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INTRODUCTION

There is increasing concern about the status and distribution of terrestrial carnivore populations throughout the world (Schaller, 1996). Changes in land-use practices, habitat loss and fragmentation, sanctioned human persecution, declines in natural prey, disease, illegal poaching, and increased competition within carnivore guilds have brought about a general decline in several carnivore populations with some species now occupying a fragment of their former range. The continued loss of suitable habitat due to an ever expanding human population has placed the issue of conservation and protection of some carnivores as a top environmental priority and/or controversy for many agencies and organizations. Paramount to carnivore recovery, reintroduction, or development of management plans and policies, is having reliable and accurate information regarding the status, health, and well-being of the carnivore population of concern. One of the most commonly asked questions when dealing with carnivore conservation is: where are the animals, how many are there, and what is the population trend? These questions often place biologists and managers in the difficult position of determining the status of a carnivore population. Biologists need reliable methods that provide accurate data on the distribution, abundance, and population trend of a species in order to make informed decisions and recommendations to policy makers. Many carnivores are secretive, nocturnal, far-ranging, live in densely vegetated habitats or remote areas, or exist at extremely low densities, making censusing and monitoring a carnivore population very difficult, if not sometimes seemingly impossible.

Monitoring of a carnivore population may be performed at various levels of resolution. First, biologists may only need to know where a particular carnivore occurs (i.e., species distribution). Second, the biologist may need to know how many animals are in an area (i.e., species abundance).

Animal abundance may be assessed in two ways: relative and absolute abundance. Relative abundance uses indices of animal abundance (e.g., track counts, scent-post visitation rates) that can be compared over time or between areas, but of itself does not estimate animal numbers. In contrast, absolute abundance involves using methods to actually count animals and then estimate the number or density of animals in the population. With repeated sampling over time, both relative indices and absolute estimates of animal abundance can be used to monitor population trends. For many carnivore species this amount of information may be adequate. However, if the population trend indicates an increasing or declining population, then it may be important for the biologist to ask: why is the population changing? This final question involves examining the demographic processes of birth, death, emigration, and immigration that determines the persistence of a population.

The objective of this chapter is to describe the techniques that have been developed to census and monitor terrestrial carnivores and a discussion of the advantages and disadvantages of each technique. Many of the techniques described herein still need an in-depth evaluation as they pertain to accuracy and reliability in monitoring population trends of carnivores. This chapter will focus on terrestrial carnivores only (suborder Fissipedia); inclusion of aquatic carnivores would require an entire chapter to itself. Capture, handling, or immobilization procedures will not be discussed; the volume of literature is enormous and species specific (readers should consult Pond & O'Gara, 1994; Schemnitz, 1994, and references therein). Current methods for censusing or surveying wild carnivores range across the gradient of accuracy, reliability, and cost. I have included references of several studies that used, or attempted to use, a technique to determine species distribution or abundance. These references are only provided as examples of studies, and are not inclusive of all studies using that specific technique.

SOME CONSIDERATIONS BEFORE IMPLEMENTING A MONITORING PROGRAM

Before embarking on a large-scale effort to monitor a carnivore population, the biologist or manager should carefully consider what question(s) they are asking, and if an estimate of population size is needed, then one must decide on the precision and accuracy of the estimate required to answer that question (Lancia *et al.*, 1994; Zielinski & Stauffer, 1996). For example, if a biologist is assessing the abundance of a very rare carnivore that numbers 50 animals in the wild, then even a slight decline in population size

would be critical and surveys would need to be sensitive to even the smallest change in numbers. In contrast, a carnivore population numbering 5000 animals could use a survey with less sensitivity because a slight decline would not be catastrophic to that population. The precision (the measure of how close an estimate is to the expected value), accuracy (the measure of how close an estimate is to the true population size), power (the probability of rejecting the null hypothesis when it is in fact false and should be rejected), sample size, survey design, and the statistical assumptions of each method should be considered before implementing a monitoring program (Peterman, 1990; Reed & Blaustein, 1997; Van Strien *et al.*, 1997). Macdonald *et al.* (1998a) provides a thorough review of statistical considerations when designing a monitoring program. Two major problems that a biologist must typically address when developing a monitoring program is observability or catchability of the animal (the probability is generally < 1) and the size of area to be sampled because time and money constrain sampling the entire area (Lancia *et al.*, 1994, Macdonald *et al.*, 1998a). In addition, the costs, logistics, manpower, and time constraints must all be considered before deciding on the usefulness of a particular method to monitor a carnivore population. These considerations sound quite intuitive and fundamental, but success of the project may hinge on careful examination, prior planning, and development of an appropriate study design (Skalski & Robson, 1992; Macdonald *et al.*, 1998a).

METHODS EMPLOYED TO DETERMINE SPECIES DISTRIBUTION

Often biologists may only need to know if a species is present in an area. This fundamental question is needed to determine the presence and distribution of rare, threatened, or endangered species. Methods typically employed to determine species distribution include habitat mapping, questionnaires, interviews, sighting reports, or confirmation of a sign left by the species in question. Any survey method (direct or indirect measures) that provides an estimate of animal abundance provides distribution information as well. However, for discussion of those survey methods see under 'Methods of estimating animal abundance'.

Habitat mapping

Biologists should not necessarily race out into the bush and start looking for animals or signs of them. Careful consideration regarding the kind of suitable habitat required for a species followed by examination of habitat

maps or aerial photos (if available) can save time (e.g., Macdonald *et al.*, 1998a). Habitat suitability models have been developed for many carnivore species. With the continued development of satellite imagery, remote sensing, and Geographic Information Systems (GIS), areas containing suitable habitat for a particular species can be identified allowing for maximization of survey effort. Surveys can then be stratified by habitat types or land classes (Macdonald *et al.*, 1998a). In the UK, use of landscape data from the Countryside Information System (CIS), plus existing mammal records and knowledge of habitat requirements, were used to predict mammal distribution on a national scale (Macdonald *et al.*, 1998a). Use of GIS has also been instrumental in identifying potential habitat for restoration of carnivores (e.g., Mladenoff *et al.*, 1995; Mladenoff & Sickley, 1998).

