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Performance in Wild Ungulates: Measuring Population Density and Condition of Individuals

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INTRODUCTION

Measures of performance in wild ungulates must consider condition and health of individuals along with estimates of population density. Condition and health interact with population density through habitat-related factors of diet and nutritional intake (*fig. 1*). These factors form part of an intrinsic, homeostatic system that tends towards self-regulation, subject to extrinsic factors such as cover, weather, hunting, human disturbance, predation, territoriality, competition, availability of water, and others.

Density-dependent reductions in reproduction resulting from food limitation have been reported in at least 12 species of ungulates (Skogland 1986). Although the effects of population density are often nonlinear (Fowler 1981, Kie and White 1985) and may not be evident at low or moderate densities, all animals are subject to density-dependent effects, given a sufficiently high population density (May and Seger 1986). For example, increases in population size resulting from predator control (Kie and others 1979) can result in changes in diet and decreases in nutritional plane (Kie and others 1980) because more animals feed on a fixed forage supply. Declines in nutritional intake can, in turn, result in poorer body condition (Kie and others 1983), reductions in reproductive rates, increases in mortality rates, and subsequent decreases in animal numbers (Kie and White 1985). Such feedback loops insure that ungulate populations are stable in the long run, given a constant habitat.

Furthermore, estimates of population size alone are of value as measures of performance only if reproductive and mortality rates are also known. For example, high mule deer (*Odocoileus hemionus*) densities on winter range are common, despite generally poor habitat quality, and are accompanied by high rates of mortality. Conversely, high recruitment rates might be accompanied by high rates of mortality and low population densities in poor quality habitat (Van Horne 1983). In addition, large population size might be viewed as favorable if health and condition of individuals remained good, but as unfavorable if health and condition declined. Only in the former case would higher population densities be maintained because of feedbacks within the intrinsic system. Finally, forage quantity and quality are integrated rather than distinct features of habitat quality. Habitats with an abundant supply of marginal quality forage may in some cases support more animals than a habitat with a short supply of high quality forage (Hobbs and Swift 1985).

This report describes some current methods for measuring population densities, condition, and health in wild ungulates and suggests some appropriate techniques to the resource manager, along with sufficient references to allow further study. Measurement of diet and nutritional intake are beyond the scope of this report. However, two excellent reviews are available (Holechek and others 1982a, 1982b). Similarly, coverage of modeling as an approach to investigating population density, condition, and nutritional intake is also available elsewhere (Medin and Anderson 1979, Bobek 1980, Hobbs and others 1982, and Boertje 1985). Finally, Gill and others (1983) presented an excellent history of monitoring ungulates in Colorado along with an outlook for future efforts.

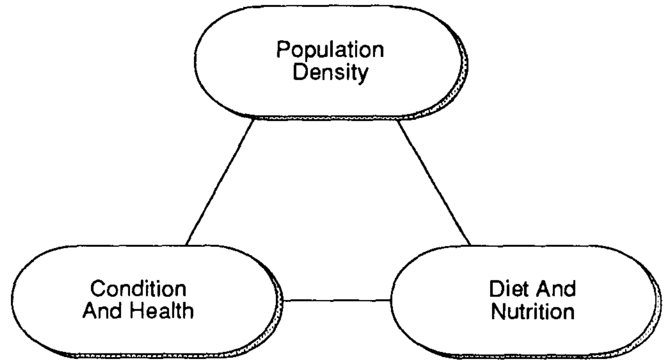

Figure 1- In wild ungulates, diet and nutrition, condition and health, and population density interact to form an intrinsic, homeostatic system that tends toward self-regulation, subject to extrinsic factors.

DETERMINING POPULATION DENSITY

Ungulate populations have specific characteristics, including population size (total number of animals) or density (animals per unit area); fertility, birth, and recruitment rates; and age-specific mortality rates. Interactions between birth and death rates lead to changes in population size and density. In many cases, information about these changes or trends is easier to obtain than absolute estimates and may be a sufficient basis for management decisions.

General census methodology was presented by Caughley (1977a) and Eberhardt (1978a) in a statistically sound manner that is understandable with limited theoretical training. Both stressed that any useful technique for estimating animal numbers must include not only an estimate but also a measure of its variability. Methods discussed in this report include both direct (drive count, aerial count, line transect count, spotlight count, remote sensing) and indirect (mark-recapture, change-in-ratio, track and trail count, fecal pellet-group) techniques.

Direct Techniques

Drive Counts

Drive counts can be used in some instances to count all deer or other ungulates present. The technique requires a large number of people, and a discrete, bounded area to be censused. People involved in counting spread out along one boundary of the area of interest, far enough apart to cover the entire boundary but close enough to remain in sight of the counters to the immediate right and left. A signal is given to advance abreast, and as the line moves forward, people count only those animals moving between them and the person to one side only (between them and the person on the right, for example). Animals moving through the line from front to back are added to the count, and those moving from back to front are subtracted.

Drive counts have been used successfully with white-tailed deer (*Odocoileus virginianus*) on the 1,146-acre (464-ha) George Reserve in Michigan (McCullough 1979), and with mule deer in a 603-acre (244-ha) predator exclosure on the Three Bar Wildlife Area in Arizona. Both areas are surrounded by a deer-proof fence. Drive counts have also been used on Axis deer (*Axis axis*) at Point Reyes National Seashore in California, moving along peninsulas from where they join the mainland down to the ocean.

Drive counts are of little use because in most cases population estimates are needed from large areas with indefinite boundaries. Drive counts are of most value in research studies on relatively small, well-defined and bounded areas, and for obtaining highly accurate estimates for comparison with estimates derived from other methods.

Aerial Counts

Aerial counts of ungulates are possible only in relatively open habitats such as grasslands, open shrublands, and deciduous forests in winter. Animals can be counted from either fixed- or rotary-wing aircraft. In either case, safety and success will depend on the skill and experience of the pilot, the suitability of the aircraft (Bleich 1983), and the skill of the observers (Dirschl and others 1981). Key references on aerial surveys include those by Caughley (1974a, 1977b) and Caughley and others (1976). A guide to conducting aerial surveys, written for moose (*Alces alces*) but applicable to other ungulate species, is also available (Gasaway and others 1986).

When censuring small areas from the air, it may be possible to obtain a count for the total area. In larger areas, aerial counts may be conducted along transects (Caughley 1977a, Gates 1979) or on randomly chosen quadrats (Kufeld and others 1980).

Aerial counts using fixed-wing aircraft usually underestimate true population densities because not all animals present are seen. Caughley (1974a) reviewed several studies and found that proportions of large mammals seen in aerial surveys ranged from 23 to 89 percent. Only 43 percent of the mule deer present were seen in a study during winter in Colorado (Gilbert and Grieb 1957). Sixty-eight percent of the moose present were seen under ideal conditions in a winter study in a boreal forest in Alaska (LeResche and Rausch 1974). Percentages of white-tailed deer observed in Minnesota mixed coniferous-deciduous forest during winter ranged from 50 to 56 percent (Floyd and others 1979). Helicopter counts may also be biased. Estimates of observability by helicopter for white-tailed deer in Texas shrublands have included 75 percent (Beasom and others 1981), 36 and 65 percent (DeYoung 1985), and 26 to 40 percent (Beasom and others 1986). From 35 to 86 percent of the mule deer in pinyon-juniper woodland were seen during winter helicopter counts (Bartmann and others 1986). Aerial counts need to be corrected for animal observability or else used only as indices of population density.

Accuracy in aerial surveys declines as altitude, speed, and strip width increase (Caughley 1974a). Other factors affecting accuracy include amount of cover, season, temperature, windspeed, and time of day (Caughley and others 1976, Hill and others 1985).

In designing an aerial survey it is desirable to minimize bias as much as possible by flying slowly at a low altitude, using narrow strip widths, and surveying when the animals are most visible. Any remaining bias may be acceptable for management purposes, such as comparing ungulate performance between years or habitats (assuming equal animal observability in all habitats). If an estimate of the true population size is required, however, then the bias must be measured and corrected. Estimates of variability in aerial censuses can be obtained through multiple counts, although it may be possible to use variability information obtained on previous censuses (Kie and White 1985).

