). Also, there is an inherent error rate in the PCR process that can produce misleading results (e.g. production of false alleles and 'allelic dropout') in terms of the number of genotypes detected. It is therefore recommended that a pilot study be carried out to quantify the genotyping error rate, and provide confidence levels for the final results (Taberlet *et al.* 1999). Commercial kits and published protocols are now available for DNA extraction from faeces (e.g. Boom *et al.* 1990; Taberlet 1996).

Despite these pitfalls, some studies of carnivores have successfully exploited this technology. Kohn *et al.* (1999) collected carnivore droppings from six transects in a 15-km² mountainous region of western USA. The samples were positively identified to species on the basis of diagnostic sections of mitochondrial DNA. Coyote droppings were then genotyped using three previously established unique microsatellite markers, and the population size was estimated by rarefaction analysis and CR. Both analyses produced results that compared favourably with results from trapping and marking. Taberlet *et al.* (1997) used a combination of DNA extraction from faeces and hair samples (see below) to estimate population size of the endangered Pyrenean brown bear (*Ursus arctos*). The results corresponded closely with those produced from an established monitoring scheme based on identification of tracks.

Recovery of hairs

Hair collection has been used to determine the presence or absence of mammals in an area (reviewed by Raphael 1994). Hairsnares usually consist of a mechanical device that removes a small number of hairs by cutting or snagging them as the animal passes or approaches a bait. However, Foran *et al.* (1997) designed a baited hairsnare consisting of a tunnel containing a plate with a covering of glue to remove a sample of hair from American martens with the follicle attached. DNA was then extracted from hair follicles and fingerprinting techniques (see above) used to distinguish individuals. Preliminary results suggested that this may provide a method of estimating population size of cryptic carnivores using CR estimators. Mowat and Strobeck (2000) estimated grizzly bear (*Ursus arctos*) population size using baited hair snares, with a sampling design that met the assumptions of CR. Although no direct validation was carried out, their results were comparable with other studies in similar landscapes in neighbouring areas of Canada.

Auditory indices

Territories of low-density species such as wolves (*Canis lupus*), coyotes and lions have been mapped from the location of calls, and estimates made of the number of groups or individuals. This has often involved simultaneous use of more than one observer to triangulate on the calling animal (Sutherland 1996). Harrington and Mech (1982) elicited wolf howling by producing simulated howls themselves from census stations. Wolf density was estimated by calculating the ratio between the area covered (i.e. the area within which they could detect howling responses) and the total number of replies, and extrapolating this ratio to the whole study area. The results depended heavily on the estimated area covered by each census station, which was in turn influenced by the effects of weather conditions on the penetration of simulated calls. The method could be used only to estimate the number of packs in an area, and as pack size varied the data could provide only a crude estimate of population size. Other workers have attempted to estimate wolf pack size from the composition of *en masse* pack replies (e.g. Pimlott *et al.* 1969), although later work suggested that this may be almost impossible even when high-quality sonographs are recorded (Harrington 1975). Fuller and Sampson (1988) carried out a howling survey to estimate wolf pack numbers in an area with a known density of radio-marked packs. The howling survey gave an artificially high estimate of pack density, and the authors concluded that the method was not suitable for surveys at a regional level, but that it could be useful in smaller areas.

Counting visible structures

Some carnivores construct conspicuous dens for protection or rearing young. For example, Eurasian badgers live in setts that can be distinguished on the basis of the size and shape of the entrance holes, and the presence of large spoil heaps (Neal and Cheeseman 1996). Some civets construct grass dens, and European otters live in recognisable waterside holts (Kruuk *et al.* 1989). Such structures are often associated with particular habitats and landscape features, which can make surveying easier. It is sometimes possible to carry out a complete survey of a small area to record the presence of all den sites of the target species. The use of den sites to estimate carnivore numbers relies upon accurate identification of the resident species. This is an important consideration as several different species may occupy similar structures. For example, in parts of Europe red foxes and raccoon dogs may opportunistically inhabit disused badger setts (R. Kowalczyk, personal communication).

When the number of individuals likely to occupy such structures is known then estimates of population density can be calculated. More often, however, these structures are used to indicate relative abundance in species that cannot be counted directly. If the species in question is solitary or lives in pairs then conversion of the number of burrows to an estimate of total population size is straightforward. If, however, the number of residents is variable, then an average group size can be used, although the wider the variation in the number of residents, the less confident is the estimate of abundance.