Questionnaires, interviews, and sighting reports

One of the simplest methods of determining species distribution, and possibly gaining a subjective estimate of animal abundance, is collecting sightings and general impressions from various people in the field. Questionnaires, interviews, and sighting reports from hunters, trappers, rangers, mail carriers, tourists, guides, and field personnel have been used with some success to measure animal distribution, and sometimes animal abundance, of different species of Canidae (Lemke & Thompson, 1960; Allen & Sargeant, 1975; Harris, 1981; W. Clark & Andrews, 1982; Fuller *et al.*, 1992a; Fanshawe *et al.*, 1997), Felidae (Tewes & Everett, 1982; Erickson, 1982), Mustelidae (Fortenbery, 1970; Hillman & Linder, 1973; Powell, 1982; Strickland & Douglas, 1984; Slough & Smits, 1985; Melquist & Dronkert, 1987), Procyonidae (Kaufman *et al.*, 1976; W. Clark & Andrews, 1982), and Ursidae (Kolenosky & Strathearn, 1987). Questionnaires were successfully used in the UK to detect the presence of elusive carnivores, such as pine marten, *Martes martes* (Strachan *et al.*, 1996), western polecats, *Mustela putorius* (Birks & Kitchener, 1999), and wildcats, *Felis silvestris* (Balharry & Daniels, 1997).

More in-depth questionnaires or interviews with persons with intimate knowledge of the area and who spend considerable time in the field (e.g., trappers, game wardens, rangers, guides) not only may provide a range and status report (Kaufman *et al.*, 1976; Fuller *et al.*, 1992a), but may also be used to obtain a general, subjective estimate of abundance (e.g., Allen & Sargeant, 1975; Harris, 1981). Many agencies compile status reports using this method to access the relative abundance and distribution of carnivores, particularly in countries that are unable to invest the considerable resources more accurate population assessment requires (e.g., Fanshawe *et al.*, 1997).

Questionnaires have been used when agencies require a large-scale assessment of carnivore distribution (e.g., Fuller *et al.*, 1992a), or in circumstances when little is actually known about the biology of the species in question. This is especially useful for rare species that have a wide distribution. For example, surveys by park staff, field workers, and rangers provided a subjective estimate (absent, rare, common, uncommon) of the abundance of African wild dogs (*Lycaon pictus*) throughout the African countries (Fanshawe *et al.*, 1997). In North America, questionnaires are often sent to trappers and field personnel to monitor trends in furbearer populations (W. Clark & Andrews, 1982; Strickland & Douglas, 1984). Drawbacks of this technique include misidentification of carnivores, low response levels to the questionnaire, and concentration of animal sightings along roads or near human habitation (i.e., rare carnivores inhabiting areas of low human density may go undetected or unreported).

Presence of sign

Sightings of the carnivore species in question allow for direct confirmation of species presence. Spotlight surveys have been commonly used to detect rare or endangered nocturnal species, such as black-footed ferrets (*Mustela nigripes*). However, in the absence of visual confirmation of the animal itself, biologists may resort to surveys of animal sign to determine whether a species is present in a given area. Sign surveys have been used to determine species distribution of most carnivore groups, including several felids (Schaller & Crawshaw, 1980; Newman *et al.*, 1985), mustelids (S. Macdonald & Mason, 1982; Melquist & Hornocker, 1983; Richardson *et al.*, 1985; Melquist & Dronkert, 1987; Macdonald *et al.*, 1998a), ursids (Pelton & Marcum, 1977; Kohn, 1982), and canids (Sargeant *et al.*, 1993). Several different methods of sign surveys have been used, including counting tracks, scats, scratches, burrows or dens, and hair samples. For example, diurnal surveys for signs (scat, tracks, fresh dirt diggings) of black-footed ferrets have been conducted throughout the prairie ecosystem to locate remnant populations (Fortenbery, 1970; Hillman & Linder, 1973; Richardson *et al.*, 1985). Trained dogs have even been used to search for ferrets and their burrows (Dean, 1979). Tewes & Schmidly (1987) describe the use of predator calls to attract ocelots (*Leopardus pardalis*) in south Texas. Conspicuous burrows of American badgers (*Taxidea taxus*) and European badgers (*Meles meles*) have been used as an indicator of species presence (Macdonald *et al.*, 1998a). Surveys at bridges crossing over rivers have been used to determine presence or absence of river otters, *Lutra canadensis* (S. Macdonald & Mason, 1982; Melquist & Dronkert, 1987). Sprainting

(defecation) surveys for otters (*L. lutra*) provide good distribution information in the UK, but appear to be unrelated to otter abundance (Conroy & French, 1987; Kruuk *et al.*, 1986). Schaller & Crawshaw (1980) identified tracks and scats to determine the presence and movement patterns of jaguars (*Panthera onca*). Hairsnares or hair tubes can be used to assess distribution through species identification by characteristics of the hair (e.g., Adorjan & Kolenosky, 1969; Moore *et al.*, 1974) or DNA techniques (Foran *et al.*, 1997a,b; Paxinos *et al.*, 1997; Kohn *et al.*, 1999).

Track plates

The use of track plates to determine carnivore presence is gaining in popularity, particularly for the detection of forest carnivores (e.g., Zielinski, 1995). This technique provides a reliable measure of species distribution or presence, but may be unreliable for determining relative animal abundance. Track counts in prepared beds have been used to estimate the extent of mink (*Mustela vison*) distribution, but not numbers of mink (Burgess & Bider, 1980; Humphrey & Zinn, 1982). Similarly, smoked track plates have been used to record tracks of weasels (Barrett, 1983; T. Clark & Campbell, 1983), marten, *Martes americana* (Barrett, 1983; Zielinski & Truex, 1995), and fisher, *M. pennanti* (Zielinski, 1995). A detailed description of tracking plates and the implementation of both enclosed track-plate boxes and unenclosed track plates is provided by Zielinski (1995). In general, track surfaces may be produced from smoked or carbon-sooted aluminum plates, contact paper (tacky, white paper), chalk, or ink. A visual and/or olfactory lure is used as an attractant to bring the animal to the tracking station and while investigating the attractant the carnivore leaves tracks on the tracking surface. Identification of tracks, getting the animal to step on the plate, transportation of the tracking plates, and protecting the track plates from the weather are all problems that require some prior planning when using this technique (but see Zielinski, 1995 and Zielinski & Truex, 1995 for suggestions).

Remote cameras

A relatively new method that is gaining popularity is the use of remote cameras set along trails, near bait stations, or nests. Remote cameras have been used successfully to detect several forest carnivores (Kucera *et al.*, 1995; Foresman & Pearson, 1998) and elusive or nocturnal felids (Joslin, 1982; Rappole *et al.*, 1985). The cameras are commercially available from several manufacturers (see a list in Kucera *et al.*, 1995). They can be set up to 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. While these camera systems are mostly used to detect the presence of carnivores (Kucera *et al.*, 1995; Naves *et al.*, 1996; Foresman & Pearson, 1998), or identify predators at bait stations or nests (Savidge & Seibert, 1988), they could potentially be used to determine animal abundance if individuals can be identified by artificial tags (e.g., ear tags, radio collars) or natural features (e.g., pelage characteristics) and then applying mark–recapture estimators. Remote cameras have the added benefit that a permanent photographic record is available for examination by other researchers. Disadvantages of remote cameras are expense (although some systems are not too costly), getting animals to trigger the camera (similar to problems associated with track plates), and the time delay between photo acquisition and development of the film (i.e., results are not instantaneous). However, development of digital cameras that download images into a computer may negate this concern.