Transect Counts

Line transect counts consist of an observer traversing a route of known length, counting the number of animals seen, and recording either their perpendicular distance to the center of the transect line or their distance from the observer and the angular deflection away from the transect line (Burnham and others 1980). Transects are often counted on foot. However, Kucera (1976) found that counting from horseback was easier and resulted in less disturbance to white-tailed deer. Where animals are accustomed to vehicles and their spatial distributions are not affected by roads, they can be counted from existing road systems (Kie and White 1985). The analytical principles of transect counts can also be applied to aerial strip counts (Gates 1979).

Line transect counts are, in effect, long quadrats. Their length is known, but the problem is one of estimating the width of the area being censused. At least 25 distinct techniques for estimating transect width have been developed (Gates 1979, Burnham and others 1980). Fewer animals are recorded as their distance from the transect line increases because the observer simply fails to detect them all. Techniques for estimating transect width attempt to mathematically portray this detection decay function, from which transect width and population density estimates are derived.

An early example of a line transect density estimator is the Kelker estimator, which assumes that all animals present are seen and counted out to a known distance W, and none are counted beyond W. If the number of animals seen is n, and the length of the transect is L, then the estimate of density is D = n/

2LW. The factor of 2 enters the denominator because animals are being counted on both sides of the transect line. The Kelker estimator can be modified to allow a linear decay in animal observability beyond W and is one of several techniques recommended by Gates (1979, 1980). It is particularly useful when ungulate densities are fairly high and the habitat is open enough to allow the choice of a large value for W, the maximum distance at which the probability of seeing an animal is 1.0 (Caughley 1977a). For example, in open savannah habitat in south Texas a value of W = 300 feet (91 m) has worked well (Kie and White 1985). However, the estimator is inefficient under other conditions because animals seen at a distance beyond W are not counted, and some authors recommend against its use (Burnham and others 1980).

All observations of animals can be used in the estimate of population density if the rate at which their observability declines with distance from the transect line can be modeled (Caughley and others 1977a). This observability decay rate has been estimated by negative exponential (Gates and others 1968), power series (Eberhardt 1968), exponential power series (Pollock 1978), and log-linear models (Anderson and others 1978), as well as numerous others (Burnham and others 1980). Several nonparametric approaches such as the Eberhardt-Cox (Eberhardt 1978b, Gates 1979), Fourier series (Crain and others 1978), and polynomial models (Gates and Smith 1980) have also been developed. Virtually all of these methods involve laborious computation that can realistically be done only by computer. Therefore, none of the formulas used in estimating animal density are presented here. However, two well-written and documented programs are available: TRANSECT (Burnham and others 1980) and LINETRAN (Gates 1980).

In designing line transect surveys, awareness of the assumptions underlying the density estimators intended for use is critical (Caughley 1977a, Anderson and others 1979). Many estimators are not robust, and if the underlying assumptions are violated, the resulting estimates will be badly biased. Surveys should be designed so that at least 40 animals are seen per transect, and 60 to 80 would be better (Burnham and others 1980). Many density estimators have theoretical variances that can be derived from data collected on a single transect, but it is generally considered best to allocate sampling time to several independent, replicate transects. Variance and standard errors of the density estimates can then be calculated directly or through jackknife techniques (Burnham and others 1980). Both TRANSECT and LINETRAN provide variances for the estimated densities.

Spotlight Counts

Ungulates can be counted at night with the aid of spotlights. Such counts may be of most value either as a nocturnal alternative to diurnal transect counts, using transect analytical methods to arrive at an estimate of population density, or as indices of population trends from year to year. Spotlight counts of mule and white-tailed deer in South Dakota were influenced by time of night, ambient temperature, forage conditions, and by the physiological changes associated with fawning and antler development (Progulske and Duerre 1964). Progulske and Duerre (1964) recommended that standardized counts be made during the 4-hour period, beginning 1 hour after sunset, and that the counts be corrected for the other factors.

McCullough (1982) conducted spotlight counts with a population of white-tailed deer of known size and composition on the George Reserve in Michigan. On average, only about 12 to 13 percent of the deer were seen in June and July, but about 30 to 45 percent in December. However, the route used covered only portions of the total reserve. When present, dense brush prevented light penetration and rendered the technique ineffective. Fafarman and DeYoung (1986) used line transect techniques to estimate the area being censused by a standardized spotlight route in south Texas. They estimated that, for counts made during the first third of the nocturnal period, between 82 and 98 percent of an assumed true population was observed.

Remote Sensing

An airborne thermal infrared scanner in the 8- to 14-micrometer band detected white-tailed deer during winter on the George Reserve in Michigan (Croon and others 1968). From images obtained at 1,000 feet (305 m) in elevation, skilled interpreters were able to detect 98 of 101 deer known to be present. The inability of infrared to penetrate green leaf canopies was listed as a major limitation. Graves and others (1972) obtained good images of cattle and white-tailed deer using both the 3- to 5-micrometer and 3- to 14-micrometer bands. They conducted their counts during late summer and early winter in Pennsylvania. Deer were best detected from 100 and 250 feet (30 and 76 m) in elevation and were not readily seen from 1,000 feet (305 m).

An infrared scanner flown at elevations of 300, 500, and 1,000 feet (91, 152, and 305 m) detected penned mule deer and pronghorns (*Antilocapra americana*) in Colorado during winter (Parker and Driscoll 1972). Three interpreters detected from 61 to 64 of 66 animals present, but were less accurate in distinguishing between species. They recommended scanning from 500 feet or less in elevation. Wyatt and others (1980) concluded that although deer could be successfully detected against a snow-covered background, the occurrence of large snow-free objects resulted in large errors. They suggested that thermal contrast, by itself, was of limited use in counting deer.

Although thermal infrared imagery alone is of little value, Trivedi and others (1982,1984) and Anderson (1987) developed a multispectral system for remotely censusing mule deer in Utah. Their device, under development since 1975, uses reflected energy in four spectral bands, contains nearly 7,000 photo-diode detectors processing 9 billion pieces of data per hour in real time, resolves a4 X4-inch (10 X 10-cm) pixel on the ground from an elevation of 1,500 feet (457 m), covers a swath about 600 feet (183 m) wide, and relies on a final classification and enumeration algorithm based on capture-recapture theory to distinguish pixels with deer from those without and to estimate deer numbers (Anderson 1987). Their approach is promising, but the system still requires additional development before widespread implementation.

Indirect Techniques

Mark-Recapture Methods

Mark-recapture techniques can be used to estimate population size, among numerous other population characteristics. They have "a long history, a plethora of designs and analyses, and a literature of daunting size" (Caughley 1977a: 133, Otis and others 1978, and Seber 1982).

The simplest mark-recapture method of estimating population size is the Peterson or Lincoln index (Caughley 1977a). It involves capturing a segment of the population, applying some sort of mark, recapturing or observing the population at some second point in time, and counting the number of marked and unmarked individuals. The intuitive estimate of density is:

$$N = Mn/m$$

in which: N = estimated population size
M = number of animals marked
n = total number of animals recaptured
m = number of marked animals recaptured

This density estimate is actually biased (Caughley 1977a, Seber 1982:60). An unbiased estimate is:

$$N = [(M + 1)(n + 1)/(m + 1)] - 1$$

which has an approximately unbiased, estimated variance:

$$\text{var}(N) = [(M + 1)(n + 1)(M - m)(n - m)]/[(m + 1)^2(m + 2)]$$

Confidence limits can be placed on the population estimate in the usual manner by taking the square root of var(n) to arrive at the standard error of the estimate, SE(N), and multiplying it by the z value at the desired alpha level (1.96 for 95 percent confidence).

The Peterson estimate requires the following assumptions (Caughley 1977a): (1) the probability of capturing an individual is the same for all animals in the population, (2) no animal is born or immigrates into the study area between marking and recapturing, (3) no animal dies or emigrates from the study area between marking and recapturing, (4) no marks are lost or overlooked, and (5) all animals are equally catchable, both before and after marking.

Assumptions 2 and 3 constrain the use of the Peterson estimate to closed populations (no births, deaths, or migrations). In actuality, deaths and emigrations are permitted, as long as they occur at equal rates among marked and unmarked individuals. In such cases, N becomes an estimate of population size at the time of the first capture (Caughley 1977a). Open populations in which births, deaths, and migrations are occurring present special analytical problems and require other, more complex models such as the Jolly-Seber method (Seber 1982).