Counts of natal dens have been widely used to estimate red fox abundance (Storm *et al.* 1976; Lindstrom 1980; Hewson 1986; Harris and Trewhella 1988; Prigioni *et al.*

1991). Sargeant *et al.* (1975) carried out an aerial den survey and located 84% of the family groups of foxes in their study area. Marks and Bloomfield (1999) estimated the density of fox groups using a combination of intensive ground searches and a media campaign asking residents to report dens. The status of the dens as breeding sites was established by detailed examination for signs of cub presence, and observation by spotlight (see below) was used to estimate mean litter size on a subsample. Estimates of fox density were calculated by multiplying the number of dens per square kilometre by group size (mean litter size plus two adults). Kruuk *et al.* (1989) found that counts of holts in coastal habitat on the Shetland Islands provided reliable estimates of the population size of European otters, as they were linearly related to the number of resident male otters present.

Several regional and national surveys of carnivore populations have used den sites as a measure of abundance. National surveys for Eurasian badger setts have been conducted in Britain (Cresswell *et al.* 1990; Wilson *et al.* 1997) and Ireland (Smal 1995). In the British surveys a random sample of 1-km squares (1% of the land area), stratified according to landscape type, was surveyed for badger setts and habitat coverage. Extrapolation gave an estimate of the number of badger social groups in Britain, and their distribution. Badger population size could, in theory, be calculated by multiplying the estimated number of social groups by the average number of residents. However, as there is considerable variation in badger group size (Neal and Cheeseman 1996), this would lead to an estimate with substantial potential error.

Methods based on observations

A census (complete count) may be possible if the target species is conspicuous. However, a survey (incomplete count) is more often conducted, as typically only a proportion of the population can be observed. Owing to the cryptic nature of most carnivores, techniques for abundance estimation based on direct observation are less widespread than methods using field signs, although in recent years increasing use has been made of remote surveillance.

Direct observations

Simply counting the total number of animals present in a target area is possible only if the species in question is clearly visible and the whole area can be covered. However, both of these requirements are rarely achievable. If a sub-sample of the total population can be observed then inferences may be drawn regarding the true population size. Transect or point counts may provide convenient sampling units to produce estimates of either relative or total abundance.

If transects or point counts are performed according to the methods described by Buckland *et al.* (1993) then the data may be treated mathematically using distance-sampling theory to generate density estimates. This method is based on the assumption that the probability of observing an animal decreases in a predictable manner as the distance from the transect or point increases. However, for many species, the threshold number of observations required to generate a density estimate from distance sampling is high relative to what may be achievable in the field. This is likely to be a particular problem when studying species that are highly cryptic or that inhabit dense cover (Duckworth 1998).

Field observations

The abundance of spotted hyena (*Crocuta crocuta*) on the Serengeti Plain was estimated using observations from ground transects (Anon. 1977). In Kruger National Park censuses of hunting dogs (Maddock and Mills 1993) and cheetahs (Bowland 1993) have been carried out using opportunistic photographs taken by staff and tourists; the distinctive coat patterns of these species allowed individuals to be distinguished. Telleria and Saez-Royuela (1984) estimated the population density of red foxes in woodland using drive counts, although this is labour intensive and potentially highly disruptive.

Estimates of group size have been carried out during detailed behavioural studies of social carnivores (e.g. banded mongoose (Rood 1975), Egyptian mongoose (*Herpestes ichneumon*) (Palomares and Delibes 1993)) where it is possible to observe them closely. Counts of individuals at dens can, however, be misleading if group members divide their time between several den sites, and if individuals cannot be clearly distinguished. Macdonald *et al.* (1998) observed that the number of Eurasian badgers counted at the sett on one occasion by a single observer correlated poorly with the number of known residents. The most reliable estimates of group size are likely to result from repeated visits to a den site over a short period.

Recorded calls of conspecifics or prey have been used to ellicit approach by predators to a location where they can be visually counted by observers (Ogutu and Dublin 1998). Auditory playback techniques can generate reliable estimates of abundance when calibrated accurately. This should involve systematic assessment of the factors that influence variability in carnivore response, and the reliability of call-in estimates compared with methods of known accuracy (Sutherland 1996).