Some considerations for sign surveys

A problem with using sign to determine carnivore distribution is the proper and consistent identification of tracks, scats, burrows, and hair samples. Species identification from scats can be assisted by the use of fecal bile acid patterns detected by thin-layer chromatography (Major *et al.*, 1980; Johnson *et al.*, 1981). Examination of hair samples with a light microscope and comparison to a hair key (e.g., Adorjan & Kolenosky, 1969; Moore *et al.*, 1974) or reference collection can provide species identification. Recent advances in DNA techniques have opened the door for more accurate assessment of species identification and carnivore distribution based upon scat or hair samples (Foran *et al.*, 1997a,b; Paxinos *et al.*, 1997; Kohn *et al.*, 1999). It should be emphasized that most sign surveys only provide distribution information. However, these DNA techniques can also be used to identify individual animals allowing for estimation of population size (Kohn *et al.*, 1999). The amount of sign left behind by an animal does not appear to correlate with animal density for most carnivores (Messick & Hornocker, 1981; Melquist & Hornocker, 1983; Messick, 1987). Also, simply because observers fail to find sign does not necessarily indicate species absence.

Surveys for species presence used as measures of animal abundance

The previously discussed sign surveys can serve a dual purpose. In their most rudimentary form they provide distributional information, but with standardization of the methodologies and the amount of effort conducting the survey, sign surveys may also be used as an index of animal abundance.

For example, if certain areas or habitats are repeatedly surveyed over time and the number of hours of searching are recorded, then biologists may standardize their surveys to tracks/hour, scats/hour, etc., allowing for trend information over time or comparisons between areas.

METHODS FOR ESTIMATING ANIMAL ABUNDANCE

Once a biologist has determined that a carnivore is present in a particular area, the next question that may need to be answered is: how many animals are there and what is the trend in abundance? Biologists may monitor animal abundance by direct methods of counting the animals themselves, or indirectly by counting animal sign (Macdonald *et al.*, 1998a). Estimating animal abundance requires consistent and standardized application of a technique to be able to detect changes or differences with some degree of accuracy, precision, and power (Macdonald *et al.*, 1998a). Thus, for any of the following techniques, biologists must maintain a standardized study protocol for the survey or count that is used and consistently apply that protocol to all future surveys to allow for direct comparisons over time. Whether biologists use sign surveys, indices of relative abundance, or measures of absolute animal abundance, caution should be exercised when examining population trends for carnivores. Assessing rates of increase or decrease from trend data should be done carefully, taking into account the precision and accuracy of the methods used to determine population size estimates or indices of relative abundance. Biologists should be aware of the influence of other variables on survey results. Biologists should consider the characteristics of the animals themselves (e.g., behavior, size, color); the topography and vegetation where the survey will be executed; temporal factors; observer experience, ability, and fatigue; and the spatial distribution of the species concerned (i.e., widely distributed versus high density). Before embarking on population trend analyses, biologists and researchers should examine the assumptions and estimate the power of the survey technique in its ability to detect population changes; see Gerrodette (1987), Eberhardt & Simmons (1992), and Kendall *et al.* (1992) for more details.

Indirect methods

Scent-station surveys

One of the most common sign surveys utilized for indexing carnivore abundance in North America is scent-post or scent-station surveys. Scent-post surveys have been widely used to estimate the relative abundance of several canids (Linhart & Knowlton, 1975; Roughton, 1979; Sumner & Hill,

1980; K. Johnson & Pelton, 1981; Morrison *et al.*, 1981; Roughton & Sweeny, 1982; Conner *et al.*, 1983; Travaini *et al.*, 1996; Sargeant *et al.*, 1998), cats (Conner *et al.*, 1983), mustelids (Brown, 1969; Lord *et al.*, 1970; Humphrey & Zinn, 1982; Melquist & Dronkert, 1987; Hein & Andelt, 1995), raccoons (Sumner & Hill, 1980; W. Clark & Andrews, 1982; Conner *et al.*, 1983; Smith *et al.*, 1994), and bears (Lindzey *et al.*, 1977; Kohn, 1982). Scent-post or scent-station surveys involve placing a scented tablet (e.g., fermented egg extract, mackerel oil) or other attractant within a 1-m circular area of sifted dirt. Tracks left by an animal are identified to species, and presence or absence of the species is recorded. Typically, stations are spaced at a predetermined interval along roads or trails and then visited for three to four consecutive nights to record tracks; the sifted area is swept smooth after each night. Biologists should consider the movement patterns and home-range size of the species of interest when determining the spacing of the stations (i.e., close spacing for close-ranging species, increased spacing for larger species). The frequency of animal visitation to operable stations (i.e., not disturbed by wind, rain, vehicles) is used as an index of abundance. For details on this method and its application, see Linhart & Knowlton (1975), Roughton (1979), and Roughton & Sweeny (1982). Biologists interested in using scent-post surveys should consult Smith *et al.* (1994) and Sargeant *et al.* (1998) prior to implementation. While some biologists reported that scent-station surveys reflect changes in raccoon abundance, Smith *et al.* (1994) found no association between visitation rates and density of raccoons. Knowlton (1984) found a positive correlation ($r^2 = 0.79$) between coyote (*Canis latrans*) scent-station indices and estimated coyote density. 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. Sargeant *et al.* (1998) makes several recommendations regarding sample unit specification and interpretation of scent-station surveys. Misidentification of tracks, problems with the weather (mostly wind and precipitation), wariness of animals in relation to the sifted substrate, and a fairly labor intensive technique are items to be addressed when considering scent-station surveys.

A variation of the scent-post survey that has been used to index dingo (*C. familiaris dingo*) populations is the activity index (Allen & Engeman, 1995, Allen *et al.*, 1996). This index of animal visitation simply uses a sifted dirt area on a road without any scent or lure to attract animals. 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 has been used as an estimate of relative abundance for some canid species, mainly coyotes (Clark, 1972; Davison, 1980; Andelt & Andelt, 1984) and wolves, *Canis lupus* (Crête & Messier, 1987). The general methodology involves designating transects or routes along a roadway, clearing all scats from the road, then returning and collecting all scats encountered two weeks later. The scat index is computed as the number of scats collected per transect per 14-day period (Davison, 1980). If transects vary in length, or the time periods vary in the number of days between collections, then the index can be standardized to scats/km/day. Scat deposition rates for coyotes were found to be correlated ($r^2 = 0.97$) with estimates of animal density derived from mark–recapture techniques using radioisotope tagging of feces (Knowlton, 1984). 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 (hence differential scat deposition rates) and seasonal changes in food items consumed (Andelt & Andelt, 1984). Misidentification of scats and heavy vehicle traffic on roadways can also be problematic when using scat deposition 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 potentially be used to estimate population size (Paxinos *et al.*, 1997, Kohn *et al.*, 1999).