Although traditional mark-recapture techniques involve a second capture period, that recapture may consist of a thorough observation of a sample of animals at some second time period to record marked and unmarked animals. For example, it may be possible to assume that no marks are overlooked when observing a sample of radio-collared ungulates. However, reception of radio signals should be avoided during the observation period to assure that radio-collared animals are no more readily observed than those without collars. Rice and Harder (1977) used such a technique by collaring 234 white-tailed deer and subsequently "recapturing" them by observing collared and uncollared deer from a helicopter to arrive at a population estimate.

The Peterson estimate may be particularly appropriate and efficient for estimating the size of small, isolated populations of ungulates such as desert mule deer, as in the following example (White 1984). Suppose an aerial radio-tracking session on 1 day shows that 29 radio-collared deer are present in a given area. The following day, an observer on foot sees 85 deer, of which 15 have radio-collars. Using these values (M = 29, n = 85, and m = 15) along with the formulas of Seber (1982), the estimated population size is 160 deer. The variance of the estimate was 581 deer, which yielded a 95 percent confidence interval of 160 ± 47 deer. An important implication of the assumption regarding equal catchability in this case is that observers should not consistently look for marked and unmarked animals at the same water holes that were originally used to capture the deer, and the observations should be made at random locations throughout the study area.

The computerized analytical package CAPTURE can calculate population estimates for mark-recapture data taken from closed populations (Otis and others 1978, White and others 1978). CAPTURE also provides models which allow some relaxation of the assumption of equal catchability.

Change-in-Ratio and Related Methods

If an ungulate population can be split into two classes, for example by sex or color phase, and if additions or removals are strongly selective towards one class, then an estimate of population size can be obtained through the change-in-ratio (CIR) method. The CIR method requires knowledge of the number of animals added or removed and pre- and post-removal estimates of the ratios between classes (Caughley 1977a). Frequently, application of the CIR method involves selective removal of males and pre- and post-hunt sex ratio counts (Hanson 1963, Rupp 1966, Paulik and Robson 1969, Otis 1980, Conner and others 1986).

If the population is divided into two classes, x and y, let:

N_1 = population size at time 1
N_2 = population size at time 2
n_1 = number of animals counted or sampled at time 1
n_2 = number of animals counted or sampled at time 2
p_1 = proportion of x-type animals at time 1
p_2 = proportion of x-type animals at time 2
C_x = number of x-type animals added or removed
C_y = number of y-type animals added or removed
$C = C_x+C_Y$

C_x and C_y may both be negative (removals), positive (additions), or one negative and one positive (Paulik and Robson 1969). Estimates of population size are:

$$N_1 = (C_x - p_2C)/(p_2 - p_1)$$
$$N_2 = N_1+C$$

Estimates of variance can be obtained by formulas given by Paulik and Robson (1969), and Conner and others (1986):

$$\mathrm{var}(p_1) = (p_1)(1 - p_1)/n_1$$
$$\mathrm{var}(p_2) = (p_2)(1 - p_2)/n_2$$
$$\mathrm{var}(N_1) = [N_1^2\mathrm{var}(p_1) + N_2^2\mathrm{var}(p_2)]/(p_1 - p_2)^2$$

The square root of $\mathrm{var}(N_1)$ equals the standard error of the estimated population size, $SE(N_1)$. The standard error multiplied by an appropriate z value yields a confidence interval about N.

Assumptions required by the CIR method include: (1) both classes of animals, males and females for example, are equally observable at time 1 and 2, (2) the population is closed with respect to migrations, births, and deaths, except for the selective additions or removals, and (3) all additions or removals are known (Caughley 1977a).

Assumption 1 may be the most difficult to satisfy (Rupp 1966, Conner and others 1986). Estimates of both sex and age ratios vary with season of the year and accurately portray true ratios under only limited conditions (Downing and others 1977). For example, deer fawns often remain hidden during the first few months of life and are not as readily seen as adult does (Jackson and others 1972, White and others 1972). Counts of does and fawns attempted before most fawns are running at heel with their dams will therefore underestimate true age ratios (Downing and others 1977). Similar biases in sex ratio estimates occur because of differences in behavior associated with reproduction. Key references to consult before designing sex- and age-ratio surveys include Downing and others (1977), McCullough (1982), Czaplewski and others (1983), Bowden and others (1984).

Assumption 3 may be relaxed somewhat, for example, by sampling the number of animals actually taken and the number reported by hunters. Actual removals can then be calculated from reported removals, but the variance formulas for estimated population size become more complex (Paulik and Robson 1969).

Precision of the CIR method depends on proportions p_1 and p_2. With a pre-hunt estimate of male deer at 10 percent of the total herd, an estimate of N_1 within 25 percent of the true value with 95 percent confidence would require pre- and post-hunt sample sizes of about 1,600 deer each (Conner and others 1986). However, if only antlerless deer were harvested from the same herd (90 percent antlerless deer at time 1), and the removal was sufficient to reduce the post-hunt estimate to 70 percent antlerless deer, the same level of precision could be achieved with pre- and post-hunt sample sizes of only 325 deer.

Eberhardt (1982) presented an index-removal method that does not require classification of individuals to estimate population size. In addition, the removal need not be selective. The index-removal method is based on a pre-removal count (x_1) that consists of some proportion (p) of the total pre-removal population size (N) and a post-removal count (x_2) that consists of the same proportion (p) of the post-removal population size. If R animals are removed, then an estimate of the population size is:

$$N = x_1R/(x_1 - x_2)$$

an estimate of the proportion of animals seen is:

$$p = (x_1 - x_2)/R$$

the estimated proportion of the population removed is:

$$p^* = (x_1 - x_2)/x_1$$

and an approximation of the standard error of the estimated mean is:

$$SE(N) = N[(q^*/p^*)^2(1/x_1 + 1/x_2)]^{1/2}$$

in which $q^* = 1 - p^*$, that is, the estimate of the proportion of animals not removed. The standard error of the mean, SE(N), multiplied by an appropriate z value yields a confidence interval about N.

An example of the index-removal method involves a pre-removal count of 301 wild horses, and a post-removal count of 76 horses after the removal of 357 animals (Eberhardt 1982). The pre-removal population size was estimated at 478 ± 41 horses with 95 percent confidence. The precision of an index-removal count is correlated with proportions of the population removed (Eberhardt 1982). Small removals result in highly variable and relatively useless estimates. Index-removal counts may be particularly useful for estimating numbers of wild horses and burros before large-scale removal operations, especially in conjunction with aerial counts before and after removal.

Track and Trail Counts

Several attempts have been made to use track counts as an index of deer population density. This method has been used successfully since 1947 with the Interstate mule deer herd that migrates south from Oregon each fall into northeastern California (Salwasser 1976). An east-west network of dirt roads is cleared periodically and all deer tracks and their direction of travel are observed and recorded. The technique, originally designed as a total counting scheme, underestimates total population size because some of the tracks during periods of heavy movement obliterate previous signs. Also, during mild winters, some deer remain in southern Oregon and their tracks are not tallied. However, the track count appears to be less dependent on annual differences in weather than other methods and provides an index to long-term trends in deer numbers.

Comparisons were made between white-tailed deer track counts and deer densities estimated by drive counts in Florida (Tyson 1959). Although there was a significant relationship between the two measures, an analysis of data given by Tyson (1959:462) indicates that the relationship was weak ($r^2 = 0.20$) and had little predictive value. All but 3 of the 68 counts averaged less than 40 tracks per linear mile, and most of the densities were 30 or fewer deer per square mile.

Daniel and Frels (1971) reported that track counts for white-tailed deer in Texas yielded 95 percent confidence limits within 18 percent of the estimated mean value when track density exceeded 45 tracks per mile. They further suggested that when such track counts were obtained, they would be sensitive to as little as a 15 percent change in deer density. Precision was increased by counting only the tracks of adult deer. The technique was not recommended for low-density deer populations.

An index to white-tailed deer densities developed in Wisconsin was based on counts of deer trails, rather than on individual sets of deer tracks (McCaffery 1976). Trail counts conducted in the fall in various hardwood and conifer forest habitats were correlated with deer densities obtained from pellet-group counts ($r^2 = 0.89$). Trail counts appeared to be useful only in dead or dormant vegetation after a severe frost. McCaffery (1976) recommended that such counts be attempted only when a -2°C freeze occurs before 20 October.