Ogutu and Dublin (1998) assessed the playback technique for lions. As responses were recorded from up to 2.5 km from the source, this was employed as the minimum interval between playback 'stations'. To avoid the possibility that individuals might move between stations during sampling, playbacks were initiated simultaneously from all stations. Lions and hyenas were stimulated to approach the stations by playing recordings of distressed prey and the predators themselves. In each sampling session, recordings were played three times at 5-min intervals, and the speakers rotated 90° after each broadcast. Lions were observed and counted through binoculars as they approached. The density of lions

in the entire study area was estimated by extrapolation from a random sample of playback stations. This estimate was within 1% of a total count from a photographic survey carried out at the same time. The response to broadcasts varied with season, and declined with increasing prey abundance. Hence, comparisons should be made only between the results of broadcast sessions carried out at the same time of day and in the same season. Taking these factors into account, the method was still considered to provide a cheap and practical means of monitoring lion populations.

Aerial observation

Aerial surveys have been used to monitor populations of several medium-sized to large carnivores. However, this method is suitable only for relatively large and conspicuous species inhabiting open habitats, and the costs of conducting regular aerial surveys may be prohibitive.

This technique is most suitable for counting species that form groups and that are therefore more conspicuous from the air (Sutherland 1996). By dividing a relatively small area into blocks, a systematic search can provide complete coverage if the species is visible enough to ensure a high probability of detection. In larger areas, sample counts from flown transects can provide mean estimates of abundance. If the transects cover representative habitat these sample counts can be used to estimate population size for the entire area by extrapolation (Wilson et al. 1996). For example, in western Canada and Alaska, aerial transects were flown to search for wolf tracks after snowfalls (Gasaway et al. 1992). Tracks were followed until visual contact was established with a wolf pack, the size of which could then be determined. This produced a pattern of wolf pack distribution from which an estimate of total population size was calculated. Experienced pilot-observer teams are required to produce reliable results with this method. A variation on this technique, where the probability of observing tracks is combined with observed pack size to produce a mathematically derived estimate of population size, has been used for wolves (Becker et al. 1998), lynx and wolverines (Gulo gulo) (Becker 1991). When the target species occurs at very low densities, this method may be preferable to direct aerial reconnaissance as similar results can be obtained for less sampling effort (Ballard et al. 1995).

Spotlight counts

As many carnivores are nocturnally active, several methods have been developed to carry out counts at night. Artificial light sources or night-vision equipment are usually employed, although under favourable conditions these may be unneccesary.

Nocturnal transect counts have been carried out using spotlights, either on foot or from vehicles. Simple indices of abundance such as the number of animals seen per kilometre driven (e.g. Mahon et al. 1998) or per unit time

(e.g. Duckworth 1992) can be calculated. Waser (1980) used spotlight sweeps from a slow-moving vehicle to collect observations of small nocturnal carnivores in the Serengeti National Park, Tanzania. Approximate population densities of several species were calculated by extrapolation from the number of observations within a sample of 110-m-wide transects. Duckworth (1998) reviewed spotlighting on foot as a method to assess the population size of nocturnal forest mammals. He concluded that the distance-sampling method for calculating density (Buckland et al. 1993) was inappropriate because the assumption of 100% detection probability on the transect line could not be met in a forest environment.

Studies of the red fox have employed spotlight counts from a moving vehicle along a transect to estimate relative abundance (e.g. Weber et al. 1991), and to calculate densities (Heydon et al. 2000) using the distance-sampling method (Buckland et al. 1993). Heydon et al. (2000) found that their density estimates were consistent with those based on den counts and sightings by gamekeepers. Schantz and Liberg (1982) produced a conversion factor to relate numbers of foxes detected by spotlighting to the number known to be present from radio-tracking. In contrast, in comparative studies of population indices for red foxes, feral cats and dingoes (Mahon et al. 1998; Edwards et al. 2000), spotlighting was found to regularly fail to detect carnivore presence in areas that had positive results from track plot surveys for footprints. This was considered to be a consequence of their low density, and the avoidance of open habitats by cats.