Track counts along a transect

Tracks left by carnivores along river beds, dry washes, sandy fire breaks or roads, or on snow-covered roads and trails have been used as a relatively simple and inexpensive measure of relative animal abundance for several species of canids (Beasom, 1974a; Crête & Messier, 1987; Palomares *et al.*, 1996), felids (Anderson, 1981; Van Dyke *et al.*, 1986; Van Sickle & Lindzey, 1991, 1992; Smallwood & Fitzhugh, 1995; Beier & Cunningham, 1996; Stander, 1998), mustelids (Ruff, 1939; Quick, 1944; de Vos, 1952; Coulter, 1966; Priklonski, 1970; Fitzgerald, 1977; Powell, 1982; S. Johnson, 1984; Slough & Smits, 1985; Golden, 1986; Melquist & Dronkert, 1987), ursids (Pelton & Marcum, 1977; Stirling *et al.*, 1980; Kohn, 1982; Kendall *et al.*, 1992), and Egyptian mongooses, *Herpestes ichneumon* (Palomares *et al.*, 1996). Carnivores that occupy regions that receive snow have been monitored through the use of counting tracks along established transects within one to two days following fresh snowfall. Winter track counts along standard transects have been routinely used to index the relative abundance

and population trends of marten (Slough & Smits, 1985), weasels (Ruff, 1939; Quick, 1944; Priklonski, 1970; Fitzgerald, 1977), and fisher (de Vos, 1952; Coulter, 1966; Powell, 1982; S. Johnson, 1984). Similarly, counts of tracks left by cougars (*Puma concolor*) along dry washes has been used to index animal abundance (Beier & Cunningham, 1996). Golden (1986) was able to conduct aerial track counts for wolverines (*Gulo gulo*) in unforested areas of Alaska. Ballard *et al.* (1995) reported good precision between line-intercept sampling of tracks and estimates of wolf density based upon radiotelemetry. This technique was repeatable, efficient, reasonably accurate, and relatively inexpensive. Biologists attempting transect counts of tracks should be aware of some pitfalls. Misidentification of tracks and low power to detect population changes can occur when using track counts (Van Sickle & Lindzey, 1991; Kendall *et al.*, 1992; Ballard *et al.*, 1995; Beier & Cunningham, 1996). Precision can be increased by increasing sampling effort (more transects), or increasing the length of transects if dealing with a far-ranging species (e.g., cougars: Van Sickle & Lindzey, 1991), although see Kendall *et al.* (1992). 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, variables one must consider include the condition and consistency of the snow, variable depth of snow (i.e., no snow negates data collection), temperature, and time of year. 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 as a method of indexing relative abundance of some carnivore species. Annual den surveys have been used to monitor populations of arctic fox (*Alopex lagopus*) in northern dry tundra (Macpherson, 1969; Garrott *et al.*, 1983), but appear to have little application in areas of coastal wet tundra (Anthony, 1996). Ground and aerial surveys for dens has been used to monitor kit fox (*Vulpes macrotis*) populations in desert environments (O'Farrell, 1987) and red fox (*V. vulpes*) populations on the prairie (Trautman *et al.*, 1974). The key to this survey technique is relatively open habitat with little vegetative cover and a carnivore species that makes conspicuous dens or burrows. These surveys can be relatively expensive (aerial searches) and/or labor intensive (ground searches). In general, this survey entails personnel walking or flying along a route or transect searching for active dens. The presence of feces or tracks at the burrow or den can assist in species identification. Ground surveys conducted along transects can also

be used to calculate the density of dens if biologists record the perpendicular distance from the transect to the den (Burnham *et al.*, 1980). Conspicuous burrows dug by badgers have been used to indicate species presence, but there appears to be no correlation between density of burrows and animal abundance (Messick & Hornocker, 1981; Messick, 1987). This technique would probably not work well for indexing carnivores with large social units. No matter how large the pack, coyotes and wolves typically have one natal den to rear offspring (i.e., a pair of coyotes uses the same number of dens as a pack of seven coyotes). For animals that exist in packs or clans, the number of dens would more likely indicate the number of social units present across an area, but not the number of animals in each social unit.

Vocalization response surveys

For social carnivores that utilize long-range vocalizations (roars, howls, or whoops) to communicate, biologists have been able to use the response rate to simulated vocalizations as an estimate or index of relative animal abundance. Howling surveys for coyotes (Wenger & Cringan, 1977, 1978; Okoniewski & Chambers, 1984) and wolves (Harrington & Mech, 1982; Carbyn, 1982; Fuller & Sampson, 1988), roaring for lions, *Panthera leo* (Rodgers, 1974; Maddock *et al.*, 1996; Ogutu & Dublin, 1998), and long-distance whoops for hyenas, *Crocuta crocuta* (Ogutu & Dublin, 1998) have all been used as a technique for estimating animal abundance. Vocalization response surveys typically employ recorded vocalizations, although human imitation of sounds is sometimes effective. Traveling along roads or trails and stopping at predetermined intervals, vocalizations are produced and then observers listen for a specified amount of time for a response from the target species. The biologist may conduct the survey over several nights and use the vocalization response as a means of estimating the relative abundance of the carnivore species. Standardization and consistency of this method is needed for reliable and comparable results for trend analyses. Biologists should also be aware of the seasonal, social, temporal, and spatial factors that may influence carnivore vocalization rates (Laundré, 1981; Harrington & Mech, 1982; Walsh & Inglis, 1989; Gese & Ruff, 1998). For an accurate population census, biologists need to intensively survey the area of interest to obtain adequate coverage (Fuller & Sampson, 1988). In the Masai Mara National Reserve of Kenya, Ogutu & Dublin (1998) estimated that 20% of the study area had to be sampled to acquire reliable estimates of hyena and lion abundance.

Frequency of depredation complaints

The frequency of livestock depredation complaints may be useful as an indicator of relative abundance and population trend under the general belief that animal abundance is correlated to rates of livestock predation. Because this relationship has not been explicitly tested, biologists should be cautious of this technique as depredation rates are subject to changes in livestock stocking rates, habitat type, size of area used, husbandry practices, and environmental variables (Fritts, 1982; Lindzey, 1987; Mech *et al.*, 1988a).