Pellet-Group Counts

Pellet-group counts are perhaps the most widely used indices of ungulate abundance. With the technique dating back almost 50 years (Bennett and others 1940, Eberhardt and Van Etten 1956), a large volume of literature is available, including a comprehensive review (Neff 1968). Pellet-group densities alone can be used as an index of animal abundance. However, they are often combined with information or assumptions about the length of time the pellet groups have been accumulating and the daily defecation rate per individual to estimate population density (Connolly 1981).

Pellet groups are frequently counted on bounded plots that are either circular or rectangular (Neff 1968). More plots are needed for a given level of precision when pellet-group densities are low. Large plots usually give lower estimates than small plots because observers may fail to see all of the pellet groups present (Neff 1968), and because defining what constitutes a separate pellet group is a problem (Batcheler 1975). Permanently located plots are more costly to install and monitor but have the advantage of allowing one to determine exactly pellet-group accumulation time. Temporary plots can cut the cost of installation by about half (Freddy and Bowden 1983a) but require that new and old pellet groups be distinguished. The requirements for using temporary plots appear to be met for some migratory populations of mule deer in the semi-arid portions of the western United States (Freddy and Bowden 1983a).

Small areas require more intensive sampling than do larger areas for a given level of precision. A reasonable goal is to obtain an estimate of pellet-group density within 10 percent of the true value with 70 percent confidence (Robinette and others 1958). With pellet densities between 353 and 527 groups per acre (872 and 1,302 groups per ha) in Utah, necessary sampling intensity (percent of total area sampled) ranged from less than 0.1 percent on areas over 7,000 acres (2,834 ha) to 0.8 percent on areas less than 500 acres (202 ha). Also, the number of plots needed to assess pellet-group densities at a given level of precision increases as group density decreases. Sampling intensities as high as 3.5 percent may be required with pellet-group densities of only 100 groups per acre (247 groups per ha)(Robinette and others 1958, Neff 1968). A level of precision at 10 percent of the true value with 70 percent confidence may not be practical at densities of less than 100 per acre (247 per ha)(Connolly 1981).

The deposition of pellet groups generally has been found to follow a pattern that is well approximated by the negative binomial distribution (Bowden and others 1969, McConnell and Smith 1970, Stormer and others 1977, Rowland and others 1984). FORTRAN programs for testing for differences between means among two or more sets of data are available (White and Eberhardt 1980).

Comparisons of pellet-group densities between populations or years require the assumption that the time during which pellet groups accumulate is equal between data sets. In addition, to estimate deer numbers, it is necessary to estimate the durations of these time periods.

Permanent plots that are cleared periodically provide exact knowledge about the length of time during which pellet groups are deposited. Temporary plots require that the time of deposition be estimated. In California, mule deer pellet groups in wet meadows may deteriorate in less than 1-1/2 years, but those on drier sites may persist as long as 3-1/2 years (Ashcraft 1980). During the warm, humid spring in Mississippi, all evidence of white-tailed deer pellet groups may be lost within a month (Wigley and Johnson 1981). In the absence of information on pellet-group persistence from a specific site, preliminary studies are necessary. Various kinds of paint can be used to measure the rate at which groups disappear (Kufeld 1968).

In the west, pellet groups are frequently counted on mule deer winter range after the animals have migrated in spring. Such counts usually assume that all pellet groups were deposited the previous winter and that the length of time spent by deer on the winter range is known. Care should be exercised in assuming that time spent on winter ranges is constant between populations or years. Cold, wet weather in late winter and early spring may delay migration by black-tailed deer (*Odocoileus hemionus columbianus*) in northern California and result in higher pellet-group densities on winter ranges (Kie 1984).

Estimating deer population size from pellet-group densities requires an estimate of or an assumption about daily defecation rates, which can range from 8.0 to 23.1 pellet groups per deer per day (Neff 1968). Factors that increase mean defecation rates include high intake rates, good forage conditions, high moisture content in forage, abrupt changes from native range forage to concentrates, and high percentages of fawns in the population. Assumed mean values between 12.7 and 13.0 pellet groups per deer per day are commonly used (Connolly 1981), often with little verification.

Batcheler (1975) developed a distance method for use with deer pellet-group counts based on the point-center and nearest-neighbor techniques in plant ecology. As with counts on bounded plots, the distance method can be used as an index of deer abundance or, with additional information, as an estimate of deer numbers. A series of sample points were located in mountainous terrain on New Zealand's South Island. Points were spaced 60 feet (18 m) apart on randomly located sample lines. Distances were measured between each sample point and the center of the nearest pellet group, as well as between the center of that pellet group and the center of its nearest neighbor pellet group. In both cases, only distances up to 12 feet (3.7 m) were recorded. This distance--the maximum to be searched--was chosen so that measurements were obtained at a minimum of half of the sample points. All distances were measured parallel to the ground and the resulting estimates of pellet-group density corrected for slope. Estimates of pellet-group density were obtained with formulas presented by Batcheler (1975:645), as corrected by Fisher (1979).

This distance measurement technique has the advantage of being independent of plot size (Neff 1968). The technique works best when pellet-group densities are high enough to allow a reasonably small choice for the distance to be searched around each point and each pellet group, for example 6 to 12 feet (1.8 to 3.7 m), and still find pellet groups at a minimum of half of the points. Although based on the use of permanent plots, the estimation of pellet-group density using this technique can be accomplished with temporary plots as well.

Batcheler (1975:648) also provided a method to estimate deer density using permanent plots sampled at two different times, and an estimate of pellet-group persistence rate (obtained by marking some pellet groups during the first sampling period and seeing how many were still present at the second time period). Unlike estimating pellet-group density, estimating deer population density requires the use of permanent plots, because of the need to calculate a pellet-group persistence rate. An estimate of daily defecation rate is also required, and the model assumes that the population is closed--no births, deaths, or migrations occur between sampling periods.

Pellet-group densities, either alone or with estimates of accumulation time and daily defecation rates, are probably the most commonly used of all deer census techniques. However, the validity of the underlying biological and statistical assumptions notwithstanding, a clear paradigm for their use has yet to be developed.

Wallmo (1969:4) noted that "local pellet-group concentrations do not necessarily reveal a net increase in carrying capacity, but they do indicate concentrations of some, so far undefined, kinds of deer activity. Since deer defecation rates are fairly constant (Neff 1968), differences in mean pellet-group densities, on areas large enough to encompass the activities of segments of a deer population, indicate that more of the requirements of deer are met on one area than on another."

Patton (1974:765-766), reviewing the effects of timber harvesting on mule deer in Arizona, suggested that "a change in days use per acre does not mean that there was an increase in total number of animals. It is possible or more than likely that the increase resulted from animals coming from adjacent areas ... Intuitively, however, if the changes are beneficial, animal numbers should increase over the long run." This short-term, functional response has also been demonstrated for black-tailed deer using small, burned areas in northern California (Kie 1984).

Deer population estimates obtained with pellet-group data show moderate to high agreement with estimates obtained by other methods, or with known population sizes (Neff 1968, Robinette and others 1977, Freddy and Bowden 1983b). Discrepancies are usually associated with errors in estimating time of deposition or defecation rate (Neff 1968, Freddy and Bowden 1983b). When using pellet groups as an index to or an estimate of deer abundance, careful consideration should be given to sampling design and stratification. Key references to be consulted before a sampling program is designed include Neff (1968), White and Eberhardt (1980), and Freddy and Bowden (1983a, 1983b).

Care should be taken, however, in using pellet-group information to infer habitat use patterns by deer. Collins and Urness (1981, 1984) found that on the basis of 24-hour
b ti
periods, defecation rates of mule deer were highest when the deer were most active and immediately following periods of rest. They concluded that pellet-group data could not be used to reliably assess relative habitat use. On the other hand, Leopold and others (1984) re-analyzed data from Collins and Urness (1981) and pointed out that pellet groups accurately ranked overall habitat use, although some discrepancies occurred.