Potential sources of undesirable variation in spotlight counts include the time of night and weather conditions during the survey, the habitat structure of the study area, and seasonal variation in both behaviour and population structure. Weber et al. (1991) speculated that seasonal variations in spotlight counts of foxes were related to differences in foraging patterns rather than absolute numbers. The reliabilty of spotlighting may therefore be improved by repeated counts and/or longer transects, and by standardising when, and under what prevailing conditions, the technique is used.

Thermal imagery

Mammals produce considerable body heat that can be seen against the relatively cooler natural surroundings using thermal-imaging technology (Bookhout 1996; Gill et al. 1997). To date, this technique has rarely been used to survey wildlife populations due to the unavailability and high cost of equipment, and a lack of standardised methodologies.

Potentially serious problems associated with surveys based on this technology are the lack of contrast of the thermal images, and reduced visibility in thick cover. However, mountain lions in Florida, USA, were successfully surveyed from an aircraft using thermal-imaging equipment (Havens and Sharp 1998) despite the presence of dense canopy cover in places. This was achieved by surveying when the thermal contrast was greatest between the animals and their background (i.e. early morning) and by scanning from different

perspectives. Thermal signatures were observed for black bears (*Ursus americanus*), and all mountain lions known to be in the study area from radio-tracking.

Remote surveillance

An increasing variety of equipment and methods are becoming available for the remote surveillance of wild animals using photography (reviewed by Cutler and Swann 1999) and video (reviewed by Stewart *et al.* 1997). These methods can provide extensive, continuous and simultaneous observations of target species that may be difficult, costly and labour intensive to observe by other means. However, the application of modern technology in field conditions is seldom straightforward and may involve considerable investment of time and money addressing technical problems.

Photography

Remote camera trapping involves the use of one or more strategically positioned cameras activated in response to the presence of the target animal. The mechanism often consists of a trip line or plate, which, when activated, completes a circuit causing the camera to operate. Alternatively, the camera may be triggered by photic cells (Savidge and Siebert 1988) or infra-red beams (Karanth 1995) that detect when an animal passes. Where individual recognition is possible from photographs (e.g. the stripe patterns of tigers (*Panthera tigris*)), population density can be estimated by deployment of camera traps in grids or transects, using a CR approach (e.g. Karanth 1995; Karanth and Nichols 1998). These data can be used to infer home-range sizes and may provide a basis for the estimation of population density by extrapolation (Griffiths and van Schaik 1993).

The positioning of remote-trip cameras is critical. Animal trails are often obvious locations to place the cameras, particularly where they are likely to funnel the animal traffic in front of the camera. Ideally, the camera should be placed so that a photograph of the whole animal can be obtained and any distinguishing features can be identified. However, if camera stations are placed along regularly used animal trails they will not be randomly located and data may be biased. The pattern of photo-trap deployment should therefore take into account the frequency of trail use and the behaviour of the target species (Wilson *et al.* 1996). Bait and prey stations have been used to attract predators into view of cameras (Joslin 1977; Mace *et al.* 1994).

Remote-trip camera systems are unobtrusive and can enable large areas to be monitored with minimal manpower. However, the equipment can be expensive and vulnerable to human interference (e.g. Stuart and Stuart 1991), theft, component failure and damage. Also, triggering systems can be particularly prone to malfunction, and repair and continual replacement of batteries and film can be difficult in isolated locations. Furthermore, scent left on the equipment can cause carnivores to avoid the camera station (K. S. Smallwood, personal communication).

Video surveillance

The use of video surveillance equipment in behavioural studies of wild carnivores is described by Stewart *et al.* (1997). This technology could potentially be used to estimate carnivore numbers in a similar way to camera traps, particularly when individuals can be recognised. Bait or scent stations could be used to attract animals to within the field of view. This method is likely to be most suited to studies of group-living carnivores, particularly those that share a common den site that can be periodically monitored.

Discussion

In deciding which technique to employ to estimate carnivore abundance, wildlife managers and researchers are guided by a number of factors related to the nature of the study and the target species. The aims and scale (spatial and temporal) of the study, the available resources, the ecology of the target species (e.g. territorial behaviour, movement patterns and breeding cycle) and the required levels of accuracy and precision will influence the decision.

Clearly, where animals themselves can be observed, and particularly when they can be individually identified, direct or indirect observation is likely to be the preferred choice. However, where this is not possible because of the behaviour of the target species, or is impractical (e.g. too costly) then methods based on field signs may be necessary.