Some considerations when using indirect methods

Indirect methods provide only relative abundance, not absolute abundance, and must be applied consistently for any reliable comparisons between areas, habitats, or over time. Whenever indices of relative abundance are used, biologists should attempt to learn if the relationship between relative indices and absolute abundance is positively and monotonically related, or if the relationship is nonmonotonic. Is the relationship linear with a constant slope, or linear with a variable slope? Indices that are nonmonotonic to animal abundance are of little use in monitoring trends of a carnivore population. Comparison of an inexpensive indirect method to a more expensive direct method could prove worthwhile for calibration of the less expensive technique. During such a calibration, the techniques should be performed concurrently and may need to be conducted on a species-specific, habitat-specific, and seasonal basis. Unfortunately, few indices of relative abundance have been properly tested with a known carnivore population estimate. Of those that have been examined, results are mixed. Knowlton (1984) found positive correlations between scat deposition rates along transects and estimated coyote population density. Scent-post survey indices were also positively related to coyote density. In contrast, Smith *et al.* (1994) found no association between scent-station visitation rates and density of raccoons.

Direct counts

Direct counts involve the actual counting of animals themselves, in contrast to counting sign. These counts may use either dead animals (e.g., mortality samples, road kills, harvest reports) or live animals (e.g., trapping or sightings). The assumptions of direct counts and the estimators used to determine population size should be carefully reviewed (Caughley, 1977; Burnham *et al.*, 1980; Skalski & Robson, 1992). Counts may involve total counts of the area, or a subsample of the area and extrapolation to the rest

of the area of concern. Stratification of subsamples to different habitat types or land classes may increase the validity, usefulness, and precision of the surveys (Macdonald *et al.*, 1998a).

Harvest reports and pelt registration

A method of gaining insight into abundance (and certainly distribution) of a species is examination of harvest and trapping records. Current and historical harvest records can be a valuable resource in obtaining a general, if subjective, idea of animal distribution and abundance (Seton, 1909; Hewitt, 1921). In the Canadian provinces, mandatory pelt sealing reports has also been used to estimate furbearer population trends (Novak, 1987). In the UK, a decline in otter numbers was observed through a decrease in hunting success (Strachan & Jefferies, 1996). While detailed information from harvested animals can be used to construct models for population estimation (W. Clark & Andrews, 1982), harvest data alone is generally not a reliable estimate of population trends. Pelt prices, differential harvest methods, and environmental and social factors all influence harvest rates. W. Clark & Andrews (1982) speculated that harvest surveys may indicate population trends of furbearers with low commercial value because harvest trends would be less affected by management actions and fur prices. Other problems associated with the use of harvest records include hunters and trappers not keeping records, trappers having faulty memories, only some hunters submitting reports (usually successful hunters), and sometimes trappers will give inaccurate reports to avoid tax auditors (Sanderson, 1951a; W. Clark & Andrews, 1982). For rare species (e.g., coati, *Nasua narica*), fur harvest reports are generally unreliable for population trends (Kaufman, 1987), while harvest reports for abundant furbearer populations (e.g., long-tailed weasel, *Mustela frenata*) may be reliable measures of population trend (Hamilton, 1933; Barbour & Davis, 1974).

One method for estimating harvest rate and population size of bobcats (*Lynx rufus*) uses the total number of harvested animals, the sex-specific age distribution of the harvest, and the estimates of harvest effort over the span of years represented in the age distribution (Paloheimo & Fraser, 1981; Rolley, 1987). Interpretation of the sex and age structure of harvested samples is commonly used to assess changes in black bear (*Ursus americanus*) populations (Whelan *et al.*, 1978; Lindzey & Meslow, 1980; Kolenosky & Strathearn, 1987). However, when using harvest data, the validity of the underlying assumptions should be carefully evaluated (Gilbert *et al.*, 1978). Population trends of carnivores have been examined in relationship to past and current harvest records for many species of Canidae (Elton, 1942;

Chitty, 1950; W. Clark & Andrews, 1982; Erickson, 1982), Felidae (Elton & Nicholson, 1942; Erickson, 1982; Lindzey, 1987; Rolley, 1987; Quinn & Parker, 1987), Mustelidae (Hamilton, 1933; Barbour & Davis, 1974; W. Clark & Andrews, 1982; Powell, 1982; Linscombe *et al.*, 1982; Strickland & Douglas, 1984; Melquist & Dronkert, 1987), Procyonidae (Seton, 1909; Hewitt, 1921; Sanderson, 1951a; W. Clark & Andrews, 1982; Kaufman, 1987; Novak, 1987), and Ursidae (Whelan *et al.*, 1978; Lindzey & Meslow, 1980; DeMaster *et al.*, 1980; Kolenosky, 1987). However, no in-depth testing has been conducted to confirm the relationship between animal population density and reports of fur or animal harvest statistics.

Road mortality samples

The frequency of animal carcasses found on roadways has been proposed as a measure of population trend for some carnivore species, usually as an index of relative abundance. For example, the number of raccoons (*Procyon lotor*) and skunks (*Mephitis mephitis*) killed along roads have been used as measures of relative abundance (W. Clark & Andrews, 1982; Bartlett & Martin, 1982). While this technique is intuitively simple and appealing, differences in animal behavior and movements, habitat, traffic density, road surface, and road density likely influence kill rates of some carnivores; nor has the relationship between population density and road kill rate been adequately examined. However, Birks & Kitchener (1999) calibrated road kills of polecats with numbers estimated from intensive live trapping. Road mortality samples can be used to confirm species presence.

Spotlight surveys

Spotlight surveys are a cost effective method typically used for assessing the relative abundance of nocturnal animals. Estimates of relative abundance for nocturnally active carnivores, such as raccoons (Andrews, 1979; Frederickson, 1979; Rybarczyk *et al.*, 1981; W. Clark & Andrews, 1982), badgers (Hein & Andelt, 1995), kit foxes (Ralls & Eberhardt, 1997), red foxes (Weber *et al.*, 1991), black-footed ferrets (Campbell *et al.*, 1985), and skunks (Schowalter & Gunson, 1982; Rosatte, 1987), have been determined with spotlight surveys. These surveys usually involve two observers standing in the back of a truck being driven slowly (16–24 km/hr) along roadways, scanning the road and sides for animals using spotlights of > 500 000 candlepower. When an animal is detected, usually by eye shine, the driver stops the vehicle and the observers identify the animal (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 (> 10 km), and because vegetative cover and topography can influence visibility (Whipple *et al.*, 1994; Ralls & Eberhardt, 1997) which influences survey results, these variables should be considered in survey design (Ralls & Eberhardt, 1997). For a description of this technique in assessing fox abundance, see O'Farrell (1987) and Ralls & Eberhardt (1997). Surveys can be conducted over several nights (repeated counts) to obtain a measure of sampling error (Norton-Griffiths, 1975). Large samples with replication are needed to detect changes in population size with any statistical power (Ralls & Eberhardt, 1997). Surveys can be conducted seasonally and annually for population trend analysis. Spotlight counts do not work well in areas containing low densities of carnivores. Spotlight counts may also be used to acquire a relative estimate of the abundance of certain prey species at the same time (Barnes & Tapper, 1985; White *et al.*, 1996), but Ralls & Eberhardt (1997) believed that spotlighting was not a sensitive method for assessing prey abundance.