Comparison of habitat use by mule deer in California using both pellet-group deposition patterns and radio-telemetry information showed minor differences between techniques (Loft and Kie 1988). However, 9 of 10 habitat-year combinations were correctly ranked and pellet-group data reliably determined the three most and two least frequently used habitat-year combinations. Pellet-group information likely gives adequate indications of overall habitat use, but may not accurately distinguish between 2 or more moderately used habitats.

CHOOSING A METHOD FOR DETERMINING POPULATION DENSITY

Indices of ungulate population density are often easier to obtain than absolute estimates. If an index will suffice and an extensive road system is present, then either spotlight counts or track counts might be appropriate (*fig. 2*). If no such road system exists, then simple pellet-group counts or track counts might be useful. If an absolute estimate of population density is required, and the habitat is relatively open, then aerial counts, ground transect counts, or spotlight counts may be used. With additional research and development, remote sensing techniques also show promise. If the habitat is too dense to permit such counts, and selective removals are occurring, the change-in-ratio method might be the method of choice. Heavy nonselective removals, for example of wild horses and burros, would suggest the index-removal method. In cases where the population of interest is isolated and population closure can be assumed, for example in some desert ungulates, then mark-recapture techniques may be used. Finally, pellet-group counts, along with estimates of deposition and persistence rates, may be used with deer and elk (*Cervus elaphus*)(*fig. 2*).

ASSESSING CONDITION AND HEALTH

Assessing condition in free-ranging ungulates poses certain unique problems. Almost all condition measures require that the animal of interest be captured, restrained, or killed. Furthermore, although some condition measures, such as live weight, can be obtained from live animals, many others, such as kidney fat, cannot. In addition, most condition measures are highly

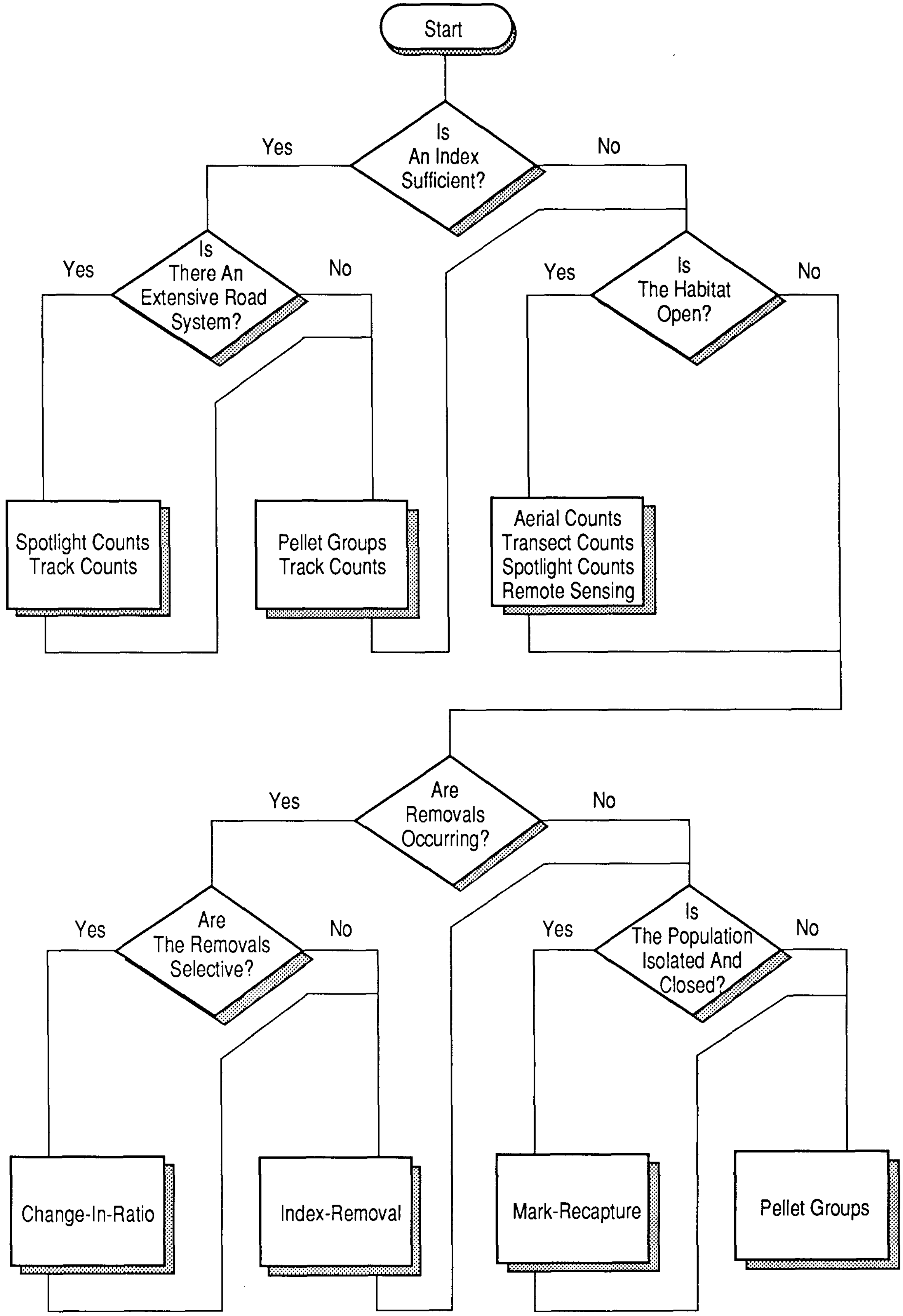

Figure 2--Methods for estimating population density in wild ungulates can be selected from a flow chart.

variable and subject to age of the individual, sex, reproductive status, and season of collection. Sample design must account for these sources of variation. Finally, some condition indices, such as subcutaneous fat, are based on subjective judgements rather than objective, quantifiable, repeatable measurements.

Reviews of assessing condition in deer (Brown 1984) and in wildlife in general (Kirkpatrick 1980) are available. Methods discussed in this report include body weights, fat reserves, blood values, reproductive rates, parasite loads, and adrenal gland weights. Because many condition measures vary as a function of age, accurate age determination is critical. References for age determinations in ungulates as well as in other wildlife species can be found in Larson and Taber (1980).

Body Weights

Body weight in deer has long been suggested as a measure of condition (Johnson 1937, Park and Day 1942, Severinghaus 1955). However, body weights are usually highly variable with respect to age, sex, and season of the year. In addition, deer may lose weight during winter even when fed a high quality diet in unlimited amounts (Nordan and others 1968, Wheaton and Brown 1983).

Body weights may be live weight, bled carcass weight (BCW), or eviscerated carcass weight (ECW). If dealing with carcasses, ECW is likely to be less variable than BCW because it is not affected by changes in visceral fat stores or by the weight of the conceptus in gravid females.

White-tailed deer in south Texas showed variations in BCW and ECW as a function of sex, age, and season of collection (Kie and others 1983). However, adult deer from a herd at a normal population density (100-120 deer per mile^2, 40-49 deer per km^2) averaged 101 lbs (46.0 kg) BCW and 76 lbs (34.4 kg) BCW, while those from a high-density herd (160-200 deer per mile^2, 64-81 deer per km^2) within a predator exclosure averaged only 90 lbs (40.8 kg) BCW and 66 lbs (29.8 kg) ECW.

Provided that consideration is given to potential sources of variation, body weights may provide useful information on condition in individual ungulates. They may also be the only information available from hunter-killed animals at check stations.

Fat Reserves

Like body weights, fat reserves in ungulates often show pronounced variations with respect to age and sex of the individual, and to season of collection. Furthermore, fat is stored and subsequently mobilized at different rates in different forms and locations throughout the body (Pond 1978). The least mobile form is in bone marrow (Riney 1955, Pojar and Reed 1974). Increasingly more mobile sources are visceral (such as that surrounding the kidneys) and subcutaneous fat reserves, and blood serum lipids, cholesterol and triglycerides. Fat reserves of lower mobility are often more desirable as measures of condition because they represent longer-term nutritional intake and are less susceptible to short-term fluctuations. Conversely, they are the last reserves to be depleted under severe stress and are not as sensitive to nutritional status as are more mobile fat reserves. Use of fat reserves to assess a wide range of conditions requires that several types of fat stores be measured (Kistner and others 1980).