Any estimate of abundance will be influenced by sources of error associated with extrinsic (environmental) and intrinsic (methodological) factors. Consideration of these potentially confounding influences is an important aspect of survey design. For example, the probability of finding droppings during faecal counts may vary in different habitats, such that apparent differences in carnivore abundance are, in fact, artefacts of different encounter rates of field signs. This is a problem when comparing between areas, but less so if the aim is to monitor the population trend over time at the same location. Counts can be standardised by sampling in similar conditions or at the same time of year. It may, for example, be appropriate to impose a set of criteria for the weather conditions under which surveying must take place. Alternatively, if comparisons between locations are required, then recording relevant incidental data such as habitat, season and weather can allow these effects to be entered as covariates in subsequent analyses.

When estimating relative abundance, the spatial distribution of transects or points from which to monitor activity, should reflect the patterns of space use (home-range size and distances travelled) and factors influencing movement (e.g. habitat structure, weather and prey availability) of the target species. This should maximise the chances of record-

ing target species but minimise the probability of repeated recording of the same individuals. However, when estimating absolute abundance, transect selection should be random with respect to object distribution (Buckland *et al.* 1993). Compromise or the use of conversion factors may, however, be necessary, as roads or tracks are usually the only practical means of access in some areas. Thompson *et al.* (1998) provides a detailed discussion of the potential errors associated with estimation of population parameters.

Several of the methods described in this paper for monitoring field signs (e.g. track count transects, track plates, faecal counts) may be sensitive to the confounding effects of environmental differences between locations. Consequently, they may be more reliable in the detection of temporal trends in abundance within locations, and particularly for identifying long-term trends.

The power of any monitoring scheme to detect significant differences in levels of index score depends on the sampling effort and the proportion of positive results (of animals or their signs) per survey. Intuitively, the greater the sampling effort (e.g. the more transects that are surveyed for tracks) the more sensitive it will be to detecting presence and therefore trends (e.g. Allen *et al.* 1996). However, high sensitivity to changes in abundance can be obtained despite low index scores where variance estimates are also calculated (Engeman *et al.* 1998). Nevertheless, resources will ultimately limit what level of sampling effort can be achieved, and it is often the case that large increases in effort are required to give only moderate or small improvements in power. The use of power analysis to aid decisions on sampling effort, and statistical treatment of survey data are discussed at length in Seber (1982), Skalski (1991), Kendall *et al.* (1992) and Zieilinski and Stauffer (1996).

It is highly recommended that the techniques described in this review are validated using populations of known size, or by using a formal estimation method (e.g. trapping and CR) on a smaller scale (Smallwood 1995). However, in practice this is seldom the case. By calibrating index scores against known populations it is possible to use them elsewhere to determine absolute abundance, assuming that the relationship between index scores and abundance is consistent in space. However, the social organisation of carnivore populations may vary with density, resulting, for example, in different patterns of scent marking and movement. To control for such variations, the validation process may need to involve more than one site. Where calibration is not possible, the parallel use of two or more complementary methods is advisable (Mahon *et al.* 1998) to provide added confidence to the results of comparisons between areas or trends in abundance. This is important as it is not always clear how variations in relative index scores relate to actual changes in abundance. The choice of which particular method (or suite of methods) to use will ultimately be a trade-off between the

available manpower and resources, and the level of sensitivity required.

Methods involving field signs are particularly prone to inter-observer variations in detection rates. Obviously, skilled fieldworkers are a highly valuable resource in this respect. Stander *et al.* (1997) illustrated the power of using highly skilled surveyors who could provide detailed and accurate interpretation of carnivore sign. On the other hand, surveys involving a large number of samples and many inexperienced staff should be designed to be simple enough to ensure consistent recording.

In conclusion, a variety of techniques are available for the direct or indirect assessment of carnivore abundance. The choice of which to use will depend on the nature of the study and the ecology of the target animal. It may be preferable to employ more than one approach to enhance the confidence associated with trends in abundance. The influence of extrinsic factors on abundance estimates is an important potential source of error and the design of the project should incorporate contingencies to deal with these. Furthermore, where possible it is highly desirable that some attempt is made to validate the chosen method by comparison with a population estimate of known accuracy.

Acknowledgments

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