Catch-per-unit-effort

Live trapping certainly gives a positive confirmation of species presence and hence distribution. The number of animals captured per trap-night can also be used as an index of relative abundance of carnivores. Live trapping is expensive and labor intensive, and can be ineffective in areas with low carnivore density. In addition, standardization of capture procedures and variation among individual trappers can cause problems with this methodology. This technique has been used to assess the relative abundance of coyotes (F. Clark, 1972; Davison, 1980; Knowlton, 1984), island gray foxes, *Urocyon littoralis* (Crooks, 1994), kit foxes (Cypher & Spencer, 1998), felids (Rolley, 1987), and some species of mustelids (Lindzey, 1971; Simms, 1979; Bjorge *et al.*, 1981; King, 1981; Hein & Andelt, 1995). For weasels, the number of animals caught per trap-night appears to be linearly related to animal density (Caughley, 1977), but few experimental tests have been conducted for other carnivore species.

Capture–mark–recapture

A technique originally developed with small mammals and proving useful for estimating carnivore populations is capture–mark–recapture. While mark–recapture is fairly time consuming, labor intensive, and costly, it does provide a reliable estimate of population size (i.e., absolute

abundance) for many carnivore species, including badger (Messick & Hornocker, 1981), ringtail (*Bassariscus astutus*) and coati (Kaufman, 1987), mustelids (Bailey, 1971; King & Edgar, 1977; Messick & Hornocker, 1981; Douglas & Strickland, 1987; Rosatte, 1987; Strickland & Douglas, 1987), bears (Pelton *et al.*, 1978; DeMaster *et al.*, 1980; Miller & Ballard, 1982; Kruuk, 1995; Miller *et al.*, 1997), canids (F. Clark, 1972; Todd *et al.*, 1981; Roemer *et al.*, 1994), felids (Schaller, 1972; Currier *et al.*, 1977; Mills *et al.*, 1978; Miller, 1980; Quinn & Parker, 1987), hyenas (Kruuk, 1972b; Sillero-Zubiri & Gottelli, 1993), and raccoons (Sanderson, 1951b). Mark–recapture can provide relatively accurate estimates of population size if sample sizes are adequate, data collection techniques are unbiased, and the basic assumptions for the population estimator are not violated (see Caughley, 1977; Wilson *et al.*, 1996; or Thompson *et al.*, 1998; and references therein for assumptions of various estimators). 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 (Pollock, 1981; Seber, 1982; Montgomery, 1987).

Marks employed to tag the animal include ear tags, radio collars, dyes, and physiological markers such as radioactive isotopes. 'Recapture' may involve actual physical recapture of the animal, resighting of the animal (Smuts, 1976; Todd *et al.*, 1981; Miller *et al.*, 1997), returns from trappers or hunters (Sanderson, 1951b), recapture via fecal analysis for a physiological marker, or a combination of these (e.g., Currier *et al.*, 1977). Kohn *et al.* (1999) estimated coyote population size by identifying individual animals through fecal DNA analysis combined with mark–recapture methodology. Several different models for population estimation (e.g., Petersen, Jolly–Seber, Schnabel) can then be used to calculate population size (Caughley, 1977; Jolly, 1982; Seber, 1982; Thompson *et al.*, 1998). Many of these models are now available on software for use on a computer (e.g., programs CAPTURE by White *et al.*, 1982; NOREMARK by White, 1996; EAGLES by Arnason *et al.*, 1991). If the area of interest or trapping effort is known, then density estimates can be derived. Researchers should review capture–recapture methodologies outlined by Caughley (1977) or Thompson *et al.* (1998) to assist in the study design prior to implementation. Various trapping designs have been used with mark–recapture estimators. Roemer *et al.* (1994) used a trapping grid to estimate population size of island gray foxes. A trapping web design was used to estimate numbers of Indian mongooses, *Herpestes javanicus* (Corn & Conroy, 1998). F. Clark (1972) captured and marked coyote pups at dens in the spring then recaptured them during late-summer trapping sessions.

The use of physiological markers has received increased interest as a means of marking animals and then using 'recaptures' of those marks to estimate animal abundance with mark–recapture estimators. The method involves capture of the animal, injection or oral dosing of the animal, then resampling the animal at a later date either by direct recapture and blood sampling, collection of labeled scats, or examination of hunter killed animals. Radioactive isotopes have been used to determine densities of black bears and other carnivores (Pelton & Marcum, 1977; Kruuk *et al.*, 1980). Radioactive zinc has been used to estimate the density of European badgers by injecting the captured individuals, then detecting the isotope in feces and estimating the population size from the ratio of radiolabeled to normal feces (Kruuk *et al.*, 1980; Kruuk & Parrish, 1982). Kruuk *et al.* (1993) used radioactive isotopes to mark otter spraints and then identify which otter deposited that spraint. With the added responsibility and permitting needed to handle and store radioisotopes, researchers have examined other compounds to serve as individual markers for carnivores. Knowlton *et al.* (1988) reported that oral doses of iophenoxic acid were detectable or traceable in coyotes up to 16 weeks post-ingestion. Johnston *et al.* (1998) tested the use of chlorinated benzenes as physiological markers for coyotes and found that injection or ingestion (oral dose) of some compounds were detectable up to 100 days later in feces and blood serum. Biomarkers have been used to estimate animal abundance in canids (Davison, 1980; Knowlton, 1984), mustelids (Kruuk *et al.*, 1980; Kruuk & Parrish, 1982; Knaus *et al.*, 1983; Melquist & Dronkert, 1987), raccoons (Conner *et al.*, 1983; Conner & Labisky, 1985), and bears (Pelton & Marcum, 1977).

Direct counts by removal

For some species of furbearers, most often species that are considered pests, the removal method has been used to estimate animal abundance. The method has been used to estimate population size mainly on skunks (Skalski *et al.*, 1984; Rosatte, 1987) and raccoons (Twichell & Dill, 1949; Fountain, 1975). 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 furbearer species, intrinsic values, and/or the social and political ramifications, the removal method is rarely employed.