Marrow Fat

Femur marrow fat (FMF) was proposed as a measure of malnutrition in white-tailed deer (Cheatum 1949a). Typically, a plug of marrow is removed for analysis from the middle third of the femur. Cheatum (1949a) used criteria of color and consistency (red or yellow and gelatinous for deer in poor condition to white and solid for deer in good condition) to rank marrow fat content. Ether extract techniques yield subjective measurements of marrow fat content (Kirkpatrick 1980), but the process is laborious and requires special apparatus. Because marrow fat is composed primarily of fat and water, with a small (less than 7 percent) nonfat solid component, simply oven drying a 10- to 30-g sample of marrow at 60-65°C and expressing the oven dry weight as a percentage of the wet weight provides a reasonably accurate estimate of fat content (Neiland 1970). Corrections for nonfat solid residue can be made if a subsample of femurs is processed with the ether extract technique, but such corrections are usually unnecessary for assessing condition in free-ranging ungulates. If a drying oven is unavailable, femur samples may be dried with a 2:1 mixture of chloroform and methanol (Verme and Holland 1973).

Estimates of FMF in white-tailed deer in south Texas fluctuated with season of collection, but not as a function of sex or age in adult deer (Kie and others 1983). Adult deer from a high-density herd averaged only 36.5 percent FMF, compared with 50.1 percent for those from a lower-density herd.

FMF is an effective measure of condition in deer and other ungulates. Because it is one of the last fat reserves to be mobilized, it is primarily of use at the low end of the condition spectrum.

Because femurs may not always be available from hunter-killed deer, Nichols and Pelton (1972, 1974) suggested that fat content in the marrow of mandibles may be used as a measure of condition. Mandibular marrow fat (MMF) was correlated with FMF ($r = 0.69$), but MMF was deposited later and mobilized earlier (Nichols and Pelton 1972, 1974, Warren and Kirkpatrick 1982). Kirkpatrick (1980) suggested that MMF be expressed on a dry-weight rather than a wet-weight basis. However, if MMF is comprised primarily of fat and water, as is FMF (Neiland 1970), then a wet-weight measurement may be more appropriate. Extreme care should be taken to prevent dehydration prior to analysis, however (Kie 1978, Kirkpatrick 1980). Assuming that MMF is more mobile than FMF, it may be of value at somewhat higher ranges of condition (Brown 1984).

Other alternatives to FMF are fat content in the marrow of other leg bones, which may be easier to obtain from hunter-killed deer. There are close correlations ($r^2 = 0.71 - 0.98$) between FMF and marrow fat in the humerus, tibia, radius, metatarsus, and metacarpus of white-tailed deer (Fuller and others 1986). However, marrow fat in the metatarsus and metacarpus appeared to be even less mobile than FMF. These fat reserves remained high even when FMF declined below 30 percent.

Kidney Fat

Visceral fat is deposited around the internal organs in ungulates when forage conditions are good. Riney (1955) developed the kidney fat index (KFI) for red deer (*Cervus elaphus*) in New Zealand by expressing the weight of the fat surrounding both kidneys along with the capsule of connective tissue as a percentage of the weight of the kidneys without the fat or connective tissue. KFI values can range from a low of only a few percent, representing solely connective tissue and no fat, to over 100 percent. Riney (1955) concluded that KFI is a valuable indicator of condition not only between populations but also within a population between seasons of the year.

The use of KFI has been criticized as measure of condition because kidney weights themselves may fluctuate during the year (Batcheler and Clarke 1970, Dauphine 1975). However, if kidney weight is viewed as a correction for the metabolic status of the animal (Flux 1971), then KFI may accurately reflect body condition. Average KFI values for adult white-tailed deer in south Texas were estimated at 15.4 percent in a normal-density herd but at only 8.7 percent in a high-density herd (Kie and others 1983). KFI values varied as a function of sex and month of collection but not with age in adult deer. These differences were significant and supported the conclusion that the deer at the higher population density were in poorer condition.

A similar conclusion was reached using total kidney fat (KF) rather than KFI, except that KF (and kidney weight) increased with age in adult deer (Kie and others 1983). KFI can be used as a measure of condition given that the sampling design recognizes that KFI varies between adult males, adult females, and fawns, as well as between seasons of the year. Other investigators still prefer KF over KFI as an index of condition (Monson and others 1974, Verme and Ozoga 1980). Because of the ease in weighing both the fat and the kidneys, both indices should be recorded and examined.

Kidney fat is more mobile than femur marrow fat. As condition in deer declines, visceral fat reserves, including kidney fat, are lost first. Not until KFI values drop below about 15 percent do white-tailed deer in south Texas begin to show declines in FMF (Kie and others 1983). Similar patterns have been observed in northern populations of white-tailed deer (Ransom 1965) and in mule deer (Pojar and Reed 1974). For a herd of white-tailed deer in Texas, Kie and others (1983) recommended the use of KFI down to a mean value of 15 percent, and the use of FMF below that. For mule deer in Oregon, Connolly (1981:334) recommended the use of KFI only down to a mean value of 20 percent and proposed a formal condition index (CONINDEX), where:

If KFI > 20,

CONINDEX = FMF + (KFI - 20)

Otherwise,

CONINDEX = FMF

Subcutaneous Fat

Subcutaneous fat reserves are even more mobile than kidney fat (Pojar and Reed 1974). Subcutaneous fat reserves used as estimates of condition include backfat depth in red deer (Riney 1955), brisket fat depth in pronghorns (Bear 1971), and tailbase, rump, and brisket fat in mule and white-tailed deer (Kistner and others 1980). In the latter case, estimates of subcutaneous fat were combined with visual estimates of heart, pericardium, kidney, and omentum fat to arrive at an overall condition score (Kistner and others 1980). However, Anderson and others (1972) found that depth of back fat was too variable to be of much use. The primary problem in using subcutaneous fat reserves is the difficulty in standardizing the point of measurement (Brown 1984).

Serum Lipids

Two additional measures of condition in deer and other ungulates are the levels of cholesterol and triglycerides in blood serum. Because these are both forms of fat, or lipids, they are discussed here rather than in the following section on blood chemistry. Levels of both serum lipids reflect changes in diet and metabolism (LeResche and others 1974). Serum cholesterol may be depressed during starvation (LeResche and others 1974), although it is relatively insensitive to less drastic dietary changes (Wilber and Robinson 1958). However, serum cholesterol declined in white-tailed deer in Michigan between October and January, presumably because of changes in diet (Coblentz (1975). White-tailed deer in south Texas showed no differences in either serum cholesterol or triglycerides with respect to population density, although cholesterol was somewhat higher in females than in males, and declined with increasing age in adult deer (Kie and others 1983). Additional research is needed on the role serum lipids play in fat metabolism, particularly in conjunction with rumen volatile fatty acid studies (LeResche and others 1974).

Blood Values

Blood values have been proposed as indices of condition in deer and other cervids (LeResche and others 1974). While some studies have been field oriented approaches to describing and comparing blood parameters (Pedersen and Pedersen 1975, Seal and others 1978a, Kie and others 1983), much recent research has been directed towards captive animals fed carefully controlled diets (Seal and others 1978b, Bahnak and others 1979). Use of blood values requires access to appropriate laboratory facilities, as well as careful handling of samples. For these reasons, blood values are of use primarily to researchers and less to wildlife managers. Reviews of blood values as condition indices are available in LeResche and others (1974), Kirkpatrick (1980), and Brown (1984). Only those blood values showing promise will be discussed here.

Blood urea nitrogen (BUN) has been suggested as a good indicator of protein intake in cervids as well as of protein dynamics (LeResche and others 1974). Diets high in protein have been shown to elevate BUN in deer serum (Seal and others 1978b, Bahnak and others 1979). Although a high-protein diet increased BUN levels in white-tailed deer fawns, diets low in energy also had the same effect (Kirkpatrick and others 1975), possibly because of the use of dietary protein as an energy source (Holier and Hayes 1977). Severe starvation and the catabolism of existing protein also elevates BUN in deer serum (deCalesta and others 1975, Bahnak and others 1979). BUN values were slightly higher among white-tailed deer from a high-density herd in Texas, although most condition indices indicated poorer nutritional intake (Kie and others 1983), and rumen crude protein levels were lower (Kie and others 1980). Therefore, although changes in BUN levels may indicate differences in health and nutritional status in ungulates, it is difficult to predict what directions those changes will follow. Information about BUN levels may be useful in assessing condition, however, along with other corroborating evidence (Kirkpatrick 1980, Brown 1984).