Transect, strip, or area sampling

In certain circumstances it may be possible for the biologist to directly count the number of animals along transects, strips, in quadrants, or within a defined area and estimate animal population size or density (Gates,

1979; Burnham *et al.*, 1980; Rao *et al.*, 1981; Bibby *et al.*, 1992a). While transect and quadrant surveys are commonly used for estimating populations of ungulates, some of the larger carnivores may be surveyed with this technique. Trends in relative abundance can be compared from direct counts; absolute abundance may be estimated if correction factors are available to account for problems with sightability (Samuel *et al.*, 1987). Population estimates can also be calculated by distance methods along line-transects (Burnham *et al.*, 1980). Software programs that will 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 carnivore occupying a relatively sparsely vegetated habitat that allows for maximum sightability. Aerial surveys have been used to estimate animal abundance of coyotes (Nellis & Keith, 1976; Todd *et al.*, 1981), brown bears, *Ursus arctos* (Erickson & Siniff, 1963), and polar bears, *Ursus maritimus* (Scott *et al.*, 1959; Prevett & Kolenosky, 1982). Air and ship censuses of polar bears have been conducted during the summer when bears are concentrated along the polar ice pack (Larsen, 1972).

The number of animals sighted can be affected by weather, vegetation, visibility, and observer experience and fatigue. Miller & Russell (1977) compared aerial transect-strip counts and ground counts of wolves and reported that the behavior of the animals, width of the survey strip, and visibility all contributed to unreliable estimates of wolves using aerial surveys over open tundra habitat. The use of ultraviolet, infrared, or thermal imagery photography has been proposed for enhancing sightability of polar bears (Lavigne & Øritsland, 1974) and cougars (Havens & Sharps, 1998) during aerial surveys. Ground surveys are practical for smaller carnivores or animals that can be readily viewed in open habitats. Population trends for coati were measured by making visual counts along walked transects (Kaufman, 1987). Hyenas were sampled by ground transects in Africa (Hanby & Bygott, 1979). In certain situations, the entire area of interest may be surveyed, and through repeated sampling and reobservation, the entire population may be counted. For example, the wolves on Isle Royale have been observed and counted for decades, with each wolf pack counted on the island each winter (Jordan *et al.*, 1967; Wolfe & Allen, 1973; Peterson *et al.*, 1998). However, the ability to count all individuals in a defined area is a rare circumstance, but correction factors from a radio-marked sample can be used for determining a more accurate estimation of population size.

Identification of individual animals

While the opportunity to directly observe carnivores 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. This technique has been used successfully in studies of large carnivores in Africa. Biologists studying African lions have been able to identify all individuals by using sketches and photographs so that all lions found could be positively reidentified by a combination of ear notches, vibrissae spot patterns, and other natural features (Pennycuick & Rudnai, 1970; Bretram, 1975; Hanby & Bygott, 1979). Similarly, identification of individual hyenas by distinct spot patterns, scars, and ear notches (East & Hofer, 1991) has been used to determine population size (Hofer & East, 1995). Throat patches have been used to identify individual European otters (Watt, 1993). Individual coyotes in Yellowstone National Park were identified through radio collars, ear tags, and unique phenotypic characteristics. Observation of these animals permitted determination of pack size, and hence population size (Gese *et al.*, 1996a). Maddock & 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 over 5000 photographs.

Common to studies using identification of individuals is relatively open habitat and a carnivore species that is readily observable and generally tolerant of human presence. In fact, the animals do not necessarily need to be marked for individual identification, as individuals may be resighted and identified indirectly. Track characteristics of cougars has been used in which tracks of individual animals were separated on the basis of characteristics and location. These individual tracks were then combined to provide a density estimate (Koford, 1976; Ackerman *et al.*, 1981; Van Dyke *et al.*, 1986; Smallwood & Fitzhugh, 1993). The main advantage of using characteristics of individual tracks for identification was that it entailed less effort than a large-scale trapping program, but the accuracy of this method in relation to changes in population size remains untested (Lindzey, 1987). While individual identification allows for a relatively complete count of animals, the time and effort for this type of monitoring avails itself only to particular situations and is often conducted in conjunction with behavior studies (e.g., East & Hofer, 1991; Gese *et al.*, 1996a). Another method that is receiving increasing attention is the use of hairsnares to acquire hair samples from carnivores, then using DNA sequencing to identify individuals in the population (Foran *et al.*, 1997b; Paxinos *et al.*, 1997; Kohn *et al.*, 1999).

Radiotelemetry

With the introduction of radiotelemetry back in the 1960s (Cochran & Lord, 1963), the ability to monitor secretive carnivores increased tremendously. This method allows researchers to estimate the home-range size or territory size of an animal. Combining territory size (and overlap) with the number of members of the social unit or pack, plus the percentage of radio-collared transients sampled from the population, density estimates can be derived for the population in question. Because canids tend to be highly social with well-defined territories, radiotelemetry is now widely accepted as a method to measure population size and density (e.g., Mech, 1973a; Fritts & Mech, 1981; Fuller, 1989; Gese *et al.*, 1989). For more solitary carnivores, 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. This method has been used for felids (Hornocker, 1970; Seidensticker *et al.*, 1973; Hemker, 1982; Rolley, 1987; Quinn & Parker, 1987), mustelids (Melquist & Hornocker, 1979; Hornocker & Hash, 1981; Magoun, 1985; Douglas & Strickland, 1987; Strickland & Douglas, 1987), ringtails and coatis (Lanning, 1976; Trapp, 1978; Russell, 1979; Lacy, 1983), and bears (Kolenosky, 1987). While radiotelemetry is very labor intensive and costly, this technique provides one of the best and reliable estimates of population density for many carnivores. Long-term studies using radiotelemetry provide the most reliable annual estimates of population density for several secretive, far-ranging, low-density carnivores, such as cougars (Hornocker, 1970; Seidensticker *et al.*, 1973; Hemker, 1982), wolverine (Magoun, 1985), and lynx, *Lynx lynx* (Quinn & Parker, 1987). With the advent of satellite and GPS technology, more intensive monitoring of large and medium-sized carnivores will be possible (Ballard *et al.*, 1998; Merrill *et al.*, 1998), but systems for smaller carnivore species will require further technological development.

MONITORING ANIMAL POPULATION DEMOGRAPHICS

The previously described methodologies provide information on how a carnivore population may be doing numerically, but do not necessarily answer questions of why the population trajectory is up, down, or stationary. In order to do this, one must know the rates of survival, fecundity, immigration, and emigration that influences the persistence of a carnivore population. Thus, in this section I will attempt to summarize the important features that one may need to measure in order to understand these important demographic processes. There are entire books devoted to the

analysis of animal population dynamics (e.g., Caughley, 1977; Royama, 1992), therefore I will not go into detail of the mathematics involved. Because most of the actual techniques used to measure survival, fecundity, immigration, and emigration are species specific, for the scope of this chapter I will only provide a listing of the various measures one may want to monitor. I strongly recommend that readers embarking on a study of carnivore population dynamics consult Caughley (1977), Royama (1992), Thompson *et al.* (1998), and White & Garrott (1990) during the design and planning stages of studies so as to maximize their effort in collecting the proper data needed for demographic analyses.

Fecundity

The fecundity rate of a female is the number of offspring she produces over an interval of time (Caughley, 1977). Measuring fecundity or reproduction is fairly involved and time consuming. However, there are several basic questions dealing with fecundity that biologists may wish to ask: (1) when does the breeding season start and how long does it last, both in terms of estrous and gestation?; (2) when are the young born?; (3) what proportion of the females in the population breed?; (4) how many young are produced?; (5) is there one (monestrous) or multiple (polyestrous) breeding seasons in a year?; (6) what is the sex ratio at birth?; and (7) what is the age of first reproduction? There are various techniques to answer these questions. For carnivores, collection of carcasses, recovery of tagged animals, and observations in the field or captivity may address some of the questions. More specifically, examination of ovaries (corpora lutea counts) and placental scar counts from recovered animals or hunter killed animals, the ratio of juveniles to females in harvest counts, and/or observation of litter size in the field will give some measure of reproductive output (e.g., age-specific fecundity). Behavioral observations of animals in the field or captivity, physical examination, or tissue histology may provide information on initiation and cessation of the breeding season, and age of first breeding or sexual maturity.

Survival

Measuring the survival rates of carnivores usually involves construction of a life table or estimation of survival from radiotelemetry data. Pertinent questions a biologist may consider when designing a study to address survival rates are: (1) what is the number of deaths in each age interval?; (2) what is the probability of dying in each age interval?; (3) does mortality vary between seasons?; and (4) what are the causes of mortality? Ages from

animals collected from hunters and trappers can be used to construct life tables. Caughley (1977) presents detailed information on various models for life-table construction and survival analysis. Measuring radio-days and numbers of deaths during defined time intervals derived from radio-collared animals can be used to calculate daily and interval survival rates (Trent & Rongstad, 1974; Heisey & Fuller, 1985). Application and assumptions of various survival estimators using radio-collared animals is covered thoroughly in White & Garrott (1990). Popular software programs that will estimate survival rates include SURVIV (White, 1983) and MICROMORT (Heisey & Fuller, 1985). The statistical package SAS (SAS Institute Inc.) will also calculate survival rates using the Kaplan–Meier product limit estimator (White & Garrott, 1990).

Immigration and emigration

Measuring emigration and immigration from a carnivore population usually involves the capture and tagging of several individuals and the subsequent recapture or radio-tracking of those individuals. Monitoring of the movements of animals out of a marked population (e.g., dispersal) is a simpler task that monitoring movements into the population, because biologists can not predict where immigration will occur from outside the known study population. Thus, biologists typically assume that the rate of movement out (egress) of their study area is equal to the rate of ingress. This assumption is usually violated, particularly if one of the populations is receiving control or some form of management. Whether the population being studied is maintained as a source or sink is pertinent to understanding the system and carnivore population in question.

DISEASE MONITORING

A subject often overlooked when monitoring carnivores is the question pertaining to the role of diseases in population dynamics. With an increasing interface between carnivores and humans and their pets, livestock, and expanding development, the possibility of disease transmission continues to escalate. Rare or endangered carnivores exposed to disease agents can have dire consequences. Canine distemper caused a rapid decline in black-footed ferret numbers and almost caused the species to become extinct (Williams *et al.*, 1988). Similarly, rabies has been implicated in the decline of African wild dogs (Woodroffe & Ginsberg, 1997b). Biologists beginning a study should investigate the possible need for a disease monitoring pro-

gram and handling protocol (for animals and samples collected), especially if dealing with a plan to reintroduce a species, or a rapidly declining carnivore population. Physical examination of living animals, blood collection for serological analysis, and post-mortem examinations of animals collected from trappers or hunters and recovery of telemetered animals can be used in a disease monitoring program. Consultations with wildlife veterinarians affiliated to a diagnostic lab or university are recommended to recognize which diseases should be screened for and then design an appropriate monitoring program.

MODELS

Computer simulations have been used to model carnivore population dynamics. Models which take into account different levels or rates of demographic variables, such as survival, fecundity, age structure, etc. have been used to develop computer simulations of population trends of various carnivore species, including coyotes (Connolly, 1978; Sterling *et al.*, 1983), river otters (Tabor & Wight, 1977; Mowbray *et al.*, 1979), polar bears (Stirling *et al.*, 1976), and black bears (Lindzey & Meslow, 1980). These models can then be used to simulate the population response when one or more demographic variables is manipulated. The use of simple population models has now expanded into more sophisticated models and software programs (e.g., VORTEX by Lacy, 1993b). Population viability analysis (PVA) and population and habitat viability assessment (PHVA) has been used to evaluate the outcomes of various management actions, environmental perturbations, and stochastic events on the population viability of a species over a predetermined period of time (Shaffer, 1981; Boyce, 1992; Reed *et al.*, 1998) using life-history data in relation to environmental factors (e.g., Shaffer, 1983). Biologists using these models should consider the 'realism' of these models. A PVA or PHVA is only a model and may not actually reflect or predict population persistence, and thus should not be the primary tool for developing a conservation plan. Macdonald *et al.* (1998a) recommended that PVAs appear to be most useful to biologists by guiding management actions and identifying practical monitoring methods. The accuracy of the data inputted into the model, levels of uncertainty, as well as the sensitivity of the model should be evaluated (Reed *et al.*, 1998). Some PVAs and PHVAs may actually be best used to raise questions and formulate hypotheses for future testing (Macdonald *et al.*, 1998a; Reed *et al.*, 1998).

SUMMARY

In closing, as with all of the techniques mentioned above, personnel utilizing these methodologies should seriously consider what questions need to be answered before starting a monitoring program. Careful thought and planning will save headaches down the road. Logistical, political, ethical, social, and economic considerations should be included in the planning process. Noninvasive techniques are becoming more prevalent for monitoring carnivore populations and will continue to be important for monitoring rare, threatened, and endangered species, particularly when capture and handling could jeopardize the health and welfare of a species. I encourage anyone planning to initiate a monitoring program to talk to other researchers and gain their insight into what works and what does not work. Regrettably, techniques that fail are usually not published. Often times, field personnel have valuable knowledge about particular aspects of carnivore monitoring that are not readily available in the published literature.

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