Total serum protein (TSP) is generally depressed only in cases of extreme distress, although it may decline in cases of chronic protein deficiency (LeResche and others 1974). Albumin, one of the major serum proteins, may be a better indicator of moderate undernutrition (LeResche and others 1974). Seal and others (1978a) reported no differences in TSP or albumin among four populations of white-tailed deer in Minnesota, although other blood values varied, presumably as functions of habitat quality. Among white-tailed deer in Texas, TSP did not vary as a function of population density, but albumin was lower in deer from a high-density herd (Kie and others 1983).

The level of nonesterified fatty acids (NEFA) in blood serum was suggested as a possible index to dietary energy intake by Seal and others (1978b). NEFA levels were significantly higher among white-tailed deer fawns on low-energy diets than among those on moderate-energy diets (Seal and others 1978b). White-tailed deer fed restricted-quantity diets (75 percent of *ad libitum* levels) showed slightly higher NEFA values than did those given abundant food (Warren and others 1981). NEFA may be of value primarily when used along with other indices of condition (Brown 1984).

Alkaline phosphatase (AP) may also be of value for assessing dietary energy intake. AP is an enzyme that is concentrated in mammalian osteoblasts, renal tubules, and intestinal mucosa (LeResche and others 1974). AP levels were reduced in white-tailed deer fawns on reduced-energy diets but were not affected by reductions in dietary protein intake (Seal and others 1978b). Kie and others (1983) found lower AP values among deer from a high-density herd of white-tailed deer than among deer at a lower population density. AP levels were also higher among adult males than adult females, higher among pregnant than nonpregnant deer, decreased with age in adults, and varied as a function of month of collection (Kie and others 1983). The sensitivity of AP to factors other than dietary energy may limit its use as an index to condition.

Some research has been done on the use of hormonal levels for assessing dietary intake, particularly using triiodothyronine (T_3) and thyroxine (T_4). Penned white-tailed deer fawns on a low-quality diet showed reduced T_4 levels (Seal and others 1972). White-tailed deer from poor-quality habitat in Minnesota were also characterized by low T_4 levels (Seal and others 1978a). In a second study, low protein intake reduced T_4 values while diets low in energy reduced T_3 levels (Seal and others 1978b). Bahnak and others (1981) reported that white-tailed deer on high-protein, moderate-energy diets had higher T_3 and T_4 values than did those on low-protein, low-energy diets. Hormonal assays may be a valuable tool for predicting dietary energy in particular, but that further research is needed on the development of assay techniques specifically for deer and other ungulates, and on the effects of drugs, excitement, age, and sex on hormone levels (Brown 1984).

In designing a sampling scheme to assess condition and dietary intake in ungulates, attention should be given to the manner in which the blood samples are collected. Many blood parameters are sensitive to the way in which the animal is captured, such as physical restraint, immobilization with drugs, or shooting (LeResche and others 1974; Wesson and others 1979a, 1979b). Also, careful consideration should be given to potential sources of variation such as age, sex, reproductive status, and season of collection. Uniformity in the manner of collection or stratification by source of variation is necessary to prevent bias and reduce residual variations in the data.

Reproductive Rates

Although reproductive rate is properly considered a population characteristic, it is obtained from examination of individual animals and can be useful as a measure of condition. Reproductive rates may be expressed as ovulation rates (corpora lutea per female), fetal rates (fetuses per female), or pregnancy rates (percent females pregnant). Ovulation and fetal rates are preferred measures of reproduction.

Ovulation rates can be determined by removing both ovaries, fixing them in a 10 percent formalin solution, and then sectioning them with a razor blade. Corpora lutea of pregnancy represent eggs that were shed and fertilized and need to be distinguished from accessory corpora lutea and related bodies (Teer and others 1965). In some cases, ovulation rates from a previous breeding season up to 8 months prior can be estimated by examination of corpora albicantia (Cheatum 1949b, Teer and others 1965). Fetal and pregnancy rates are determined by gross examination of the reproductive tract.

Ovulation and fetal rates are valuable indicators of condition because they are sensitive to changes in nutritional intake (Cheatum and Severinghaus 1950; Teer and others 1965; Verme 1965, 1967, 1969). Fetal rates among yearling white-tailed does from a high-density herd in Texas averaged only 0.86 fetuses per doe compared with 1.13 fetuses per doe among yearlings from a lower-density herd (Kie and White 1985). Comparable data for mature does, those at least 2 years old at parturition, were 1.17 and 1.60 fetuses per doe (Kie and White 1985). Ovulation rates were similar to fetal rates.

Normally, determination of reproductive rates among wild ungulates requires sacrificing the dam. However, Greer and Hawkins (1967) determined pregnancy rates in live elk by rectal palpation of the uterus, and Ramsey and Sadlier (1979) used elevated blood plasma progestin levels as indicators of pregnancy in bighorn sheep (*Ovis canadensis*). Barrett (1981) successfully used a Doppler ultrasound fetal pulse detector to determine pregnancy rates in immobilized feral hogs. Kirkpatrick and others (1988) were able to determine pregnancy rates in feral horses by collecting urine-soaked soil samples following direct observation of mares, and analyzing extracts of the samples for estrone sulfate. Additional research is needed on techniques to determine not only pregnancy rates in living animals but also fetal rates.

Parasite Loads

In the south and southeast, levels of internal parasitism in white-tailed deer are related to population density and range carrying capacity (Eve and Kellogg 1977, Foreyt and Samuel 1979). Eve and Kellogg (1977) suggested that a standardized abomasal parasite count (APC) would be a useful index of population density-carrying capacity relationships. The APC was defined as the average number of adult-sized abomasal parasites from five or more deer at least 1 year old. The deer were collected over a short time period between July and September and from a single location. APC values less than 500 indicate a herd below carrying capacity, between 500 and 1,500 a herd at or near carrying capacity, and over 1,500 a herd that exceeds carrying capacity (Eve and Kellogg 1977).

Because levels of abomasal parasites can fluctuate throughout the year, use of APC with hunter-killed deer in the fall and winter may not result in the same conclusions as those obtained from deer collected in the summer. In addition, levels of internal parasitism may not increase until the host has undergone prolonged malnutrition (Demarais and others 1983).

White-tailed deer in Texas showed significant changes in body weights, fat reserves, and some blood parameters in 1975-1976 (Kie and others 1983) following an increase in population density resulting from intensive predator control begun in 1973 (Kie and others 1979). Food habits and nutritional levels also showed changes over that time period (Kie and others 1980), but incidence of internal parasitism did not. Not until 1977 were substantial increases in lungworms and abomasal parasites detected (Foreyt and Samuel 1979). Parasite counts may not be sensitive indicators of annual changes in population density-carrying capacity relationships but may be of value in detecting chronic levels of malnutrition.

Adrenal Gland Weights

The size of the adrenal glands in mammals is thought to be an indicator of social stress. Christian (1950) suggested that high population densities would lead to increases in pituitary-adrenocortical activity and adrenal gland size. It was further suggested that such increases would lead to impairment of reproduction and to increased mortality, either indirectly through increased susceptibility to such factors as disease and parasitism, or directly through shock-related phenomena.

Christian and Davis (1964) stated that adrenal weight is an indicator of some value for estimating changes in adrenocortical function. However, they cautioned that other factors may influence adrenal weight. For example, they pointed out that androgens decrease adrenal weight in adults while estrogens increase adrenal weight. In conclusion, they stated that "changes in adrenal weight can only be considered strong presumptive evidence of changes in adrenocortical function until validation is obtained" (Christian and Davis 1964:1551).

Christian and others (1960) reported the die-off of sika deer (*Cervus nippon*) on James Island in Chesapeake Bay, Maryland. Introduced to the island in 1916, the herd reached a density of 1 deer per acre (2.47 per ha) by 1955. Subsequently, 60 percent of the population died. Mortality was greatest among young deer and among females of all age classes. During the die-off, absolute adrenal weights increased, particularly among juveniles, and declined afterwards. "All deer appeared well nourished and free of parasitism throughout the study, although there was a marked inhibition of growth at the time of the die-off, which primarily affected those in their first three years of age ... It was concluded that physiological disturbances, induced by factors of high population density, probably hierarchical-behavioral, were responsible for the deterioration and death of these deer..." (Christian and others 1960:94-95).

Hughes and Mall (1958) found significant inverse correlations between adrenal gland weights and visual estimates of kidney fat as well as body weight in black-tailed deer in California, although variation between individuals was great. Kie and others (1984) found no such correlations in a later study of two other herds of black-tailed deer.

Kie and others (1983) found no significant differences in relative adrenal gland weights (expressed as a function of body weight) between high- and low-density white-tailed deer herds in Texas. Absolute adrenal weights, suggested as a better measure than relative weights (Kirkpatrick 1980), were actually slightly lower among the lighter weight deer from the high-density herd, although the difference was thought to be of little biological significance (Kie and others 1983).

In general, heavier adrenal weights were associated with higher population densities among white-tailed deer in North Carolina, although the data were inconclusive (Welch 1962). Bubenik and Bubenik (1967) found relative adrenal weights to be higher among a high-density population of roe deer (*Capreolus capreolus*) in Germany than among a lower-density population in Yugoslavia.

The increases in adrenal weight described by Christian and others (1960) for sika deer occurred at unusually high population densities. Data presented for black-tailed deer by Hughes and Mall (1958) were also from a herd suffering from chronic overpopulation. The data discussed by Bubenik and Bubenik (1967) were from roe deer, in which social interactions, particularly territoriality, play important roles in population regulation (Strandgaard 1972). In addition, Georgii (1973) found no relationship between adrenal gland weights and kidney fat in roe deer from Bavaria, except for large adrenal glands taken from diseased animals in weakened condition. Data presented by Welch (1962) were not without interpretive problems, and he later concluded that adrenal weight was not a good indicator of population conditions (Welch 1966). Adrenal gland weights appear to be of little practical use in monitoring condition in most ungulates, although they may still have some interest to the research biologist.

CHOOSING A METHOD FOR ASSESSING CONDITION AND HEALTH

Determining condition in live animals is currently limited to the use of live weights, reproductive rates measured by nondestructive techniques, and blood values (*fig. 3*). For assessing protein intake, BUN, TSP, albumin, and T_4 show the most promise (Kie and others 1983, Brown 1984). For assessing energy intake, NEFA, T_3 (Brown 1984), and possibly AP may be of value (Seal and others 1978b). Serum cholesterol (Coblentz 1975) and triglycerides may be of use in some cases.

If entire carcasses are available, ECW, BCW, FMF, KFI, KF, and possibly APC should be recorded (*fig. 3*). Ovulation, fetal, and pregnancy rates should be recorded for females. If condition must be assessed from hunter-killed animals (usually males) at check stations, then ECW, MMF, and possibly some measure of carcass fat (Kistner and others 1980) may be the only measures available.

Multiple measures of condition are preferable to any single measure (Brown 1984). When comparing condition between herds, univariate analysis of covariance with age as a covariate is an appropriate analytical technique (Kie and others 1983). The possibility of nonlinear response in dependent variables should be considered, for example in KFI and FMF expressed as percentages, or in a bimodal response in BUN. Multivariate analyses are possible but may lead to a series of univariate analyses of covariance in the case of a significant multivariate response. Univariate analyses, coupled with judicious consideration of biological significance, are usually sufficient.

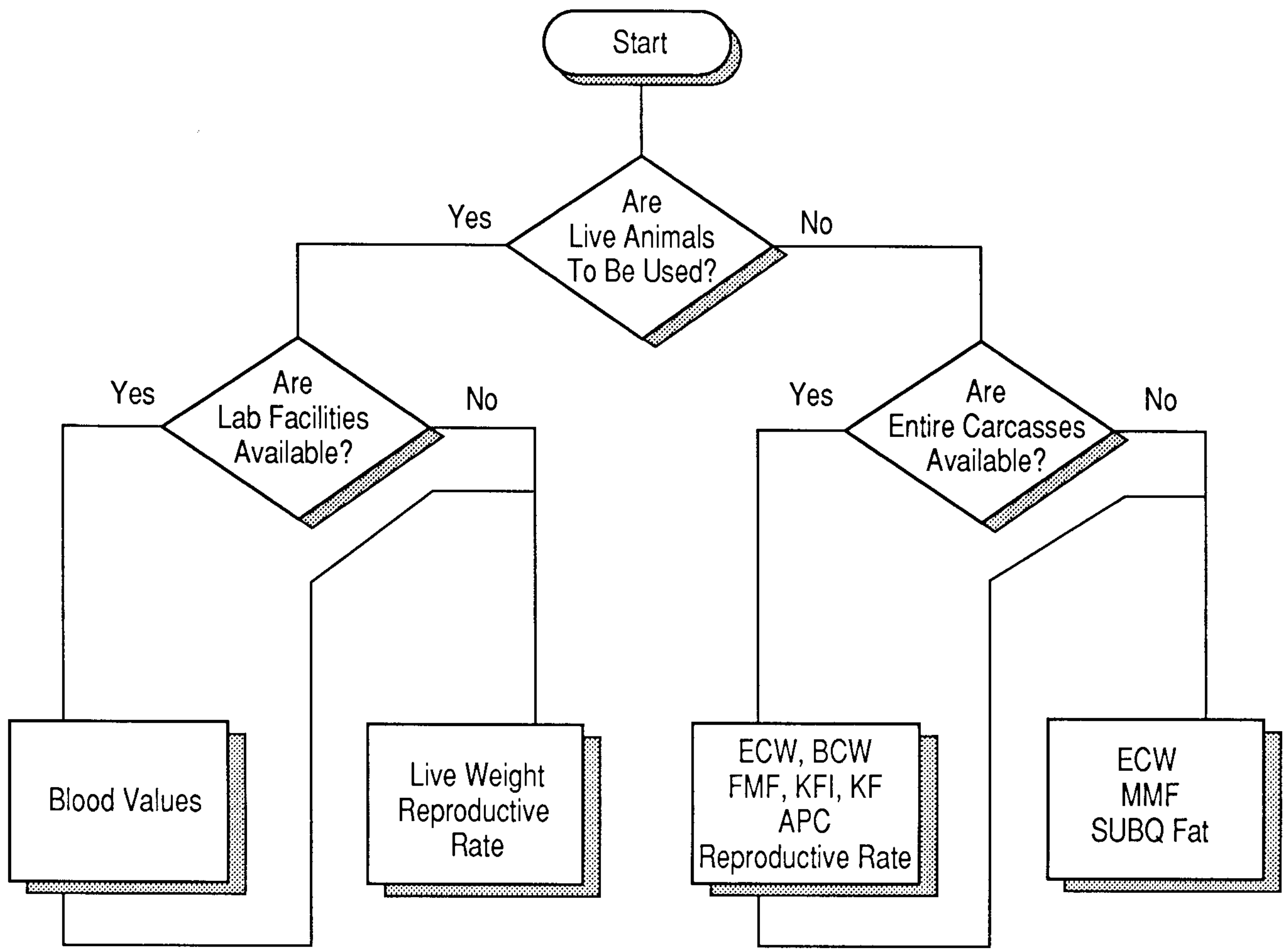

Figure 3--Methods for assessing condition in wild ungulates can be chosen from a flow chart. (ECW = eviscerated carcass weight, BCW = bled carcass weight, KFI = kidney tat index, KF = kidney fat, APC = abomasal parasite count, MMF = mandibular marrow fat, SUBQ = subcutaneous).

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Measures of performance in wild ungulates can include characteristics indicative of condition and health such as body weights, fat reserves, blood values, reproductive rates, and parasite loads. Performance may also be inferred from habitat-related factors, such as diet and nutritional intake. However, these parameters interact with population density to form a homeostatic system that tends towards equilibrium over time, subject to other extrinsic variables. Therefore, performance in ungulates should be judged with reference to a specific population density. Estimates of population density can be derived from direct methods such as drive counts, aerial counts, line transect counts, spotlight counts, and remote sensing, as well as from indirect techniques such as mark-recapture methods, change-in-ratio methods, track and trail counts, and fecal pellet-group counts. Flowcharts presented offer help in choosing appropriate methods to determine population density and assess condition and health of individuals.

Retrieval Terms: ungulate populations, census methods, condition indices